



Neural differences in the mapping of verb and noun concepts onto novel words

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ABSTRACT

A dissociation between noun and verb processing has been found in brain damaged patients leading to the proposal that different word classes are supported by different neural representations. This notion is supported by the facts that children acquire nouns faster and adults usually perform better for nouns than verbs in a range of tasks. In the present study, we simulated word learning in a variant of the human simulation paradigm that provided only linguistic context information and required young healthy adults to map noun or verb meanings to novel words. The mapping of a meaning associated with a new-noun and a new-verb recruited different brain regions as revealed by functional magnetic resonance imaging. While new-nouns showed greater activation in the left fusiform gyrus, larger activation was observed for new-verbs in the left posterior middle temporal gyrus and left inferior frontal gyrus (opercular part). Furthermore, the activation in several regions of the brain (for example the bilateral hippocampus and bilateral putamen) was positively correlated with the efficiency of new-noun but not new-verb learning. The present results suggest that the same brain regions that have previously been associated with the representation of meaning of nouns and verbs are also associated with the mapping of such meanings to novel words, a process needed in second language learning.

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Introduction

Nouns and verbs are universal building blocks of all languages subserving very different grammatical functions. Nouns and verbs might be retrieved by different neural networks thereby honoring syntactic structure as an organizational principle (Caramazza and Hillis, 1991; Damasio and Tranel, 1993). Neuropsychological evidence indeed suggests that verbs are relatively more impaired by left frontal lesions, whereas the processing of nouns is relatively more impaired after left temporal damage (Breedin et al., 1998; Damasio and Tranel, 1993; Daniele et al., 1994; Miceli et al., 1984; Shapiro and Caramazza, 2003). Functional neuroimaging in normal participants has yielded more variable results: Greater activation for verbs relative to nouns has been found in the left posterior middle temporal gyrus and/or left inferior frontal gyrus (Warburton et al., 1996; Davis et al., 2004; Fiez et al., 1996; Kable et al., 2002; Perani et al., 1999; Shapiro et al., 2005, 2006; Tranel et al., 2005; Tyler et al., 2004; Yokoyama et al., 2006; Bedny et al. 2008). A few studies have revealed greater activation

associated with nouns in left inferior temporal regions (Shapiro et al., 2005, 2006), whereas others failed to show differences between noun and verb processing (Tyler et al., 2001; Vigliocco et al., 2006).

Importantly, nouns and verbs differ also in their conceptual-semantic, syntactic and morphological characteristics. Verbs play a different syntactic role than nouns and are characterized by an argument structure. Conceptually, most nouns are pointers to entities (people, places and things), whereas verbs generally refer to actions and states and can be described more “relational” in their semantics than nouns. The referents of nouns are more easily individuated, stable and defined by sensory properties and in turn concepts that display these properties are more susceptible to be defined as (concrete) nouns in virtually all languages. On the other hand, verb referents rely less on sensory properties, are bound to specific relations between concepts and are more variable across languages (Gentner, 1982; Gentner and Boroditsky, 2001).

From the learning perspective, it has been shown that verb meanings are acquired later than noun meanings, harder to remember, more variable cross-linguistically and broader than noun meanings (Gentner, 1981, 1982; Gentner and Boroditsky, 2001). The fact that verbs are learned later than nouns cannot exclusively be attributed to maturational limitations as second language learners show the same profile as young children (Lennon, 1996). No prior study has investigated the mapping between novel words and noun or verb concepts and the neural networks recruited in this process, a

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process that could be considered to simulate word learning. Therefore we investigated to which degree this mapping process might differ between nouns and verbs by modifying a paradigm that we used previously to simulate contextual learning (Mestres-Misse et al., 2007, 2008). We hypothesized that regions engaged in noun and verb processing (see above) will also support the mapping of new words to their appropriate concepts.

Materials and methods

Participants

Twenty-one native German speakers (11 women, mean age 24 ± 1.8 years) without a history of neurological or psychiatric disease were enrolled. All participants were right-handed according to the Edinburgh Handedness Scale (Oldfield, 1971) and gave written informed consent. The study was approved by the ethical committee of the University of Magdeburg.

Task and stimulus materials

While in the scanner, participants silently read pairs of German sentences. In the critical conditions, the two sentences ended in a new word (standing for either a noun, henceforth Nn for new-noun, or a verb, henceforth Nv for new-verb). They had to discover the meaning of the hidden word. In all cases, hidden words were nouns and verbs of middle frequency. In addition, as a control, sentence pairs ending in existing nouns (Rn for real-noun) or verbs (Rv for real-verb) were also presented. An example for the Nn condition follows:

1. “Die Frau bekam zu Weihnachten einen *Jatt*.” (The lady received a *jatt* for Christmas)
2. “Der Trauzeuge vergaß vor Aufregung den *Jatt*.” (Due to excitement, the best man forgot the *jatt*) Hidden word: Ring (ring)

An example for the Nv condition was

1. “Der Student hat zum Essen Nudeln *genischt*.” (The student *has nished* noodles for lunch)
2. “Der Mann hat für sie lecker *genischt*.” (The man has nished deliciously for her) Hidden word: kochen (to cook)

In order to minimize possible differences due to phrase construction, sentences were systematically rotated across the two critical conditions by creating different sentence lists. Sentences uniformly had a length of 7 words. New-nouns/verbs respected the phonotactic rules of German and were created by changing one or two letters of an existing word.

The hidden words were 80 nouns and 80 verbs. The nouns and verbs were selected from the CELEX database (Baayen et al., 1995) and matched for frequency (nouns; mean frequency of 46.5 per million occurrences, verbs: 43.8). For each target word, two sentences were built, in which an increasing degree of contextual constraint was created (Mestres-Misse et al., 2007, 2008). Cloze probability patterns were assessed by presenting each sentence in isolation to 150 students. The cloze probability of a word in a given context refers to the proportion of people who complete a particular sentence fragment with that particular word (Taylor, 1953). The students were thus required to complete the sentence with the first word that came to their mind and that fit well with the sentence. Mean cloze probability for the final pool was as follows: for nouns, first sentence (low constraint) 14.8% (SD = 7.6) and second sentence (high constraint) 89.1% (SD = 9.2); and for the verbs, first sentence (low constraint) 13.1% (SD = 6.9) and second sentence (high constraint) 84.8% (SD = 9). A second pilot study (15 new student participants) was conducted in order to determine meaning extraction after sequentially reading the two sentences. The probability of meaning resolution was 91.2% (SD = 8.7) for the nouns and 89% (SD = 9.1) for the verbs.

