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ABSTRACT

We used fMRI to investigate competition during language production in two word production tasks: object naming and color naming of achromatic line drawings. Generally, fMRI activation was higher for color naming. The line drawings were followed by a word (the distractor word) that referred to either the object, a related object, or an unrelated object. The effect of the distractor word on the BOLD response was qualitatively different for the two tasks. The activation pattern suggests two different kinds of competition during lexical retrieval: (1) Task-relevant responses (e.g., *red* in color naming) compete with task-irrelevant responses (i.e., the object's name). This competition effect was dominant in prefrontal cortex. (2) Multiple task-relevant responses (i.e., target word and distractor word) compete for selection. This competition effect was dominant in ventral temporal cortex. This study provides further evidence for the distinct roles of frontal and temporal cortex in language production, while highlighting the effects of competition, albeit from different sources, in both regions.

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1. Introduction

Whenever we produce a word, we have to select the correct lexical concept from a multitude of other lexical concepts that are also active in memory (in the so-called mental lexicon). The notion that lexical retrieval entails selection from co-activated elements was established through research on speech errors in the 1970s and 1980s. For example, [Fromkin \(1971\)](#) and [Garrett \(1980\)](#) used speech errors to draw conclusions about the nature of the language processing system. Specifically, semantic substitution errors are taken as evidence of selection difficulty: If I say “Can you pass me the salt, uh, the pepper, please?”, the unintended, but semantically related, lexical concept *salt* was temporarily more active than the intended lexical concept *pepper*.

In the present article, we investigate semantic retrieval processes using functional magnetic resonance imaging (fMRI). We explore whether the blood oxygen level dependent (BOLD) signal can inform us about the nature of the competitor set for two differ-

ent tasks that both require semantic retrieval and overt language production.

A well-established paradigm for investigating semantic retrieval during language production is picture–word interference (PWI): Participants are instructed to name a picture as quickly as possible while ignoring a printed word superimposed on the picture. However, their inability to ignore this distractor word is evidenced by the effects of the relationship between picture and word on naming latencies. When the word and the picture are semantically related, naming latencies are longer than when they are unrelated. Because the activation of a semantic competitor is boosted by the presentation of the written word, competition increases and reaction times are prolonged. PWI has been used to study the time course of lexical retrieval (e.g., [Schriefers, Meyer, & Levelt, 1990](#)) as well as graded effects of semantic relatedness ([Vigliocco, Vinson, Lewis, & Garrett, 2004](#)).

[Levelt et al. \(1991\)](#) used a different paradigm to investigate semantic activation. Participants named pictures. On some trials, the picture was followed by an auditory probe. Participants had to decide if this probe was a word or a non-word by pressing a button. After this lexical decision, participants had to give the naming response. The dependent measure was the speed of the lexical decision as a function of the relationship between the picture name and the probe word. During the shortest SOA (the probe was presented 47 ms after picture onset), participants' responses were significantly slower to a probe semantically related to the picture name than to an unrelated probe. Again, the representations of picture name and related probe word compete for selection.

[Jescheniak, Schriefers, Garrett, and Friederici \(2002\)](#) used event-related brain potentials to study the activation of semantic and

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phonological codes in language production, using a variant of the delayed naming paradigm described above. Participants had to prepare a naming response but withhold it until the appearance of a cue. On some trials, auditory probe words were presented during the delay period. Jescheniak and colleagues found a reduced N400 component for both semantically- and phonologically-related probe words relative to unrelated probe words. The N400 is usually interpreted as an indication of integration difficulty and hence probe words that were related in some lexical property to the prepared picture name were better integrated than unrelated probe words. In a second experiment, participants performed a non-lexical task. Instead of naming the objects, they made a real-life size judgment. During this non-lexical task, there was still a reduction in the N400 for semantically-related probe words, but no reduction for phonologically-related probe words. The authors conclude that the semantic effect indexes semantic activation involved in object processing, while the phonological effect indexes activation that is specifically linked to lexical retrieval. A different way to think about the findings is that recognition of an object activates semantically-related concepts in both lexical and non-lexical tasks, but that activation includes concepts with phonologically-related names only if the task entails retrieval of a name.

To recapitulate: Co-activation of competing representations during semantic retrieval is often measured with PWI or probe paradigms. Inhibition effects observed in PWI and the behavioral probe paradigm (Levett et al., 1991) highlight the greater competition due to the simultaneous (or near-simultaneous) activation of target word and related competitor. The electrophysiological probe paradigm (Jescheniak et al., 2002) demonstrated that the set of competitors is altered by the task demands.

Here, we investigate semantic retrieval during two different linguistic tasks, using fMRI. These two tasks are object naming and color naming of achromatic line drawings. The paradigm is a hybrid between PWI and the probe paradigm: Participants generated responses for pictured objects. The pictures were followed by a word that either named the pictured object or a different object that was either semantically related or semantically unrelated to the pictured object. Although participants knew which task to perform prior to the presentation of the object, they were instructed to withhold their response until they had seen the subsequent word. Underlying this paradigm is the following rationale: As soon as participants see the picture, they start to retrieve the appropriate response for the designated task (either its name or its color). During this ongoing process, a word is presented. We measure the effect of this word on the magnitude of the BOLD response. Ideally, this paradigm could reflect both processes of semantic integration (*apple* and *peach* are both fruit, hence, *peach* should be easier to integrate into the context created by the preparation of the picture name *apple* than, for example, *table*) and competition effects (*apple* and *peach* are stronger competitors than *apple* and *table*). The critical question is whether the pattern of activation in the *same*, *related*, and *unrelated* cases will be comparable in object naming and in color naming. If the retrieval of an object's name is an automatic "by-product" of the object recognition process (cf. Moss et al., 2005), then the name *apple* will become active, even when naming the picture *apple* with *red* (in the color naming task). In this case, the relatedness of the probe words should yield the same activation pattern in both tasks. The alternative view is that retrieving an object's name and retrieving its color highlight different aspects of the semantic representation. Retrieval of an object name might activate related objects to a greater extent than does retrieval of an object's properties, such as color. If this were the case, we should observe different patterns of activation as a function of relatedness in object naming and in color naming.

