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# Research



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# Sentential negation of abstract and concrete conceptual categories: a brain decoding multivariate pattern analysis study

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We rarely use abstract and concrete concepts in isolation but rather embedded within a linguistic context. To examine the modulatory impact of the linguistic context on conceptual processing, we isolated the case of sentential negation polarity, in which an interaction occurs between the syntactic operator not and conceptual information in the negation's scope. Previous studies suggested that sentential negation of concrete action-related concepts modulates activation in the fronto-parieto-temporal action representation network. In this functional magnetic resonance imaging study, we examined the influence of negation on a wider spectrum of meanings, by factorially manipulating sentence polarity (affirmative, negative) and fine-grained abstract (mental state, emotion, mathematics) and concrete (related to mouth, hand, leg actions) conceptual categories. We adopted a multivariate pattern analysis approach, and tested the accuracy of a machine learning classifier in discriminating brain activation patterns associated to the factorial manipulation. Searchlight analysis was used to localize the discriminating patterns. Overall, the neural processing of affirmative and negative sentences with either an abstract or concrete content could be accurately predicted by means of multivariate classification. We suggest that sentential negation polarity modulates brain activation in distributed representational semantic networks, through the functional mediation of syntactic and cognitive control systems.

This article is part of the theme issue 'Varieties of abstract concepts: development, use and representation in the brain'.

# 1. Introduction

Research on conceptual knowledge has provided consistent neuropsychological and neuroimaging evidence that abstract and concrete concepts are represented in distributed brain networks, which are best differentiated at the level of structural and functional connectivity [1]. In so-called 'hubs and spokes' models of conceptual knowledge, modality-specific nodes (i.e. spokes), for example in sensory-motor or limbic areas, are linked together with modality-invariant and graded hubs (though it is debated whether there are several hubs in the fronto-parieto-temporal cortices [2] or a single hub in the anterior temporal lobe [3]). According to multiple representation accounts developed within the grounded cognition framework, the differential involvement of these distributed networks for processing abstract and concrete concepts, and their more fine-grained sub-categories, reflects the type of experiential information that is more relevant for either concept type during acquisition [4,5]. Concrete concepts mostly draw on sensory-motor experience [6], whereas abstract concepts mostly draw on emotional, introspective, social and linguistic experience [5,7–10].

Whether and to what extent experiential information also contributes to a context-dependent appropriate use of concepts is debated. Previous work revealed differential contextual effects on abstract and concrete word processing. These were explained in terms of either lower context availability [11] or higher context diversity [12] for abstract versus concrete words. However, the neural mechanisms through which linguistic contextual information modulates multiple grounded representations are still poorly understood [13].

In the present study, we isolated the case of sentential negation as a benchmark for testing the role of linguistic context on neural conceptual representations, for two reasons. First, by reversing the truth value of conceptual information, sentential negation has clear-cut, discrete effects on its semantic interpretation, applying equally to concrete (e.g. She doesn't kick the ball) and abstract (e.g. She doesn't remember the past) concepts. Second, there is evidence that the sentential negation of concrete, action-related concepts reduces the access to experience-related sensory-motor brain networks. In a previous functional magnetic resonance imaging (fMRI) study [14], we showed that sentential negation of action-related concepts reduces activation and effective connectivity within the left-hemispheric premotor-parietotemporal action representation system. Concordant evidence of motor cortex activity reduction in the presence of sentential negation was obtained in other fMRI [15], electroencephalography (EEG) [16] and transcranial magnetic stimulation (TMS) [17] studies. This effect has been interpreted as a reduced grounding in the sensory-motor system for the semantic processing of negative action-related sentences [18], possibly due to action inhibition mechanisms [16].