Two lists of 160 sentence pairs were created comprising 40 Nn, 40 Nv, 40 Rn and 40 Rv sentence pairs each. The critical words of the two lists were matched in frequency for hidden nouns and verbs within and across lists. For the Rn and Rv conditions, the sentences were presented with the appropriate real word in the terminal position. Each list of 160 sentence pairs was divided into 8 experimental runs comprising 5 sentence pairs per condition as well as 5 additional fixation trials of 8 s.

Each run started with four baseline images (8 s) to allow the magnetic resonance signal to reach equilibrium. Each trial began with a fixation cross lasting 500 ms, then sentence stems (all six words simultaneously) were presented centrally for 2000 ms. After a variable interval between 1 and 2 s, the critical word was presented for 500 ms. The screen remained dark for a variable 1- to 6-s interval. Subsequently, the second sentence was presented in the same fashion, after which participants were required to think covertly about the hidden word or, in the case of a real word, about a semantically related word. The order of the four experimental conditions within an experimental run was pseudo-randomized with the restriction that the same condition could not occur more than two times in a row. Stimulus presentation was controlled by Presentation 9.20 software (Neurobehavioral Systems) and synchronized with MRI data acquisition with an accuracy of 1 ms. Stimuli were presented in white on a black background and projected onto a screen and could be viewed by the participant through a mirror system mounted onto the head-coil.

Prior to the scanning session, participants were carefully trained outside the scanner using test trials to ensure that they fully understood the task. Scanning began with a 15-min structural scan followed by the 8 experimental runs, each lasting about 7 min. A short rest was given between runs.

As the fMRI design did not allow direct testing for correct meaning assignment, a short behavioral test was performed during breaks between functional runs. Participants were shown a new word together with the correct and an alternative meaning (the meaning of another new word presented in the same run) and had to choose the appropriate meaning by button press (10 trials after each block; random SOA of 1000–2000 ms). Subsequently, participants performed a word recognition task. For each of 20 words (5 from the Rn and 5 from the Rv conditions and 10 new real words), participants had to indicate whether it had been presented in the preceding block. This task served to induce participants to attend to the Rn and Rv sentences (which otherwise could have been neglected).

MRI data acquisition

Images were acquired on a 3-T whole-body MRI system (Siemens Magnetom Trio, Erlangen, Germany). Whole-brain T2*-weighted functional magnetic resonance images were obtained (200 scans per run) using axially oriented echo-planar imaging (TR = 2000 ms TE = 30 ms; flip angle = 80°; 32 slices; 4-mm thickness; no gap; matrix size: 64 × 64; field of view: 224 mm; resolution 3.5 × 3.5 × 4 mm³). The first four volumes of each session were discarded owing to T1 equilibration effects. For anatomical reference, a high-resolution T1-weighted anatomical image was obtained (magnetization-prepared, rapid-acquired gradient echoes (MPRAGE), TR = 2500 ms, TE = 4.77 ms, T1 = 1100 ms, flip angle = 7°, 192 slices, 1 mm isotropic voxels).

MRI data preprocessing

Data were analyzed using standard procedures implemented in SPM2 (<http://www.fil.ion.ucl.ac.uk/spm>): First, functional volumes were phase-shifted in time with reference to the first slice to minimize purely acquisition-dependent signal-variations across slices. Head-movement artifacts were corrected based on an affine rigid body transformation, where the reference volume was the first

image of the first run (e.g., Friston et al., 1996). Functional data were then averaged and the mean functional image was normalized to a standard stereotactic space using the EPI-derived MNI template (ICBM 152, Montreal Neurological Institute) provided by SPM2. After an initial 12-parameter affine transformation, an iterative non-linear normalization was applied using discrete cosine basis functions by which brain warps are expanded in SPM2 (Ashburner and Friston, 1999). Resulting normalization parameters derived for the mean image were applied to the whole functional set. Finally, functional EPI volumes were resampled into 4-mm cubic voxels and then spatially smoothed with an 8-mm full-width half-maximum (FWHM) isotropic Gaussian kernel to minimize effects of inter-subject anatomical differences.

MRI data analysis

The statistical evaluation was based on a least-square estimation using the general linear model by modeling the different conditions with a regressor waveform convolved with a canonical hemodynamic response function (Friston et al., 1998). Specifically, the event-related design matrix included all conditions of interest, that is, 1Nn (Nn within 1st sentence) and, analogously, 2Nn, 1Nv, 2Nv, 1Rn, 2Rn, 1Rv, 2Rv. The data were high-pass filtered (to a maximum of 1/128 Hz), and serial autocorrelations were estimated using an autoregressive model (AR(1) model). Resulting estimates were used for non-sphericity correction during model estimation. Confounding effects in the global mean were removed by proportional scaling, and signal-correlated motion effects were minimized by including the estimated movement parameters. Contrast images were calculated for each subject. The resulting contrast images were submitted to a second-level analysis using a 3-way within-subject ANOVA with correction for non-sphericity. Main effects and interactions were tested with linear contrasts (*t*-test, instead of *F*-tests). Unless mentioned otherwise, contrasts were thresholded at FEW $P < 0.05$ with a cluster extent of > 20 contiguous voxels, and only clusters significant at $P < 0.05$ corrected for multiple comparisons are reported and interpreted (Worsley and Friston, 1995). The maxima of suprathreshold regions were localized by rendering them onto the volunteers' mean normalized T1 structural images on the MNI reference brain (Cocosco et al., 1997). Maxima and all coordinates are reported in MNI coordinates as used by SPM and labeled according to the Talairach atlas.

Maps of parameter estimates (β values) were computed from the generalized linear model to assess the magnitude of activation during each condition. The mean parameter estimate of each regressor was then calculated at the cluster activation maximum for each participant and region. These mean parameter estimates were used as dependent variables in 2-way repeated measures ANOVAs conducted separately for new-word and real-word conditions with the following factors: Word exposure (1st vs. 2nd sentence) and Grammatical class (noun vs. verb). Further statistical analyses with planned comparisons (two-sided, paired-sample *t* tests) were used to test differences ($P < .05$) between the parameter estimates from the different conditions.

Finally, to investigate the possible relationship between individual participants' behavioral performance and the activation changes of those areas that were found to be modulated by meaning acquisition, the contrast images (from the contrast $2Nn > 1Nn$ for new-noun analysis and $2Nv > 1Nv$ for new-verb analysis) were entered into a random effects correlation analysis in SPM2 that highlighted the voxels showing a significant correlation between the correct meaning derivation (expressed as the percentage of correct responses on the meaning recognition task for new-nouns and new-verbs, respectively) and the intensity of task-related BOLD activity. For this analysis, activation clusters at a significance level of $P < .05$ corrected for multiple comparisons were interpreted.