Given the extant literature on neural systems involved in language production, we expected to observe activation during these

naming tasks in left prefrontal cortex and in left temporal cortex. For example, Price, Moore, Humphreys, Frackowiak, and Friston (1996) report modality-independent activation in the left inferior frontal gyrus (LIFG) during naming tasks. Similarly, Chao and Martin (1999) found left ventral temporal activity in a color naming and color generation task.

Wheatley, Weisberg, Beauchamp, and Martin (2005) report fMRI results from a primed lexical decision task employing the same conditions as our experiment: Participants read words that could either be identical (crow–crow), semantically related (fork–cup), or unrelated (ankle–carrot), and they had to decide whether the second word was a real word. The authors found a stepwise pattern of activation in the left inferior frontal gyrus and the left posterior region of the fusiform gyrus: The activation was lowest in the identical condition and greatest in the unrelated condition. The negative relationship between activation and semantic relatedness was explained as fMRI adaptation, due to a reduction in neural firing in response to a repeated stimulus (cf., Grill-Spector et al., 1999). Direct comparison of our results to Wheatley and colleagues will highlight differences between language comprehension and language production.

2. Materials

Experimental blocks: The set of experimental items comprised 80 line drawings of objects and animals (Alario & Ferrand, 1999). Half of the participants saw 40 line drawings during object naming and the other 40 line drawings during color naming. For the other half of the participants, the assignment of images to tasks was reversed.

The line drawings had high name agreement (mean 93%, standard deviation 7%, range 76–100%) and high color agreement (mean 89%, standard deviation 8%, range 71–100%), based on ratings obtained by Kan and Thompson-Schill (2004).

During presentation, a picture was followed by a written word (henceforth referred to as the "distractor"). The combinations of pictures and words formed three conditions, *same*, *related*, and *unrelated*. In the *same* condition, a picture was followed by its name, in the *related* condition, it was followed by a semantically-related noun, and in the *unrelated* condition, it was followed by an unrelated noun. The actual picture names were used once as a distractor (in the *same* condition) during the course of the experiment. The other words were used twice, once as *related* distractor and once as *unrelated* distractor.

Semantic relatedness values were obtained from latent semantic analysis (Landauer, Foltz, & Laham, 1998) pairwise comparisons. The mean relatedness in the *related* condition was 0.47 (standard deviation 0.19, range 0.11–0.88) and 0.06 in the *unrelated* condition (standard deviation 0.06, range –0.06 to 0.21). We also obtained relatedness ratings from a separate group of 12 participants. The mean relatedness on a 7-point scale was 4.82 (standard deviation 1.03, range 1.42–6.75) in the *related* condition and 1.05 (standard deviation 0.14, range 1.00–1.83) in the *unrelated* condition.

The relatedness of the picture–word pairs was further established with a behavioral pilot study using the classic PWI procedure. The typical pattern of results is interference for *related* relative to *unrelated* trials and facilitation for *same* relative to *unrelated* trials. We tested a separate group of 12 participants from the same pool from which participants in the fMRI study were drawn. An ANOVA on naming latencies in the classic PWI paradigm, with the three-level factor 'relatedness' (*same*, *related*, *unrelated*), revealed a significant effect of distractor relatedness on naming latency, $F_1(2, 22) = 72.95$, $MSE = 1071$, $p < .001$; $F_2(2, 158) = 77.09$, $MSE = 7597$, $p < .001$. Paired *t*-tests confirmed that the pattern was as expected: Reaction times were slower for *related* (858 ms)

than *unrelated* (795 ms) trials, $t_1(11) = 4.92$, $p < .001$; $t_2(79) = 5.02$, $p < .001$. Reaction times were faster for *same* (697 ms) than *unrelated* (795 ms) trials, $t_1(11) = -8.32$, $p < .001$; $t_2(79) = -7.24$, $p < .001$. Replication of the effects in the classic PWI paradigm established the presence of semantic competition among the stimuli used in the experiment reported below (where behavioral effects are obscured with the use of the delayed probe paradigm).

Baseline blocks: For a perceptual baseline task (described below), images of dots were created from the experimental pictures. The experimental pictures were distorted with the “spatter” filter in Adobe Photoshop® (radius 25, smoothness 5). Half of the pictures were presented with a line superimposed on the image.

The dot images were followed by letter strings. The letter strings were made by taking the letters from all the words in the experimental blocks and randomly rearranging them into nonsensical letter strings of equal length as the experimental words. Care was taken that none of these letter strings formed an existing word. We did not scramble the letters on a word by word basis, because in that case participants could unscramble them. Rather, letters for the non-words were drawn from the pool of all letters belonging to the 120 distractor words.

2.1. Participants

Twenty-one students of the University of Pennsylvania participated in the experiment (14 women, 7 men). Their mean age was 21 years, with a range from 19 to 27. All participants were right-handed and native speakers of English. None of the participants suffered from psychiatric or neurological disorders or had ever sustained a head injury. Participants gave informed consent before their participation and were paid 30 dollars.

Three participants failed to comply with the experimental instructions. For another participant, recordings were not obtained due to a technical error. The data from these participants were excluded from the analyses conducted on the final sample of 17 subjects (10 women, 7 men).

2.2. Procedure

The experiment consisted of four runs: Two color naming runs alternated with two object naming runs (order of task-runs was counter-balanced across subjects). A given run comprised ten blocks with 16 events each. In a given experimental task (object naming or color naming), all 40 pictures were used in all three conditions. The order of the 120 picture-trials was randomly interspersed with 40 null events (i.e., fixation-only). The resulting 160 events were divided into the ten blocks. Five blocks were experimental blocks and five blocks were baseline blocks. Experimental and baseline blocks alternated (again, order of blocks within each run was counter-balanced across subjects but was constant within a subject).

A trial began with a fixation cross (500 ms), followed by a 100 ms blank screen. Then the picture was presented for 500 ms, and after another blank screen (50 ms), the word was presented for 500 ms. The screen was blank for 1350 ms before the next trial started; that is, total trial length was 3000 ms. In the null events, a fixation cross stayed on the screen for 3000 ms.