Building on this evidence, in the present study we tested not only concrete but also abstract concepts in order to address the questions of whether processing of specific semantic categories entails activation of brain areas coding for the corresponding experiential information and whether this activation is modulated by negation. We applied multivariate pattern analysis (MVPA) to fMRI data obtained while participants processed fine-grained abstract (mental state, emotion, mathematics) and concrete (related to mouth, hand, leg actions) concepts, presented in either the affirmative or negative polarity context (electronic supplementary material, table S1). Compared with univariate methods, MVPA can attain increased sensitivity, by considering activation across multiple voxels that may even be distributed in non-adjacent anatomical regions, rather than accepting or rejecting individual voxels based on a given significance cut-off [19,20]. Based on machine learning classification algorithms, MVPA aims at solving a classification problem (CP), by predicting the stimuli associated with a given activation pattern. Sentential negation for abstract and concrete conceptual categories was examined by specifying the following classification problems:

The first classification problem (CP1) tested whether sentential negation differentially modulates abstract and concrete semantic representations. According to multiple representation accounts and to 'hubs and spokes' neuroanatomical models, abstract and concrete concepts are represented in partially distinct and distributed brain networks. Sentential negation may therefore operate on abstract versus concrete networks independently, yielding in principle four distinct neural representation levels: affirmative abstract, negative abstract, affirmative concrete and negative concrete. By means of CP1, we tested whether our fMRI data contained sufficient information to discriminate between these four sentence types. Previous evidence demonstrated the feasibility of decoding abstract versus concrete semantic content processing, with classification sensitive regions widely distributed across the cortex [21]. To the best of our knowledge, this study provides the first decoding attempt applied to concreteness categories and negation polarities jointly, as reflected by their  $2 \times 2$  factorial interaction.

The second classification problem (CP2) examined the sentential negation of abstract and concrete concepts at a fine-grained semantic level, based on grounded, multiple representation hypotheses that concepts representing different types of experience are represented by distinct modality-specific networks, and that negation operates on each of these networks independently. By applying an MVPA decoding approach, we aimed at predicting the brain activation patterns of each fine-grained conceptual category (mental state, emotion, mathematics, mouth, hand, leg) presented either in the affirmative or negative polarity context ( $6 \times 2$  factorial interaction).

We leveraged MVPA classification to also investigate the main effects nested in our factorial manipulation. Namely, sentential negation polarity (CP3: affirmative versus negative); concreteness (CP4: abstract versus concrete), and fine-grained conceptual category (CP5: mental state, emotion, mathematics, mouth, hand, leg). CP3 sought confirmation for a neural correlate of negation at the syntactic level (i.e. independently of the semantic meanings on which negation operates), an aspect for which limited evidence obtained by means of univariate analysis techniques is available [14,22]. CP4 and CP5 tackled the important question of replicability of previous results for concreteness [21] and fine-grained conceptual categories [23,24].

# 2. Methods

#### (a) Participants

Fifty subjects (25 females, mean (*M*) age = 23.02 years, s.d. age = 4.88) volunteered in the study. All subjects were Italian native speakers with a comparable level of education and with no reported history of neurological or psychiatric disorders. All subjects were right-handed (Edinburgh Inventory score: M = 0.94, s.d. = 0.05). Two subjects (one female) were excluded owing to brain structural anomalies.

#### (b) Experimental design

We applied a within-subject factorial combination of conceptual category (three abstract: mental state (Ms), emotion (Em), mathematics (Ma); three concrete: hand (Ha), mouth (Mo), leg (Le) action-related), and polarity (affirmative (A), negative (N)). This resulted in 12 experimental conditions: AMs, NMs, AEm, NEm, AMa, NMa, AMo, NMo, AHa, NHa, ALe, NLe.

#### (c) Experimental stimuli

The set of stimuli consisted of 35 Italian sentences for each of the six conceptual categories, each sentence presented in the affirmative and negative form (total = 420 sentences) (electronic supplementary material, table S1). The set of affirmative sentences was validated in a previous rating study [9] with respect to linguistic variables, namely: number of words (all four-word sentences), number of syllables (chi-square  $d_{25} = 36.37$ , p = 0.07); number of letters ( $F_{5,204} = 1.25$ , p = 0.29); lexical frequency for,

respectively, nouns ( $F_{5,204} = 1.86$ , p = 0.10), verbs ( $F_{5,204} = 1.72$ , p = 0.13), and noun–verb combinations ( $F_{5,204} = 1.82$ , p = 0.11). In addition, sentences were rated with respect to semantic variables, including category-specific association, body-part association, concreteness, context availability and familiarity (see tables 2–4 in [9]).