Results

Behavioral performance

Meaning recognition for Nn was significantly higher than for Nv ($71.5 \pm 13.1\%$ vs. $59.7 \pm 12.5\%$, respectively, $t_{20} = 4.18$, $P = 0.0001$), and both were significantly different from chance (Nn: $t_{20} = 25.02$; $P < 0.0001$; Nv: $t_{20} = 21.98$, $P < 0.0001$). Furthermore, fewer false alarms (Nn $25.4 \pm 12.7\%$ vs. Nv $31.9 \pm 9\%$, $t_{20} = -2.9$, $P = 0.009$) and omissions ($3.2 \pm 6.7\%$ vs. $8.2 \pm 12.3\%$, $t_{20} = -2.8$, $P < 0.009$) were observed for Nn. Reaction times were significantly shorter for Nn ($1598 \text{ ms} \pm 316$ vs. $1841 \text{ ms} \pm 351$, $t_{20} = -10.13$, $P < 0.0001$).

In the word recognition task, the overall hit rate was 87.2% ($SD = 6.8$) and false alarms occurred in 10.3% ($SD = 5.9$), indicating that participants paid attention to the real-word sentence conditions. Differences between nouns and verbs were found for hits (Rn: $91.2 \pm 5.9\%$, Rv: $84.2 \pm 8.9\%$; $t_{20} = 5.3$, $P < 0.0001$) and false alarms (Rn $7.3 \pm 5.7\%$, Rv: $13.3 \pm 7.2\%$; $t_{20} = -5.04$, $P < 0.0001$), but not for omitted responses (Rn: $1.5 \pm 2.2\%$, Rv: $3.1 \pm 5.4\%$; $t = -1.5$, $P = 0.142$). Participants were faster to judge nouns (Rn: $1174 \text{ ms} \pm 207$; Rv: $1430 \text{ ms} \pm 264$, $t_{20} = -9.2$, $P < 0.0001$). These differences in memory judgment for verbs and nouns replicate previous findings (Reynolds and Flagg, 1976; Wearing, 1970).

Functional imaging

The functional imaging data were subjected to a within-subjects ANOVA. Main effects of Type of word (defined as differences between new-real and real-new words), Word exposure (defined as differences between first-second and second-first sentences) and Grammatical class (defined as differences between noun-verb and verb-noun) were investigated. We created statistical parametric maps with *t*-contrasts in order to further assess these effects.

Type of word effect

Real words showed greater activation than new words in the left anterior cingulate cortex (BA 32), bilateral posterior cingulate gyrus (BA 31) and right inferior parietal lobule (BA 40) (see Supplementary data; Table S1 and Fig. S1a). New words displayed larger BOLD responses than real words in left superior and middle frontal gyrus (BA 6), left inferior frontal gyrus (BA 44, BA 45 and BA 47), left middle temporal gyrus (BA 21 and BA 37) and left inferior parietal lobule (BA 40) among other regions (see Table 1 and Fig. 1A).

Table 1
Activation clusters for main effect of Type of word.

Brain region	Coordinates				P corrected
	x	y	z	Z	
<i>Type of word effect (Nw > Rw)</i>					
L superior frontal gyrus (6)	-4	8	60	Inf	0.0001
L inferior frontal gyrus (44)	-48	8	24	Inf	0.0001
L middle frontal gyrus (6)	-52	4	48	Inf	0.0001
L inferior frontal gyrus (45)	-44	20	20	Inf	0.0001
L inferior frontal gyrus (47)	-48	32	0	Inf	0.0001
R cerebellum	32	-60	-32	Inf	0.0001
L middle temporal gyrus (37)	-44	-60	-8	Inf	0.0001
L inferior parietal lobule (40)	-36	-44	44	7.82	0.0001
R inferior frontal gyrus (47)	32	24	-4	6.99	0.0001
R middle occipital gyrus (18)	36	-96	0	6.77	0.0001
L middle temporal gyrus (21)	-56	-40	4	5.58	0.0001
L cuneus (18)	-20	-104	-4	5.48	0.0001

MNI coordinates and Z-score for the peak location in a particular identified anatomical cluster (FWE $P < 0.05$; 20 voxels spatial extent) for the statistically significant differences of the corresponding activated regions.