Participants were told to name the pictures (in the object task) or to identify their typical color (in the color task). To ensure that participants processed the words following the pictures, participants were instructed to respond if the item following the picture was a real English word, but to withhold their response if the picture was followed by a non-word. Across the experimental blocks, 8 trials were catch trials in which the picture was followed by a non-word. These trials, on which the participant withheld the naming response, were excluded from subsequent fMRI data anal-

ysis but were used to verify that each participant performed the task as instructed. Note that, while the catch trials did allow us to verify that participants processed the distractor words and did not just ignore them, catch trials were very rare events (there were 30 times as many go trials as no-go trials). Hence, the demands that no-go trials made on executive control mechanisms, were expected to be minimal.

In the baseline task, participants were instructed to respond by saying ‘yes’ if there was a line in the image or ‘no’ if there was no line in the image. Participants were told to execute their response if the picture was followed by scrambled letters but to withhold it if the picture was followed by a series of #-signs. Across the baseline blocks, 8 trials were catch trials. We used this rather elaborate baseline because it was parallel to the experimental task in that it involved presentation of an image, presentation of letters that provided a go/no-go cue, and a spoken response. In contrast to the experimental task, there was no semantic processing involved in the baseline task.

Participants used a directional optical microphone with adaptive noise reduction (Litemic 3140, OptoAcoustics, Israel). The responses were recorded and the scanner noise was filtered from the recorded volume. Participants were instructed to speak quietly, reducing potential movement artifacts.

Before fMRI scanning commenced, participants were familiarized with the line drawings by naming them once. Participants also completed two short practice blocks of the color naming, object naming, and baseline tasks, composed of items that were not used elsewhere in the experiment.

2.3. Data acquisition

Structural and functional data were collected on a 3.0 Tesla Siemens Trio scanner, using a transmit/receive multicoil surface array (Nova Medical). High resolution T1-weighted structural images were collected in 160 axial slices and near isotropic voxels (0.9766 mm × 0.9766 mm × 1.0000 mm; TR = 1620 ms, TE = 30 ms, TI = 950 ms). Functional, blood oxygenation level dependent (BOLD), echoplanar data were acquired in 3 mm isotropic voxels (TR = 3000 ms, TE = 30 ms). BOLD data were acquired in 46 axial slices, in an interleaved fashion with 64 × 64 in plane resolution. The functional data were collected in four runs of 9 min and 24 s each. The first 21 s of each run consisted of a ‘dummy’ gradient and radiofrequency pulse to allow for steady state magnetization.

2.4. Image processing

Off-line data analysis was performed using VoxBo (www.voxbo.org) and SPM2 (www.fil.ion.ucl.ac.uk). At any time point when the strength of the global signal deviated more than 3.5 standard deviations from the average global signal (i.e., a “spike” in the data), the measurement was defined as an outlier, eliminated, and replaced using cubic spline interpolation. The data were then sinc interpolated in time to correct for the slice acquisition sequence. Motion correction was performed on the data with a six parameter least squares rigid body realignment routine using the first functional image as a reference. The data were normalized in SPM2 to a standard template in Montreal Neurological Institute (MNI) space. Normalization maintained 3 mm isotropic voxels and used 4th degree B-spline interpolation. The normalized data were smoothed with an 8 × 8 × 8 mm full width at half maximum Gaussian smoothing kernel.

2.5. Data analysis

The general linear model modified for serially correlated error terms was used to analyze the BOLD activation of each subject

on each trial as a function of condition (Worsley & Friston, 1995; Zarahn, Aguirre, & D'Esposito, 1997). fMRI signal change was modeled by creating covariates for all event types (object naming/*same* word, object naming/*related* word, object naming/*unrelated* word, color naming/*same* word, color naming/*related* word, color naming/*unrelated* word, null events, and baseline trials). We modeled neural activity as a brief impulse at stimulus onset (Zarahn et al., 1997), and then convolved covariates of interest with a standard hemodynamic response function.

Nuisance covariates for effects of scan, global signal, and motion were included in the model. A nuisance covariate corresponding to time points at which spikes in the global signal were removed was also included in the analysis. Time series data were subjected to a high-pass (.0177 Hz) filter, and serial autocorrelation of error terms was modeled as described by Zarahn et al. (1997).

Instead of defining *a priori* regions of interest with anatomical criteria, we initially identified areas across the entire brain that were more active during the experimental tasks than during the baseline task. The false positive rate ($\alpha = .05$) was controlled by performing 2000 Monte-Carlo permutations of the data and empirically-deriving the critical threshold (Nichols & Holmes, 2002). We extracted the coordinates of the peak activation in MNI space and converted them to Talairach space. The Talairach demon was used for a first localization of the activated area. The localization was then verified or adjusted using the Duvernoy atlas (1999). Data from clusters (10 or more voxels) identified in this omnibus whole brain analysis were then subjected to subsequent region of interest (ROI) analyses of effects of interest: Data were spatially averaged across the suprathreshold voxels in each cluster identified in the omnibus analysis. We calculated the β -value relating each covariate of interest to the spatially-averaged signal, in each ROI for each subject. Each effect was evaluated in a random-effects analysis across subjects, at an uncorrected threshold of $p < .05$.

3. Results

3.1. Behavioral results

3.1.1. Behavioral control experiment

Because we could not acquire voice-onset times with the microphone used in the scanner, we conducted a parallel experiment outside of the scanner, in order to provide an estimate of the response times in the scanning session. We recruited 12 additional participants (who did not take part in the fMRI study) from the same participant pool. These participants named the items in the experimental blocks only. Voice onset latencies and errors were recorded (see Table 1). A name or color that was different from the intended response, but a valid alternative, was accepted as a correct response. 7.2% of the object responses were alternative names, and 19% of the color responses were alternative colors. Reaction

Table 1
Average reaction times and error rates by task (object vs. color) and relatedness condition (*same*, *related*, *unrelated*) for participants ($N = 12$) in the behavioral control experiment^a

	Object naming	Color naming
Same	596 (239) 2.5% (3.0%)	712 (225) 1.0% (1.7%)
Related	609 (247) 2.5% (3.5%)	750 (201) 3.3% (3.6%)
Unrelated	601 (233) 3.1% (4.9%)	725 (227) 2.7% (4.9%)

(Standard deviations are given in parentheses).