All affirmative and negative sentences were read aloud by a female native Italian speaker and recorded in a sound-proof room. Intensity was normalized for all sentences at 70 dB. Pitch was balanced across the six conceptual categories, both for affirmative,  $F_{5,204} = 1.43$ , p = 0.21, and negative sentences,  $F_{5,204} = 0.65$ , p = 0.66.

In order to avoid repetition effects that could arise if participants were exposed to the same sentences in both polarities, the pool of 420 sentences was split in two lists of 210 experimental stimuli, each including only one version of each sentence, either with affirmative or negative polarity. Each list was assigned to one of two groups of subjects (Group A: 24 subjects, 12 females, M age = 23.71 years, s.d. = 6.14, Edinburgh score M = 0.94, s.d. = 0.06; Group B: 24 subjects, 12 females, M age = 22.42 years, s.d. = 3.61, Edinburgh score M = 0.95, s.d. = 0.05).

#### (d) Experimental procedure

Presentation 14.9 (Neurobehavioral Systems Inc.) was used for stimulus presentation. Sentences were presented in an event-related design. The acquisition session for each participant comprised four runs of 12 min 40 s each. Each run consisted of 67 randomized trials: 51 experimental, nine catch and seven null trials. Experimental trials began with the auditory presentation of one sentence, followed by a 2000 ms interval, after which a visual fixation cross appeared for 500 ms. In catch trials, the fixation cross was replaced by a question mark, followed by a written sentence presented for 1000 ms, and participants were instructed to blink their eyelids once in case the written sentence matched the auditory sentence, or twice in case of mismatch (for full details, see [24], where the same procedure was applied).

#### (e) Data acquisition

MRI scans were acquired with a 3 T Intera Philips body scanner (Philips Medical Systems), equipped with an eight-channel head coil (SENSE factor = 2). In order to prevent scanner noise from affecting auditory sentence presentation, fMRI sparse sampling was employed [25,26]. Whole-brain T2\* blood-oxygenation-level dependent (BOLD) images were acquired with a gradient-echo, echo-planar imaging (EPI) pulse sequence (repetition time, TR = 2915 ms acquisition time + 7585 ms silent period = 10 500 ms; echo time, TE = 30 ms). Each functional image comprised 35 axial slices (3.2 mm thick, 0.8 mm gap) acquired in ascending order (field of view, FOV: 240 × 240 mm; matrix size: 128 × 128). Each participant underwent four fMRI scanning sessions, each comprising 71 scans, plus two initial dummy scans, which were discarded prior to data analysis.

A high-resolution T1 anatomical image was acquired for each participant (TR = 7.2 ms; TE = 3.5 ms), comprising 200 axial slices (1 mm slice thickness,  $1 \times 1$  mm in-plane resolution).

#### (f) Data analysis

#### (i) Data preprocessing

Data were preprocessed with SPM8 (www.fil.ion.ucl.ac.uk/ spm), including slice time correction, realignment, and normalization to the Montreal Neurological Institute (MNI) space. Smoothing was not performed to provide optimal sensitivity for high-frequency multi-voxel patterns in MVPA [27]. The time series of each subject were high-pass filtered at 128 s. No pre-whitening and no global normalization was applied. For each subject, we modelled a  $6 \times 2$  factorial design (conceptual category  $\times$  polarity) with four separate sessions and one regressor for each experimental condition. Additional regressors modelled the catch trials and movement parameters. For each subject, we defined a set of Student's *t*-contrasts, with a weight of +1 for one of the experimental condition regressors and a weight of zero for all the other regressors. The resulting 12 *t*-contrast images (AMs, NMs, AEm, NEm, AMa, NMa, AMo, NMo, AHa, NHa, ALe and NLe) of each participant were used for the MVPA [28].