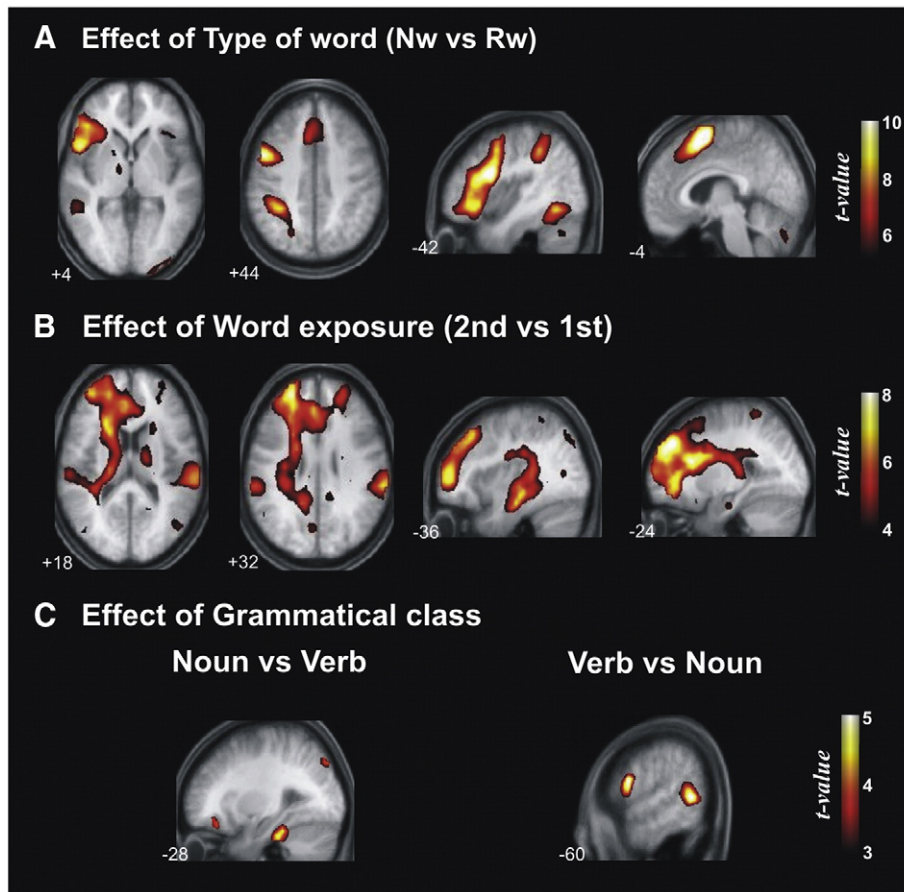


Fig. 1. (A) Group-average comparisons between new words and real words (Type of word effect). (B) Group-average comparisons between second and first sentence for new words (Word exposure effect). (C) Grammatical class effect. Left: Group-average comparison between new-nouns and new-verbs. Right: Group-average comparison between new-verbs and new-nouns. Activations were superimposed on the mean anatomical image formed by averaging all 21 subjects' T1 structural MRI scans mapped into normalized MNI space.

Word exposure effect

The comparison of first versus second sentence showed greater activation in bilateral lingual gyrus (BA 17), left middle temporal gyrus (BA 21) and left inferior frontal gyrus (BA 47) (see Supplementary data; Table S1 and Fig. S1b). The second sentence revealed, compared to the first sentence, larger activation in bilateral middle frontal gyrus (BA 8, BA 9 and BA 10), left anterior cingulate gyrus (BA 32), left

hippocampus, bilateral caudate, left thalamus and bilateral inferior parietal lobule (BA 40) among other regions (see Table 2 and Fig. 1B). Notice also in Fig. 1B the spread activation observed between the different regions in the left hemisphere activated network, extending from the temporal lobule until more anterior prefrontal regions, through the thalamus, the basal ganglia and the insular cortex.

Grammatical class effect

Nouns showed greater activation than verbs in left fusiform/parahippocampal gyrus (BA 20/36). Verbs displayed larger activation than nouns in left middle/superior posterior temporal gyrus (BA 21/22) and left inferior frontal gyrus (BA 44) (see Table 3 and Fig. 1C). In order to ascertain that these activations reflected general grammatical class

Table 2
Activation clusters for main effect of Word exposure.

Brain region	Coordinates				P corrected
	x	y	z	Z	
<i>Word exposure effect (2Sentence>1Sentence)</i>					
L middle frontal gyrus (9)	-28	40	40	7.80	0.0001
L anterior cingulate cortex (32)	-4	36	28	7.13	0.0001
L middle frontal gyrus (10)	-16	48	12	6.87	0.0001
R inferior parietal lobule (40)	64	-32	24	6.62	0.0001
L hippocampus	-36	-20	-16	6.60	0.0001
L caudate	-16	20	-4	6.59	0.0001
R cerebellum	40	-80	-36	6.46	0.0001
L precuneus/cingulate gyrus (7/31)	-4	-36	48	6.28	0.0001
R inferior/middle frontal gyrus (10)	40	44	4	5.87	0.0001
R caudate	16	20	-4	5.82	0.0001
L transverse temporal gyrus (41)	-32	-32	8	5.82	0.0001
L inferior parietal lobule (40)	-60	-32	32	5.76	0.0001
R middle frontal gyrus (8)	28	32	44	5.50	0.0001
R middle temporal gyrus (21/37)	52	-60	4	5.08	0.0001
L thalamus	0	-4	8	4.98	0.0001

MNI coordinates and Z-score for the peak location in a particular identified anatomical cluster (FWE $P < 0.05$; 20 voxels spatial extent) for the statistically significant differences of the corresponding activated regions.

Table 3
Activation clusters for main effect of Grammatical class.

Brain region	Coordinates				P corrected
	x	y	z	Z	
<i>Grammatical class effect (N>V)</i>					
L fusiform/parahippocampal gyrus (20/36)	-28	-32	-24	4.65	0.056
<i>Grammatical class effect (V>N)</i>					
L middle/superior temporal gyrus (21/22)	-64	-52	12	5.20	0.013
L inferior frontal gyrus (44)	-60	8	24	5.17	0.023

MNI coordinates and Z-score for the peak location in a particular identified anatomical cluster ($P > 0.001$; 20 voxels spatial extent) for the statistically significant differences of the corresponding activated regions.

Table 4
Activation clusters for interactions.

Brain region	Coordinates				P corrected
	x	y	z	Z	
<i>Type of word × Grammatical class</i>					
R precuneus (19)	40	−72	40	4.71	0.0001*
L inferior parietal lobule (7/40)	−32	−68	48	4.32	0.0001*
Cingulate gyrus (29)	0	−44	12	4.16	0.012*
R middle frontal gyrus (9)	48	20	36	4.13	0.027*
<i>Word exposure × Type of word</i>					
R cerebellum	4	−80	−24	7.80	0.0001
L inferior parietal lobule (40)	−48	−52	44	7.79	0.0001
L middle frontal gyrus (10)	−36	52	4	7.48	0.0001
L anterior cingulate cortex (32)	−4	32	40	7.05	0.0001
R inferior parietal lobule (40)	44	−56	44	6.59	0.0001
R thalamus	16	−8	16	6.45	0.0001
L thalamus	−20	−16	16	6.43	0.0001
R putamen	28	0	0	6.19	0.0001
L putamen	−24	16	0	6.10	0.0001
R middle frontal gyrus (10)	32	48	20	5.84	0.0001
L superior frontal gyrus (6)	−4	12	68	5.81	0.0001
L middle temporal gyrus (21)	−64	−40	−4	5.61	0.0001
L lateral globus pallidus	−24	−16	0	5.54	0.0001
L inferior frontal gyrus (47)	−40	16	−4	5.42	0.0001
L precuneus (7)	−4	−68	44	5.17	0.0001
L thalamus (pulvinar)	−20	−28	8	5.16	0.0001
R medial globus pallidus	8	0	−4	4.90	0.0001
<i>Word exposure × Grammatical class</i>	No significant activations				
<i>Word exposure × Grammatical class × Type of word</i>	No significant activations				

MNI coordinates and Z-score for the peak location in a particular identified anatomical cluster (FWE $P < 0.05$; 20 voxels spatial extent; $*P > 0.001$) for the statistically significant differences of the corresponding activated regions.

effects, each contrast (Noun vs. Verb; Verb vs. Noun) was exclusively masked with the contrast Type of word by Grammatical class interaction ($P < 0.001$, uncorrected). All three regions survived the masking procedure ($P < 0.001$, uncorrected), suggesting that these regions were indeed involved in noun and verb processing independent of word type.