^a Only 'real' errors are reported, voice key malfunctionings are not included in the percentages.

times deviating more than two standard deviations from both a participant's and an item's mean were coded as outliers (2.5% of all responses) and excluded from the analyses. Trials with errors or invalid response latencies (hesitations, self-corrections, a color response in an object trial or vice versa, no response, and voice key malfunctioning) were also excluded from the reaction time analyses (3.4% of all responses).

We subjected response time data and error rates to a 2 (task) by 3 (relatedness condition) within-subjects ANOVA, with either subjects (F_1) or items (F_2) designated as a random variable. The effect of task was significant, $F_1(1,11) = 12.33$, $MSE = 23584$, $p < .01$, $F_2(1,79) = 22.29$, $MSE = 82748$, $p < .001$; with longer reaction times in color naming (729 ms) than in object naming (602 ms). The main effect of relatedness was also significant, $F_1(2,22) = 5.12$, $MSE = 801$, $p < .05$, $F_2(2,158) = 4.25$, $MSE = 6894$, $p < .05$. Planned comparisons revealed that reaction times in the *same* condition were faster than those in the different (*related* and *unrelated*) conditions, $F_1(1,11) = 10.33$, $MSE = 5713$, $p < .01$, $F_2(1,79) = 5.54$, $MSE = 93566$, $p < .05$, but the related and unrelated conditions were not reliably different from each other ($F_1(1,11) = 2.92$, $MSE = 4502$, $p > .10$, $F_2(1,79) = 2.57$, $MSE = 23967$, $p > .10$). The interaction of task and relatedness was not significant, $F_1(2,22) = 1.17$, $MSE = 886$, $p > .25$, $F_2 < 1$. There were no significant effects for the error rates. Note that these effects were, predictably, different from those reported above in the classic PWI paradigm used to verify the suitability of our materials for this study.

3.1.2. Performance errors in the fMRI experiment

Subjects made overt responses during fMRI scanning; although we could not record response latency, we could analyze error rates across conditions (see Table 2). Four percent of the responses were missing due to recording errors. In 3.2% of the object naming trials, participants used a name that was different from the intended target, but acceptable. In 10.4% of the color naming trials, participants used an alternative color. This is the same pattern as in the behavioral control experiment (i.e., more alternative names on the color task than on the object task), although the overall rates are lower. Errors were coded in the same way as in the behavioral experiment. Erroneous responses amounted to 2.8% of all responses.

As above, accuracy data were subjected to a 2 (task) by 3 (relatedness condition) within-subjects ANOVA, with either subjects (F_1) or items (F_2) designated as a random variable. The effect of task was not significant, $F_s < 1$. The main effect of relatedness was significant by participants, $F_1(2,32) = 4.26$, $MSE = 0.001$, $p < .05$, but not by items, $F_2(2,158) = 2.15$, $MSE = 0.016$, $p > .10$. Planned comparisons showed that the difference between *related* and *unrelated* was not significant ($F_s < 1$). The error rates in the *same* condition were less than in the different (*related* and *unrelated*) conditions, $F_1(1,16) = 8.19$, $MSE = 0.007$, $p < .05$, $F_2(1,79) = 5.5$, $MSE = 0.15$, $p < .05$. The difference between *same* and *unrelated* was significant, ($F_1(1,16) = 5.25$, $MSE = 0.003$, $p < .05$, $F_2(1,79) = 4.08$, $MSE = 0.054$, $p < .05$). The interaction of task and relatedness was not significant, $F_1(2,32) = 1.25$, $MSE = 0.001$, $p > .25$, $F_2 < 1$.

Table 2
Average error rates by task (object vs. color) and relatedness condition (*same*, *related*, *unrelated*) for participants ($N = 17$) in the fMRI experiment

	Object naming	Color naming
Same	1.5% (1.8%)	2.0% (3.5%)
Related	3.5% (3.7%)	2.7% (3.6%)
Unrelated	2.7% (2.9%)	4.0% (6.6%)

(Standard deviations are given in parentheses.)

3.2. Functional imaging results

3.2.1. Functional region of interest analysis

Seven regions were identified as more responsive during the experimental task than during the baseline task in the omnibus whole-brain analysis (see Table 3 and Fig. 1): left ventral temporal cortex (fusiform/parahippocampal gyri); left frontal cortex (three clusters in anterior inferior frontal gyrus; posterior inferior/middle frontal gyri; and superior/middle frontal gyri); left parietal cortex; and right cerebellum (two distinct clusters). As described above, we calculated percentage signal change associated with each condition (versus baseline) in each ROI (see Table 4 and Fig. 2).

In each ROI, percent signal change data were subjected to a 2 (task) by 3 (relatedness condition) ANOVA, with subjects designated as a random factor. Table 5 presents the statistical analyses for the seven functional ROIs.

The effect of task was significant in the anterior cerebellar region, the more posterior part of the prefrontal cortex, the superior and middle part of the prefrontal cortex and the parietal lobule.

The effect of relatedness was significant in the posterior cerebellar region, and marginally significant in the left temporal region and the parietal lobule. Collapsed over tasks, in the posterior cerebellum, activation was stronger for *related* trials than *unrelated* trials, $F(1,16) = 10.69$, $MSE = 0.05$, $p < .01$, and marginally stronger for *same* trials than *unrelated* trials, $F(1,16) = 3.51$, $MSE = 0.08$, $p = .08$. In the left temporal region, activation was stronger for *related* trials than *unrelated* trials, $F(1,16) = 5.04$, $MSE = 0.06$, $p < .05$. In the left parietal region, activation was stronger for *same* trials than *unrelated* trials, $F(1,16) = 5.15$, $MSE = 0.04$, $p < .05$, and marginally stronger for *related* trials than *unrelated* trials, $F(1,16) = 3.64$, $MSE = 0.03$, $p = .075$.