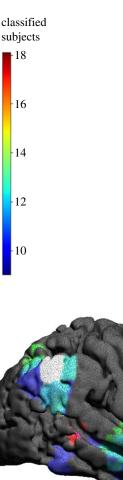
#### (ii) Multivariate pattern analyses

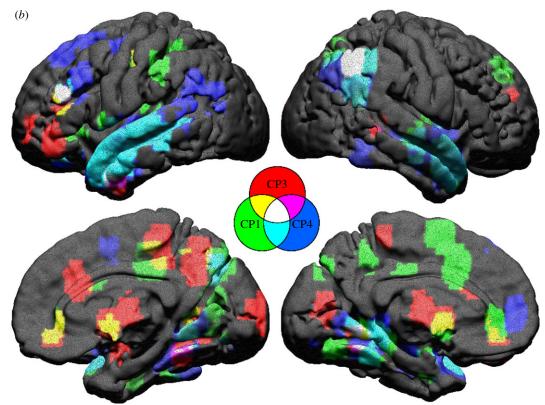
PyMVPA 2.5.0 (www.pymvpa.org; [29]) running under Python 2.7.9 (www.python.org) was used for MVPA. The *t*-contrast images (spmT) were inclusively masked by an image defining the set of non-zero voxels shared by all subjects, with grey matter tissue probability >0.1 (for an equivalent procedure, see [24]). Subject-wise *z*-scoring normalization was applied to correct for noise-related inhomogeneities in voxel intensities. The *t*-contrast images were averaged subject-wise and condition-wise.

A linear support vector machine (SVM) algorithm was used for all CPs (CP1:  $2 \times 2$  factorial interaction, and *post hoc* classification of affirmative versus negative sentences, separately for the abstract and concrete conditions, see §3a; CP2:  $6 \times 2$  factorial interaction; CP3: main effect of polarity; CP4: main effect of concreteness; CP5: main effect of fine-grained conceptual category). Classifications were performed between subjects in order to examine whether brain activation patterns were consistent across subjects, by means of a leave-one-subject-out cross-validation [24]. We report the mean cross-individual classification accuracies across all inclusive mask voxels (i.e. at the whole-brain level).

In addition, we used searchlight analysis [30] with 4 mm radius spheres and a Gaussian Naive Bayes classifier [31] to localize anatomically the brain regions that significantly contributed to accurate discrimination of the different classification problems, as determined through a Monte Carlo permutation testing procedure. The condition labels were permuted in each sphere 1000 times [32], and the actual classification accuracy was then compared against the random permutation distribution with a declared p < 0.001 threshold. We report the mean classification accuracies across leave-one-subject-out cross-validations and the corresponding confusion matrices for the significant searchlight spheres.

For CP5, in order to gain a deeper insight into the brain coding of semantic information for the target conceptual categories, we adapted the procedure described in [24], which is based on recursive feature elimination and the sensitivity weights it provides. Sensitivity weights reflect the contribution of each voxel to the discrimination of one category from the others [33]. For each category, we calculated the spatial intersection of all pairwise sensitivity maps involving that category (e.g. for Ms: Ms-Em, Ms-Ma, Ms-Mo, Ms-Ha, Ms-Le). Before calculation of the category-specific intersections, the pairwise sensitivity maps were filtered for a minimum cluster extension of 20 voxels, only the clusters with sensitivity weights in the 9.5 highest percentile were retained, and smoothing with a 3mm full width at half maximum (FWHM) Gaussian kernel was applied. The sensitivity intersection maps were then inspected anatomically and projected to the Automated Anatomical Labeling Region Of Interest (AAL ROI) atlas [34], in order to identify four distinct levels of semantic coding, derived from 'hubs and spokes' models [2,3]: (i) categoryspecific spokes: brain regions that were specific for just one particular category; (ii) multi-category spokes: AAL ROIs presenting distinct and non-overlapping clusters for two or more category-specific intersection maps; (iii) category-invariant hubs: AAL ROIs presenting clusters with spatial overlap from all the category-specific intersection maps; (iv) graded hubs: AAL ROIs presenting both category-specific and overlapping clusters from all the category-specific intersection maps.





**Figure 1.** MVPA classification of the main effects of sentential negation polarity, concreteness, and their  $2 \times 2$  factorial interaction. (*a*) Confusion matrix for CP1, featuring the means of the classified spmT maps across the significant (p < 0.001, against 1000 permutations) searchlight spheres. Cell numbers represent the mean number of subjects that were classified either correctly (diagonal) or incorrectly (off the diagonal), with respect to the four concreteness by polarity factorial combinations (AA, affirmative abstract; NA, negative abstract; AC, affirmative concrete; NC, negative concrete). (*b*) Anatomical localization of the searchlight spheres yielding significant (p < 0.001, against 1000 permutations) classification accuracy for CP1, CP3 and CP4. Colour codes are indicated by the colour palette inset. The effects are displayed on lateral and medial wall surface renderings of the average anatomical image of all participants. Left and right hemispheres are displayed according to the neurological convention.