Interactions

The interaction between Type of word and Grammatical class showed significant activation in left inferior parietal lobule (BA 7/40), right precuneus (BA 19), posterior cingulate gyrus (BA 29) and right middle frontal gyrus (BA 9) (see Table 4 and Fig. 2A, see also Fig. S2).

In all these regions, new-nouns showed, overall, larger activation than new-verbs except in the right middle frontal gyrus where no differences were observed. The interaction between Word exposure and Type of word showed large activations (see Table 4 and Fig. 2B) in bilateral inferior parietal lobule (BA 40), bilateral middle frontal gyrus (BA 10), left anterior cingulate cortex (BA 32), left superior frontal gyrus (BA 6), left middle temporal gyrus (BA 21), left inferior frontal gyrus (BA 47) in the vicinity of the anterior insula, bilateral thalamus, globus pallidus and putamen. In general, new words showed an increase in activation for the second sentence compared to the first in these regions, while real words showed no differences or in some

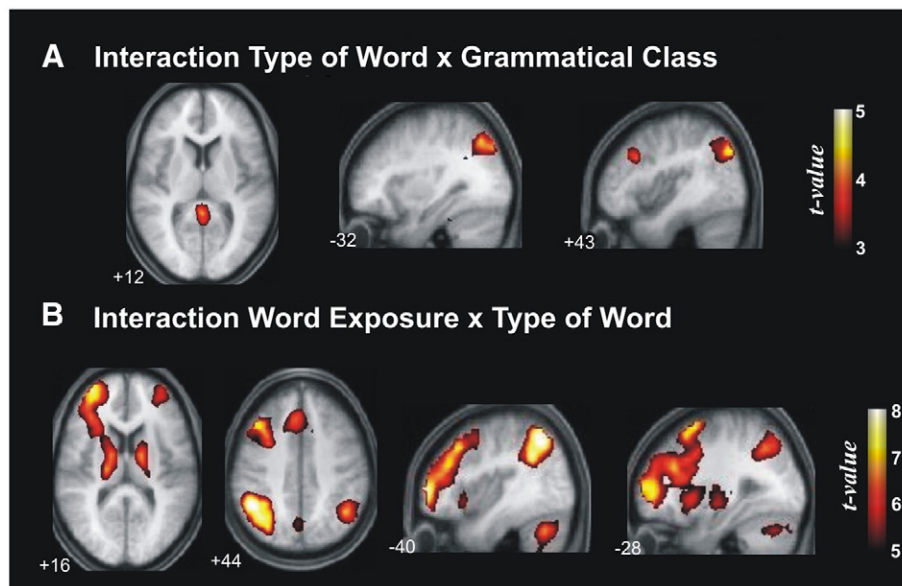


Fig. 2. (A) Group-average interaction between Type of word (word/new word) and Grammatical Class (verbs/nouns). (B) Group-average interaction between Word exposure (first/second exposure) and Type of word. Activations were superimposed on the mean anatomical image formed by averaging all 21 subjects' T1 structural MRI scans mapped into normalized MNI space.

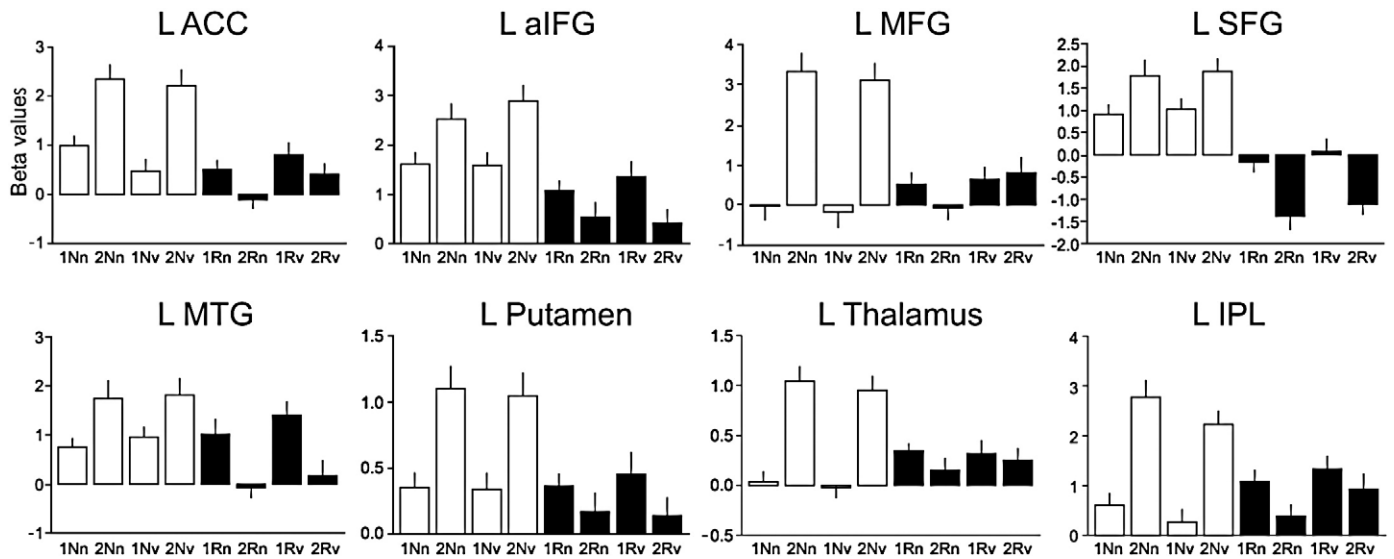


Fig. 3. Group-average beta values for each condition in selected regions showing an interaction between Word exposure and Type of word: left anterior cingulate cortex (L ACC), left anterior inferior frontal gyrus (L aIFG), left middle frontal gyrus (L MFG), left superior frontal gyrus (L SFG), left middle temporal gyrus (L MTG), left putamen, left thalamus and left inferior parietal lobule (L IPL).

cases a decrease in activation reflecting, most probably, priming effects (see Fig. 3). The other interactions did not display any significant activation.