The interaction of the two factors was only significant in the left temporal region and marginally significant in the two cerebellar regions. For these regions, the effect of relatedness was investigated separately for color naming and object naming. The effect was not significant for color naming in any of the regions (posterior cerebellum: $F(2,32) = 1.58$, $MSE = 0.017$, $p < .221$; anterior cerebellum: $F(2,32) = 1.62$, $MSE = 0.013$, $p < .215$; left temporal: $F < 1$). The

Table 3

Regions more active during the experimental tasks than during the baseline task (omnibus whole-brain analysis, $p < .05$ corrected)^a

Brain region (Brodmann's area)	Peak voxel <i>t</i> -value	Cluster size (in voxels)	X	Y	Z
Right cerebellum	7.29	10	15	-80	-26
	8.54	30	36	-71	-19
Left fusiform gyrus/left parahippocampal gyrus (37, 20)	13.35	297	-33	-44	-15
Left anterior inferior frontal gyrus (47)	8.00	11	-56	32	-7
Left posterior inferior frontal gyrus/left middle frontal gyrus (45, 46, 10)	12.39	637	-48	36	9
Left superior parietal lobule/left inferior parietal lobule/precuneus (7)	11.08	59	-27	-54	44
Left superior frontal gyrus/left middle frontal gyrus (6, 8, 32)	8.78	64	-3	15	52

^a Peaks of activation which reached significance at the $p < .05$ level corrected for multiple comparisons with at least 10 contiguous voxels. Coordinates are reported in Talairach space.

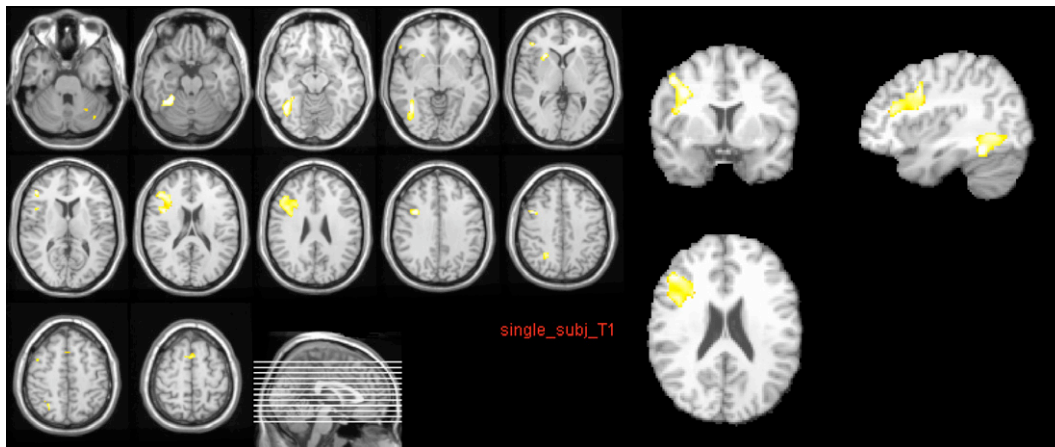


Fig. 1. Regions more active during the experimental task than during the baseline task, $p < .05$ corrected. Activations are superimposed on the MNI template.

Table 4

Average percentage signal change, from baseline, for the seven ROIs identified in the omnibus whole brain analysis

Region	Object naming			Color naming		
	Same	Related	Unrelated	Same	Related	Unrelated
Right cerebellum (15, -80, -26)	0.16	0.25	0.11	0.28	0.24	0.20
Right cerebellum (36, -71, -19)	0.11	0.12	0.04	0.23	0.16	0.21
Left fusiform/parahippocampal ("temporal")	0.18	0.27	0.16	0.25	0.24	0.22
Left inferior frontal gyrus, anterior (IFG)	0.21	0.38	0.22	0.34	0.35	0.33
Left inferior frontal gyrus, posterior/left middle frontal gyrus (IFG/MFG)	0.10	0.13	0.11	0.23	0.18	0.16
Left parietal	0.16	0.15	0.10	0.23	0.22	0.19
Left superior/middle frontal (SFG/MFG)	0.12	0.11	0.13	0.23	0.23	0.18

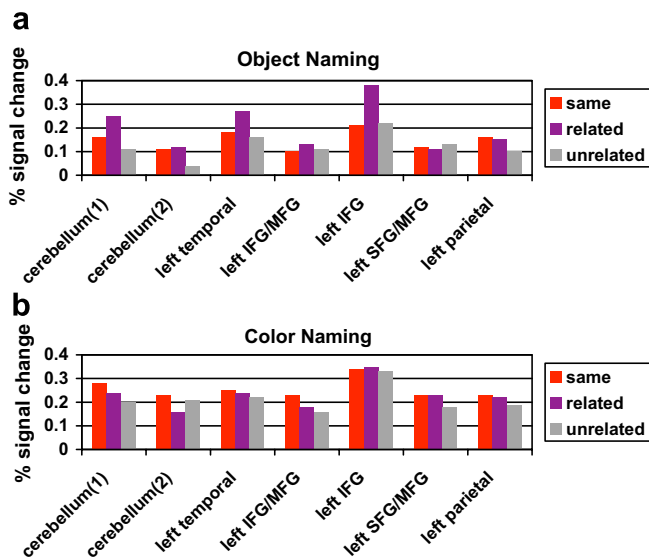


Fig. 2. In each ROI, average percentage signal change, from baseline, is plotted as a function of condition for (a) object naming and (b) color naming tasks.

relatedness effect was significant for object naming in the posterior cerebellar region, $F(2, 32) = 5.60$, $MSE = 0.016$, $p < .01$, and the temporal region, $F(2, 32) = 5.06$, $MSE = 0.011$, $p < .01$; but not in the anterior cerebellar region, $F(2, 32) = 2.23$, $MSE = 0.013$, $p < .124$. Pairwise t -tests were carried out in the posterior cerebellar and the temporal region (corrected $p = .016$). In the posterior cerebellar region, only the difference between *related* and *unrelated* in object naming was significant, with the activation level higher for *related* than for *unrelated* trials. In the left temporal region, the activation level was significantly higher in *related* than in *same* while the difference was marginally significant for *related* and *unrelated* ($p < .018$).