# 3. Results

*(a)* 

AA

NA

AC

NC

prediction

AA

18.11

11.03

9.03

9.83

target

NA

10.45

9.79

AC

10.54

9.85

11.56

NC

10.68

9.07

#### (a) CP1: 2 $\times$ 2 concreteness by polarity interaction

The four concreteness by polarity factorial combinations were classified with a mean accuracy of 35.42% across participants (chance level: 100%/4 = 25%) at the whole-brain level. Searchlight permutation testing indicated that there were 135 searchlight spheres that significantly discriminated between the four factorial combinations (p < 0.001 against 1000 permutations), with a mean classification accuracy of

38.41% (figure 1*a*). The significant searchlights were localized over extensive bilateral regions of the brain, including the medial and lateral frontal and parietal cortices, the anterior temporal lobes, the anterior and middle cingulate cortex, the caudate, and the cerebellum (figure 1*b*; electronic supplementary material, table S2A).

Given successful discrimination of the  $2 \times 2$  concreteness by polarity interaction, we further examined our experimental hypothesis that sentential negation modulates the modality-specific brain networks not only for concrete but

also for abstract concepts, by *post hoc* classification of affirmative versus negative sentences, separately for the abstract and concrete conditions.

For abstract concepts, affirmative and negative sentences were discriminated with a mean classification accuracy of 41.66% (chance level: 100%/2 = 50%). Classification accuracy in individual searchlights was more successful. Searchlight permutation testing indicated that there were 23 spheres that significantly discriminated between affirmative and negative sentences (p < 0.001 against 1000 permutations), with a mean classification accuracy of 76.32%, and the mean confusion matrix [34.35 13.65; 13.65; 34.35].

For concrete concepts, affirmative and negative sentences were discriminated with a mean classification accuracy of 56.25% (chance level: 100%/2 = 50%). Again, classification accuracy in individual searchlights was more successful. Searchlight permutation testing indicated that there were 44 spheres that significantly discriminated between affirmative and negative sentences (p < 0.001 against 1000 permutations), with a mean classification accuracy of 76.91%, and the mean confusion matrix [34.82 13.18; 13.18 34.82].

The abstract and concrete conditions partially differed with respect to the macro-anatomical distribution of the searchlights, significantly discriminating between affirmative and negative sentences (electronic supplementary material, figure S1). For the abstract conditions, there was a unique involvement of the left temporal pole, right medial temporal lobe (amygdala, hippocampus and parahippocampal gyrus), right precuneus, and cerebellum (electronic supplementary material, table S2B). Only the concrete conditions, in turn, involved the left posterior middle temporal gyrus, the left angular gyrus, the pars opercularis of the right inferior frontal gyrus, the right superior frontal gyrus, the calcarine and lingual gyri, and, bilaterally, the postcentral gyrus and the putamen (electronic supplementary material, table S2C).

# (b) CP2: $6 \times 2$ fine-grained conceptual category

### by polarity interaction

The mean whole-brain accuracy for the classification of the 12 classes of sentences was 14.93% (chance level: 100%/12 = 8.33%). However, the confusion matrix showed a meaningless structure, that is, an inconsistently populated leading diagonal, and a disproportionally high rate of densely populated off-the-diagonal cells, representing incorrect predictions-to-target correspondences (electronic supplementary material, figure S2). Therefore, no further analysis of CP2 was carried out.

#### (c) CP3: main effect of polarity

Affirmative and negative sentences were discriminated with a mean classification accuracy of 62.50% (chance level: 100%/2 = 50%). Classification accuracy in individual searchlights was more successful. Searchlight permutation testing indicated that there were 47 spheres that significantly discriminated between affirmative and negative sentences (p <0.001 against 1000 permutations), with a mean classification accuracy of 75.66%, and the mean confusion matrix [33.28 14.72; 14.72 33.28]. These searchlights were localized in the left dorsolateral and medial frontal cortex, anterior and middle cingulate gyrus, precuneus and calcarine gyri, left caudate nucleus, right putamen and left thalamus, and cerebellar hemispheres (figure 1*b*; electronic supplementary material, table S3).