Analysis of the areas modulated by grammatical class

To further assess the effects of grammatical class, ANOVAs were performed on the parameter estimates at the peak coordinates of the regions showing Grammatical class effects. The three regions, namely, left fusiform gyrus, left posterior middle temporal gyrus and left inferior frontal gyrus, revealed only Grammatical class effects for new words and no word exposure effects (see Table 5 and Fig. 4). New-nouns showed greater activation than new-verbs in the left fusiform gyrus while the opposite pattern was observed in the left posterior middle temporal and inferior frontal gyrus. Despite the fact that new words showed a Word exposure \times Grammatical class interaction for the left fusiform gyrus, further pairwise comparisons revealed no differences between sentences for either new-word type (1Nn vs. 2Nn: $t = 1.33$, $P = 0.19$; 1Nv vs. 2Nv: $t < 1$), while significant differences were observed between new-nouns and new-verbs in both sentences (1Nn vs. 1Nv: $t_{20} = 4.87$, $P < 0.0001$; 2Nn vs. 2Nv: $t_{20} = 3.86$, $P < 0.001$).

In a similar vein, real-verbs showed larger activation than real-nouns in the left posterior middle temporal gyrus and left inferior frontal gyrus, while real-nouns showed a significant greater activation than real-verbs in the left fusiform gyrus (1Rn vs. 1Rv: $t_{20} = 2.53$, $P < 0.020$) (see Table 5 and Fig. 4).

Table 5
Parameter estimates analysis.

	Peak coordinates	New word			Real word		
		WE	GC	WE \times GC	WE	GC	WE \times GC
L FFG	-28, -32, -24	n.s.	25.43***	4.45*	n.s.	n.s.	5.36*
L pMTG	-64, -52, 12	n.s.	35.12***	n.s.	13.46**	8.01**	n.s.
L pIFG	-60, 8, 24	n.s.	19.40***	n.s.	4.23*	13.20**	n.s.

F-values corresponding to pairwise ANOVAs restricted to new word and real word, respectively, comparing the different conditions and regions of interest. WE, word exposure (1st vs. 2nd sentence); GC, grammatical class (nouns vs. verbs) and corresponding interaction; L FFG, left fusiform gyrus; L pMTG, left posterior middle temporal gyrus; L pIFG, left posterior frontal gyrus. Degrees of freedom: 1, 20. n.s., non-significant. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Activation correlated with meaning acquisition

Several brain regions showed a significant correlation between correct responses to new-nouns in the meaning recognition task (but not for new-verbs) and activation changes associated with repeated exposure (see Fig. 5). The highest correlations were obtained for the 2Nn > 1Nn contrast and were located in the right and left hippocampus (coordinates of the peak of the cluster, $x = 32$, $y = -12$, $z = -20$, $r = .70$, $P < 0.0001$; $x = -20$, $y = -20$, $z = -16$, $r = .63$, $P < 0.002$, respectively). In addition, the right and left putamen ($x = 24$, $y = -12$, $z = 16$, $r = .69$, $P < 0.001$; $x = -24$, $y = -8$, $z = 12$, $r = .49$, $P < 0.023$), right thalamus ($x = 20$, $y = -28$, $z = 0$, $r = .46$, $P < 0.035$), left anterior cingulate cortex (BA 24, $x = -8$, $y = 28$, $z = 20$, $r = .58$, $P < 0.007$), left middle frontal gyrus (BA 9, $x = -28$, $y = 32$, $z = 28$, $r = .51$, $P < 0.019$) showed significant correlations.

Discussion

We investigated the mapping of novel words to existing noun or verb concepts derived from sentential context using fMRI. Whereas, words from both classes were successfully learned from contextual information, nouns were learned and remembered better and were associated with faster reaction times. These results agree with previous studies showing that nouns of a second language are learned easier than verbs (Gillette et al., 1999; Kallkvist, 1999; Lennon, 1996). These learning differences might be due to the differential conceptual organization of nouns and verbs. Whereas nouns usually point to individual referents, the meaning of verbs is constructed in a relational sense with other elements of the sentence (Gentner, 1982, 2006). Thus, grasping the meaning of a verb from a context imposes a greater cognitive load, because participants need to infer the relationships between several elements present in the sentences and correctly select the right set of semantic components that need to be attached to the hidden concept. Indeed, Bowerman (1982) showed that infants made semantic errors even after the acquisition of verbs (e.g., “Don’t dead him”, produced by a 5-year-old, when seeing someone picking up a spider), suggesting that learning the meaning of verbs is an extended and incremental process. Verbs are more challenging because the underlying concepts are more abstract and relational, depend on the speaker’s perspective and do not directly label an event or refer to a physical entity. The meaning of a hidden noun can be inferred easily by binding it to the object-referent (Gleitman et al., 2005). By contrast,

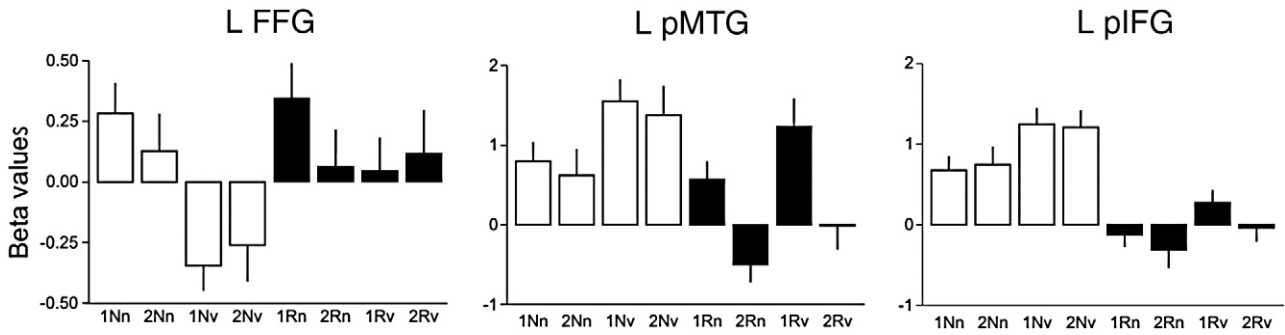


Fig. 4. Group-average beta values for 1st sentence new-noun (1Nn), 2nd sentence new-noun (2Nn), 1st sentence new-verb (1Nv), 2nd sentence new-verb (2Nv), 1st sentence real-noun (1Rn), 2nd sentence real-noun (2Rn), 1st sentence real-verb (1Rv) and 2nd sentence real-verb (2Rv) in regions showing a main effect of Grammatical class: left fusiform gyrus (L FFG), left posterior middle temporal gyrus (L pMTG) and left posterior inferior frontal gyrus (L pIFG). For real words, the same tendency of the Grammatical class effect was observed in the three regions although the size of the effects was less. Bars indicate standard error of the mean.

inferring a verbal concept usually requires to assess the semantic relations between objects and events occurring in the context.