Fig. 2 illustrates that a qualitatively similar activation pattern was present in most ROIs, although the interaction was only reliable for the left temporal ROI.

3.2.2. Anatomical regions of interest

In order to further characterize the regional variation in the response to these tasks, we reexamined the above analyses in four ROIs with additional anatomical constraints: We defined distinct regions for the left inferior frontal gyrus ROI (LIFG) and the left middle frontal gyrus ROI (LMFG). We also defined an ROI specific to the left fusiform gyrus, and another ROI specific to the left superior parietal lobule. Anatomical ROIs were drawn on each participant's anatomical scan. Effects were assessed on the average signal change across all voxels in the ROI that exceeded a threshold of $t = 2.0$ in the omnibus whole-brain analysis.

LIFG. The area between the inferior frontal sulcus (dorsal bound) and the circular insular sulcus (ventral bound). The anterior bound was formed by the inferior frontal sulcus and the posterior bound by the precentral sulcus.

LMFG. The area between the inferior frontal sulcus and the superior frontal sulcus. The dorsal and ventral bounds were marked by the disappearance of the sulcus.

Lfusiform. The region of interest was confined laterally by the lateral occipito-temporal sulcus, medially by the collateral sulcus and the medial occipito-temporal sulcus, rostrally by the anterior transverse collateral sulcus and caudally by the posterior transverse collateral sulcus.

LParietal. The region of interest contained a large area between the parieto-occipital sulcus posteriorly and the postcentral sulcus anteriorly.

Table 5
Statistical analyses of percentage signal change in the BOLD-signal

	Source	<i>F</i>	<i>df</i>	<i>p</i>	<i>MSE</i>
<i>Functional ROI</i>					
Cerebellum 1	Task	2.03	1, 16	.174	0.052
	Relatedness	4.02	2, 32	<.05	0.019
	Task × Relatedness †	2.95	2, 32	.067	0.015
Cerebellum 2	Task	5.02	1, 16	<.05	0.060
	Relatedness	1.23	2, 32	.307	0.012
	Task × Relatedness †	2.52	2, 32	.097	0.014
Left temporal	Task	1.45	1, 16	.246	0.019
	Relatedness †	3.18	2, 32	.055	0.012
	Task × Relatedness *	3.27	2, 32	<.05	0.007
Left IFG/MFG	Task **	10.24	1, 16	<.01	0.014
	Relatedness	1.37	2, 32	.269	0.005
	Task × Relatedness	1.83	2, 32	.177	0.010
Left IFG	Task	<1	1, 16	.459	0.205
	Relatedness	1.42	2, 32	.257	0.068
	Task × Relatedness	1.11	2, 32	.341	0.065
Left SFG/MFG	Task **	14.26	1, 16	<.01	0.016
	Relatedness	<1	2, 32	.694	0.011
	Task × Relatedness	<1	2, 32	.605	0.023
Parietal	Task *	5.33	1, 16	<.01	0.030
	Relatedness †	2.55	2, 32	.094	0.010
	Task × Relatedness	<1	2, 32	.935	0.016
<i>Anatomical ROI</i>					
Left fusiform gyrus	Task	1.86	1, 16	.191	0.024
	Relatedness	3.72	2, 32	<.05	0.011
	Task × Relatedness	1.33	2, 32	.278	0.008
Left MFG	Task **	11.11	1, 16	<.01	0.037
	Relatedness *	3.53	2, 32	<.05	0.017
	Task × Relatedness	<1	2, 32	.661	0.022
Left IFG	Task *	6.41	1, 16	<.05	0.031
	Relatedness *	3.56	2, 32	<.05	0.011
	Task × Relatedness	2.01	2, 32	.151	0.018
Left parietal lobule	Task *	6.30	1, 16	<.05	0.033
	Relatedness **	4.96	2, 32	<.01	0.014
	Task × Relatedness	<1	2, 32	.962	0.018

† $p < .10$.

* $p < .05$.

** $p < .01$.

The same analyses were conducted as described in Section 3.2.1. The results of the analyses are reported in Table 5 and illustrated in Fig. 3.

The effect of task was significant for LIFG, LMFG, and for the left parietal lobule. The effect of relatedness was significant for all four

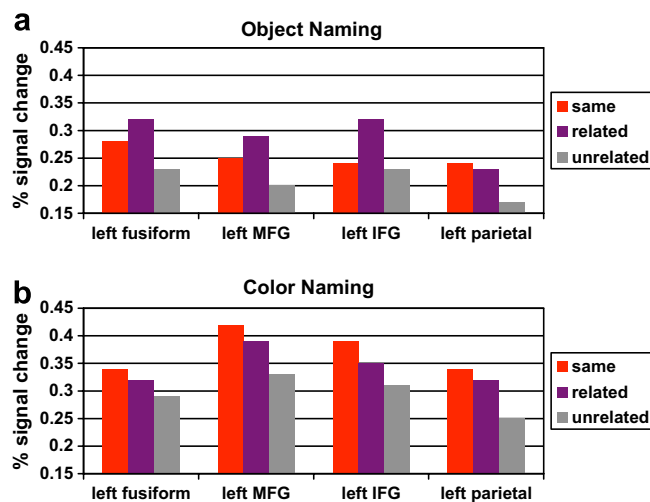


Fig. 3. Average percentage signal change, from baseline, by relatedness condition in four functional-anatomical regions of interest for (a) object naming and (b) color naming tasks.

regions. Collapsed over tasks, the activation for *same* was higher than for *unrelated* in all four regions, LIFG ($F(1,16) = 5.43$, $MSE = 0.03$, $p < .05$), LMFG ($F(1,16) = 4.54$, $MSE = 0.07$, $p < .05$), left fusiform ($F(1,16) = 4.42$, $MSE = 0.04$, $p < .05$), and left parietal lobule ($F(1,16) = 6.80$, $MSE = 0.07$, $p < .05$). The activation for *related* was higher than for *unrelated* in all regions, too, LIFG ($F(1,16) = 6.17$, $MSE = 0.05$, $p < .05$), LMFG ($F(1,16) = 9.92$, $MSE = 0.04$, $p < .01$), left fusiform ($F(1,16) = 4.49$, $MSE = 0.06$, $p < .05$), and left parietal lobule ($F(1,16) = 14.56$, $MSE = 0.02$, $p < .01$). None of the regions showed a significant task by relatedness interaction.