Importantly, the present results show that the linguistic differences discussed above are accompanied by a neural dissociation in specific brain regions engaged in mapping verb or noun meanings to new words: left fusiform gyrus was associated with significantly greater activity for mapping meaning to new-nouns, whereas the posterior middle temporal gyrus and left posterior inferior frontal gyrus showed greater activity for new-verb stimuli. Furthermore, activity in the hippocampus (bilateral), putamen (bilateral), right thalamus, anterior cingulate gyrus and left middle frontal gyrus showed a positive correlation with the efficiency of mapping meanings to new-nouns. At the chosen threshold, no brain region showed a positive correlation with new-verb learning. At present, we do not have a clear explanation about the lack of a significant relationship between functional activation and learning rates in verbs. Indeed, participants were clearly able to extract the hidden meaning in both conditions. Although meaning recognition was more efficient in the new-noun condition, it is important to consider that the behavioral test was performed at the end of each run, which means that participants needed to remember 10 new words–meaning pairs per

run. In a self-paced reading experiment with the current materials, using a similar setting as described in Mestres-Misse et al. (2007), we also encountered a significant difference in the percentage of correct meaning extraction when participants were tested immediately after each trial (nouns 98.08% vs. verbs 94.23%; $t_{25} = 2.3$; $P < 0.030$) (see Supplementary data for additional analyses showing that the effects of new-verb learning are distinguishable from task difficulty effects).

The overall pattern of the present results dovetails nicely with previous findings from our group demonstrating a word-learning network comprising prefrontal regions, ACC, basal ganglia, middle temporal, inferior parietal and medial temporal lobule (Mestres-Misse et al., 2008, in press). In the process of inferring the meaning of a new word, a set of initial candidate semantic features might be activated based on the information conveyed by the initial context and might be narrowed down during more encounters of the new word in different contexts. This process is mediated by the interplay between the MTG and the ventral IFG, with the latter likely involved in guiding semantic selection/retrieval processes (Badre and Wagner, 2002; Badre et al., 2005; Wagner et al., 2001; Moss et al., 2005; Bedny et al., 2007). However, this mechanism of semantic selection and retrieval might require the monitoring of conflict between candidate

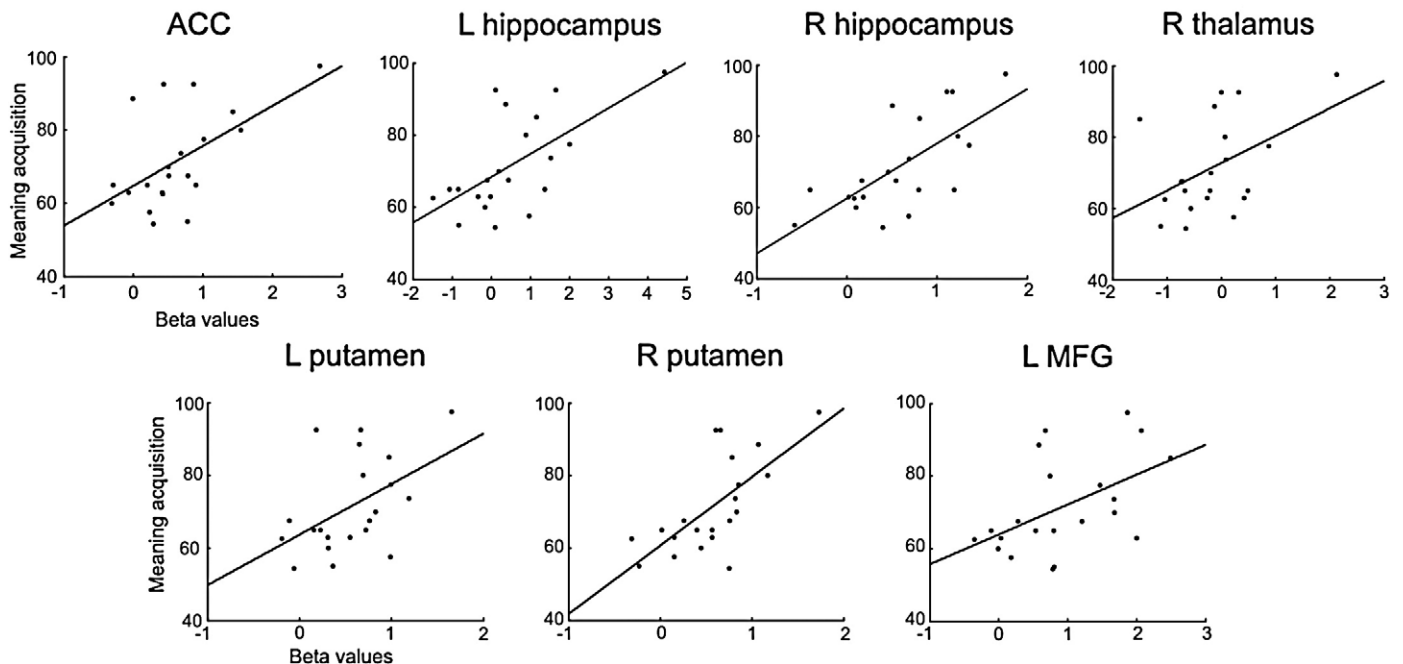


Fig. 5. Scatterplots of the beta values against meaning recognition rate for new-nouns (Nn) for the left anterior cingulate cortex (BA 24, coordinates $-8, 28, 20$), left hippocampus ($-20, -20, -16$), right hippocampus ($32, -12, -20$), left putamen ($-24, -8, 12$), right putamen ($24, -12, 16$), right thalamus ($20, -28, 0$) and left middle frontal gyrus (BA 9, $-28, 32, 28$).

meanings or lexical items pre-activated in the semantic network and the final selection of the best fitting candidate concept. This monitoring and selection of the final lexical candidate is probably mediated also by the ACC-striatum-thalamic loop (Mestres-Misse et al., 2008, 2009). The basal ganglia and the thalamus may provide a bias signal towards the selection of a candidate lexical item. Once an appropriate lexical item has been selected, the bias may be overridden allowing further processing of the selected item by frontal structures (Crosson et al., 2003; Nadeau and Crosson, 1997) and later storage in medial temporal regions (Breitenstein et al., 2005; Mestres-Misse et al., 2008; Davis et al., 2009). Based on this hypothesis, the prefrontal cortex and basal ganglia monitor and gate lexical information generated in the cortex when the language system cannot rely entirely on automatic mechanisms but strategic-controlled mechanisms are required (Copland et al., 2000; Friederici, 2006; Johnson and Ojemann, 2000; Ketteler et al., 2008).