4. Discussion

We investigated the effect of the semantic relatedness between a prepared response and a distractor word in color naming and object naming. Two questions were addressed: First, is semantic retrieval task-dependent, resulting in a task by relatedness interaction? Or does presentation of an object entail full activation of this object and its semantically related associates, independent of the task? Second, is there a dissociation between brain regions sensitive to the amount of semantic relatedness between picture name and distractor word, and brain regions sensitive to retrieval demands (cf., Bedny, McGill, & Thompson-Schill, 2008)? Sensitivity to the amount of semantic relatedness should result in a monotonic relation between the amount of semantic relatedness and the BOLD-signal, with the least activation in the *same* condition and the greatest activation in the *unrelated* condition (cf. Wheatley et al., 2005, for language comprehension). Sensitivity to conflict resolution between active competitors should lead to high activation when the need for suppression is high. In object naming, semantically related distractors are highly effective competitors, increasing naming latencies for the target (the classical PWI effect). In color naming, the challenge is to avoid naming the picture with its object name and produce a color instead. In this condition, presentation of the object name should cause the highest competition.

Unlike the results for language comprehension (Bedny et al., 2008; Wheatley et al., 2005), in a language production study, we did not find clear evidence for a monotonic relation of semantic relatedness and activation. In line with the findings in behavioral PWI, the BOLD signal seems to reflect competition during the retrieval of a target word. Additionally, the results of our study suggest that prefrontal cortex and temporal cortex are sensitive to different kinds of competition. Activation in prefrontal cortex is driven by competition between task-relevant and task-irrelevant information (i.e., task effect), while activation in temporal cortex is driven by competition between a target and semantically related distractors.

Before turning to each of these effects in more detail, we want to highlight one unusual aspect of the current design. As explained above, in order to ensure that participants read the words prior to responding, we included rare catch trials in both experimental and baseline blocks in which case the response was to be withheld. This aspect of the task is similar to go/no-go paradigms that are thought to elicit executive control during response inhibition. In the omnibus comparison of experimental and baseline tasks, we did not find activation in areas associated with conflict monitoring and response inhibition (i.e., anterior cingulate cortex). Presumably, this is because the go/no-go decision required equal processing demands in the experimental trials and in the baseline. While it could be interesting to compare go/no-go trials, our study was not designed to allow such a contrast (i.e., there were only eight no-go trials across all of the experimental blocks).

4.1. Task effects

The activation for color naming was higher than for object naming in frontal and parietal regions and in the anterior cerebellar re-

gion. Heightened activation during color name retrieval might reflect the need to suppress the object name. Presumably, an object's name is more strongly activated by a black and white line drawing than is its real life color (cf. Price et al., 1996). This creates an asymmetry between the two tasks, similar to that described between word meaning and ink color in the Stroop paradigm. Of note, it has been demonstrated that activation of LIFG is modulated by demands to bias competitive interactions among incompatible representations in a variety of language production and comprehension tasks (Kan & Thompson-Schill, 2004; Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997; Thompson-Schill, Aguirre, D'Esposito, & Farah, 1999; Thompson-Schill, D'Esposito, & Kan, 1999; Thompson-Schill et al., 1998).

The task effects in parietal cortex were unexpected but not unprecedented: This region is often active in task-switching contexts (cf. Wager, Jonides, & Reading, 2004). Some types of task-switching require disengaging attention from previous task demands or previous response sets. We alternated object and color naming; therefore, participants had to disengage attention from the response set of the previous run. Because the different types of responses are not equally preferred, switching demands are not symmetrical. Presumably, switching is more difficult from object naming to color naming than the other way round. This would explain why parietal activation is higher for color naming than for object naming. Two areas implicated by Wager and colleagues (BA 7, -20, -66, 46, and BA 40/BA 7, -32, -44, 50) are close to the peak of activation we found in the left parietal lobe (-27, -54, 44, see Table 3).

While Wager et al. (2004) investigated shifts in visual or spatial attention, Hirshorn and Thompson-Schill (2006) found bilateral activation in the parietal cortex during shifts in conceptual space. Increased neural activation in the parietal cortex during shifts might reflect the disengagement from previous semantic associations.

4.2. Task by relatedness interaction

Trying to tease apart effects of semantic relatedness and competition effects, we had predicted two different types of activation patterns. Regions that reflect competition during semantic retrieval should show the highest activation in the condition that yields the highest competition (*related* for object naming, *same* for color naming). Regions that are sensitive to semantic relatedness should reflect the amount of semantic overlap as a monotonic effect of relatedness on activation. Figs. 2 and 3 illustrate that the posterior cerebellar region, and the temporal and frontal regions showed the activation pattern we predicted for areas involved in competition. However, these patterns were only reliable in the functionally defined temporal region and in the posterior cerebellum. In these two regions, the effect of relatedness was significant for object naming (with higher activation for *related* than for either *same* or *unrelated*) but not for color naming. For all other regions, the effect of relatedness was not affected by the task.

The pattern for object naming in left temporal cortex resembles the one obtained in the reaction times in behavioral PWI: Reaction times are longest when the distractor word is semantically related to the target. In the present experiment, the distractor word appeared after the picture. Delaying the onset of the distractor had eliminated the interference effect in the reaction times. This is often observed in delayed naming experiments, since participants can prepare their response in advance and the delayed distractor does not slow down response execution (but see Janssen, Schirm, Mahon, & Caramazza, 2008). However, the interference effect is present in the BOLD response, with the hardest condition (*related*) producing the most activation. That is, neuronal activity reflects competition during the selection of the target word.

4.3. Relatedness effects

There was a main effect of relatedness in all anatomically constrained regions of interest and the functionally defined left parietal region. Both *same* and *related* conditions show higher activation than the *unrelated* condition while these two conditions do not differ significantly. These regions do not show the stepwise activation progression with the least activation in the *same* condition, as the semantic adaptation account (Grill-Spector et al., 1999; Wheatley et al., 2005) would let us predict. Nonetheless, these regions are sensitive to the manipulation of semantic relatedness independent of task.

The relatedness effect in the left fusiform gyrus is in accordance with findings that show that this region is active in semantic tasks (Fiez, 1997; Wheatley et al., 2005). The relatedness effect in left frontal and parietal regions of interest parallels findings that, in some tasks but not others, prefrontal areas are also activated during the retrieval of semantic knowledge (Roskies, Fiez, Balota, Raichle, & Petersen, 2001; Wheatley et al., 2005).

Our failure to find semantic adaptation anywhere in the brain highlights the difference between language comprehension studies and language production studies and particularly the fact that semantically related words compete for selection during language production.

Even though there was no interaction between relatedness and task, we performed separate *t*-tests for color naming and object naming in regions with a main effect of relatedness to estimate how much each task contributed to the relatedness effect. The only clear difference we found was in the anatomically constrained LIFG where the difference between *same* and *unrelated* was significant for color naming ($t(16) = 2.16, p < .05$) but not for object naming ($t < 1$).

4.4. Region-specific differences

The magnitude of the patterns described above varied across the different ROIs we examined: The anatomically constrained left fusiform gyrus showed only a main effect of relatedness. Some regions showed both an effect of relatedness and an effect of task, namely the left parietal region (both functionally defined and anatomically defined), and the anatomically defined LIFG and LMFG. Finally, the functionally defined left ventral temporal region, the posterior cerebellar region, and the anatomically defined LIFG seemed to yield task-specific patterns of activation, with the temporal region and the cerebellum displaying sensitivity to relatedness effects during object naming and the LIFG displaying sensitivity to relatedness effects during color naming.

The response of the functionally defined temporal region and the anatomically defined LIFG was the most interesting result of our study. The temporal region was the only region that showed a significant interaction of task and relatedness, with the posterior cerebellar region displaying the same pattern in a slightly weaker fashion. In this region, the BOLD response reflected the reaction time pattern obtained in PWI for object naming. The region was not sensitive to manipulations in the color naming task. In contrast, the overall relatedness effect in the LIFG was mainly due to color naming, where the difference between *same* and *unrelated* was significant. Another difference between these two regions was that the main effect of task was significant for the LIFG but not for the temporal region. We interpret the task effect as competition from task-irrelevant information (cf. Thompson-Schill et al., 1997, 1999), in our case, the object's name during the color naming task. Presumably, suppressing the object name is made even more difficult when the distractor word is the object name, hence the higher activation in the *same* trials.

The temporal region seems to be relatively unaffected by task-induced retrieval demands. Instead, it is sensitive to the presence of semantic competitors within the object naming task. Usually, prefrontal cortex rather than temporal cortex is associated with competition during selection, but semantic competition effects in left temporal areas are not without precedent (Noppeney, Phillips, & Price, 2004). The posterior cerebellar region shows the same pattern, in line with observations (e.g., Price et al., 1996) that the right cerebellum is often activated alongside the more typical language areas in the left temporal and inferior frontal cortex during language processing.

The statistical analysis yielded greater effects when computed across the entire, functionally defined, ventral temporal region of interest than when restricted to the anatomically-defined fusiform gyrus. Ricci et al. (1999) report a similar finding: In their experiment, the fusiform gyrus was active in conditions requiring semantic retrieval on real objects, but it was part of a larger inferior temporal activation. With high semantic processing demands, activation increased in the left parahippocampal gyrus, not the left fusiform gyrus. Possibly, the same is true for our data and excluding the left parahippocampal region weakened statistical power.

At first sight, it is surprising that the ventral temporal region and particularly the fusiform gyrus do not show higher activation for color naming, since this region has been regularly implicated in color naming or color generation tasks (e.g., Martin, Haxby, Lalonde, Wiggs, & Ungerleider, 1995; Price et al., 1996; Price, Noppeney, Phillips, & Devlin, 2003). Chao and Martin (1999) found fusiform activation only when color naming was compared to a low level viewing baseline and they argue that naming either objects or colors already involves automatic retrieval of semantic knowledge from the fusiform gyrus. Findings from Thompson-Schill et al. (1999) partly support this argument: These authors found that visual knowledge for living things (indicated by activation in the fusiform gyrus) is active whether participants have to retrieve visual or non-visual knowledge. And in a study looking at the retrieval of semantic knowledge, Noppeney and Price (2003) found more activation in the fusiform gyrus for the generation of origin than for color generation. They concluded that the fusiform gyrus has a more general strategic role during semantic retrieval than described elsewhere.

5. Conclusions

In a task that measures the effect of distractor words on lexical retrieval, we observed task-dependent differences: Generally, color naming led to increases in the BOLD signal relative to object naming. These increases are observed in brain regions known to be involved when competition increases. Therefore, a compelling interpretation of the task effect is that object names are active, but have to be suppressed during color naming, while the opposite is not true for object naming.

In addition to the main effect of task which may result from competition between color and object names, the effects of relatedness may also reflect competitive interactions among active object representations: During the object naming task, activation in the temporal region was increased in the *related* condition relative to the *same* and the *unrelated* condition. We know from PWI studies that competition is higher when participants have to name an apple when the distractor *peach* is presented than when either the distractor *apple* or the distractor *table* is presented. Hence, this activation pattern is readily interpreted as reflecting competition between the target and semantically-related alternatives.

The frontal and parietal regions were more sensitive to competition effects between tasks (color naming vs. object naming), while the temporal region was more sensitive to competition with-

in object naming (increased BOLD activation for related distractor words). These regional differences are consistent with the hypothesis that prefrontal cortex plays a more general, regulatory function in cognition, whereas posterior regions subserve more domain-specific processes.

In sum, this study illustrates that different types of competition occur during word production. A speaker's challenge consists in (a) selecting a task-relevant response over a task-irrelevant response and (b) selecting the correct task-relevant response from a pool of competing related, task-relevant responses.

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