Finally, the activation of left middle/superior frontal gyrus in the present study contributes to the mentioned word-learning network with an extra step, that is, inductive reasoning (Ferstl et al., 2008; Ferstl and von Cramon, 2001; Friese et al., 2008; Keil et al., 2005). Our results suggest a relationship between left anterior frontal cortex and the ability to integrate information necessary to infer the meaning of a new word. The activation observed in more posterior prefrontal regions, like in the dorsolateral prefrontal cortex, could be related to the effort of maintaining in working memory the information gathered across the two sentences (Chein et al., 2003; Petrides, 2005). The on-line integration of this information is necessary in order to discover the underlying meaning.

Importantly, pure grammatical class effects were seen in a number of regions (see Fig. 4). New-nouns led to greater activation in the left anterior fusiform gyrus, a region that has classically been associated with visual object processing (Chao et al., 1999; Martin and Chao, 2001). As pointed out above, a main difference between nouns and verbs is their semantic representation with most nouns being more concrete than verbs (Bird et al., 2003; Marshall et al., 1996a,b). Thus, it might be hypothesized that the fusiform gyrus activation is driven by the greater imageability of nouns, but dissociations between nouns and verbs in the fusiform gyrus have been shown to remain even after imageability was controlled (Crepaldi et al., 2006; Luzzatti et al., 2006; Shapiro and Caramazza, 2003; Shapiro et al., 2005, 2006). It follows that imageability cannot be the only cause of the noun-verb dissociation.

New-verbs were associated with greater activation in left posterior inferior frontal gyrus and left posterior middle temporal gyrus. As mentioned in the Introduction, several neuroimaging and neuropsychological studies have associated activation in these areas with verb processing. Specifically, activation in the left posterior inferior frontal gyrus has been suggested to reflect greater cognitive demands in processing verbal inflectional morphology compared to nominal morphology rather than differences in verb-noun neural representations (Tyler et al., 2001, 2004; Yokoyama et al., 2006; Longe et al., 2007). These studies suggest that noun and verb stems do not differ in their representation, however, when verbs are inflected, and therefore, morphologically more complex than nouns (even when also inflected), greater involvement of the neural systems engaged in morphosyntactic processes is observed (de Diego et al., 2006). Nonetheless, this activation could also reflect greater general processing demands imposed by verbs (Siri et al., 2008; Berlinger et al., 2008; Crescentini et al., in press).

Importantly, previous word-learning studies have also shown increased activation in the inferior frontal gyrus for recently acquired new words (Gronholm et al., 2005, 2007; Davis et al., 2009; Mestres-Misse et al., 2009). Also, James and Gauthier (2004) showed that visual processing of novel objects which were associated with arbitrary semantic information activated the inferior frontal cortex compared to non-trained novel objects or new objects which were

associated with proper names. Similarly, Gronholm et al. (2005; see also Gronholm et al., 2007) showed larger activation in the posterior IFG for new objects which were trained to be associated with real names and/or definitions. These results are in agreement with the proposal that the IFG is involved in the control and/or selection of semantic features (Thompson-Schill et al., 1997; Wagner et al., 2001). From a controlled semantic retrieval perspective (Wagner et al., 2001), the IFG might be involved in the activation of semantic features in situations where no automatic semantic retrieval is possible. A more integrative perspective (Wagner, 2002) suggests that controlled semantic retrieval and selection are facets of the same and more general top-down bias signal originating in the IFG. This signal facilitates the recovery of goal-relevant knowledge in a particular context. Importantly, the posterior part of the IFG, which in the present study showed greater activation for new-verbs, has been implicated in selection of competing semantic features (Gabrieli et al., 1998; Poldrack et al., 1999; Wagner et al., 2000), whereas more anterior ventral parts appear to be involved in controlled semantic retrieval.

Thus, the question arises whether the increased IFG activation for new-verbs compared to new-nouns is related to the higher demands imposed by relational processing. The processing of the semantic features associated to a new-verb might require to focus on semantic relations between objects and events occurring across the sentences. Selection of the fitting features will then lead to the assignment of a meaning to the new-verb. In contrast, less semantic features (mainly based on the detection of possible object referents) will be activated in the new-noun condition resulting in less competition between the different candidates. Less competition and less effort in the retrieval of semantic features in the new-noun condition goes in line with less activation in the IFG as observed in the present study.

The posterior middle temporal gyrus lies just anterior to area MT (Culham et al., 2001; Dukelow et al., 2001; Zeki et al., 1991) and has been associated to action observation and imitation (Grezes and Decety, 2001), verb processing (Davis et al., 2004; Fiez et al., 1996; Kable et al., 2002; Liljestrom et al., 2008; Longe et al., 2007; Perani et al., 1999) and action word generation (Martin et al., 1995). Lesions in this region impair the retrieval of knowledge for actions (Tranel et al., 2003). Furthermore, certain classes of verbs, such as manipulation verbs, psychological verbs (Perani et al., 1999) and cognition verbs (Grossman et al., 2002), lead to prominent activations of this area and increased activation for verbs compared to nouns regardless of imageability suggesting that it reflects semantic aspects of action associated to verbs in general rather than mere tool utilization or motion (Bedny et al., 2008). What the current results add is that the very same regions differentially engaged in the processing of nouns and verbs are also engaged in the mapping of noun and verb concepts to novel words.

Finally, correlational analysis showed that activity in bilateral hippocampus, ACC, left prefrontal cortex, putamen and thalamus was related to the quality of noun learning. This suggests a positive relationship between activation and word learning. The greater activation for new-nouns than new-verbs in these regions thus corresponds with the behavioral finding of a better performance for new-nouns. These differences in brain activation and behavior can be explained by representational differences: noun meanings refer to stable, individuated and tangible entities which should facilitate rapid mapping of meaning and engage circumscribed stable brain networks. As verbs meanings might involve multiple semantic aspects such as motion, change, manner or direction and encode relations between things, the information encoded in verbs is more complex and abstract (Gentner, 1982, 2006), which should lead to more extended and less stable brain activations on the one hand and a more difficult mapping of verb meanings to new words on the other hand. The current results contribute to the word-learning literature by showing that word learning and mapping of meaning is not accomplished by

language domain-specific but rather by domain-general cognitive mechanisms (Bloom, 2000; Gentner and Namy, 2004).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.neuroimage.2009.10.018.

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