#### (d) CP4: main effect of concreteness

Abstract and concrete sentences were discriminated with a mean classification accuracy of 83.33% (chance level: 100%/2 = 50%) at the whole-brain level. Searchlight permutation testing indicated that there were 464 spheres that significantly discriminated between abstract and concrete sentences (p < 0.001 against 1000 permutations), with a mean classification accuracy of 77.82%, and the mean confusion matrix [34.9 13.1; 13.1 34.9]. These searchlights were localized in the left dorsolateral frontal cortex and, bilaterally, in the anterior, posterior, and medial temporal lobe, the angular gyrus, and the cerebellum (figure 1*b*; electronic supplementary material, table S4).

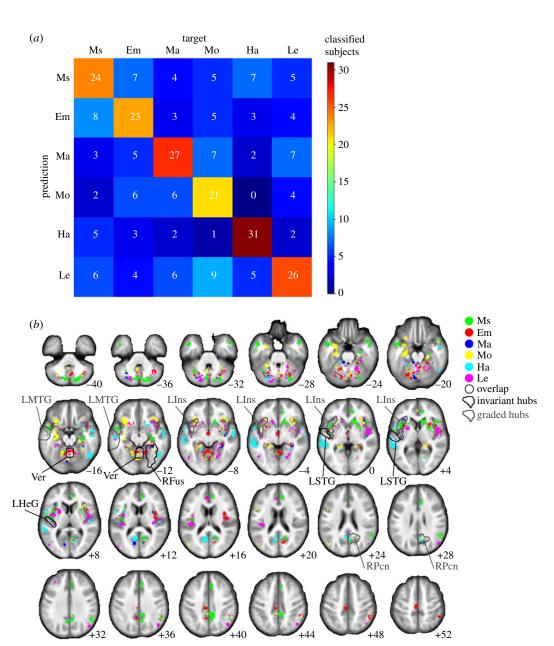
## (e) CP5: main effect of fine-grained conceptual category

The mean whole-brain accuracy for the classification of the fine-grained conceptual categories was 52.78% (chance level: 100%/6 = 16.67%) (figure 2*a*). Searchlight permutation testing yielded a much lower mean classification accuracy (18.17%), indicating that the to-be-discriminated patterns distinguishing between the six categories are sparse and distributed over broad neural territories.

To further investigate this broadly distributed categoryspecificity we applied an alternative whole-brain approach based on sensitivity weights, yielded by recursive feature elimination. We calculated all pairwise classifications among the six categories. For each and every pair, the mean classification accuracy was well above the 50% chance level, with a significant rate of correct predictions-to-targets correspondences (p < 0.001 for all pairs) (electronic supplementary material, table S5). Based on these successful pairwise classifications and on the corresponding sensitivity weights' anatomical distribution, we identified brain regions that might be ascribed to four distinct levels of semantic coding, reflecting multiple representations (figure 2b; electronic supplementary material, table S6; see also §2f(ii)): (i) brain regions that were specific for just one particular category ('category-specific spokes'), and (ii) regions presenting distinct and non-overlapping clusters for two or more categories ('multi-category spokes'): both these coding levels were sparsely distributed over large portions of the heteromodal cortices in both hemispheres, including the cerebellum; (iii) regions of spatial overlap of all categories ('category-invariant hubs'): these were identified in the left superior temporal gyrus/Heschl's gyrus, right fusiform gyrus, and the cerebellar vermis; (iv) regions presenting both spatial overlap and specific clusters for all six categories ('graded hubs'): these were identified in the left insula, left anterior middle temporal gyrus, and right precuneus.

## 4. Discussion

This study investigated how the neural processing of abstract and concrete concepts expressed at the sentence level is modulated by negation polarity. Sentential negation polarity is thought to operate at the syntax-semantic interface [35,36], thus representing a case of interplay between a linguistic



**Figure 2.** MVPA classification of the main effect of fine-grained conceptual category. (*a*) Confusion matrix for CP5, with cell numbers featuring the number of subjects that were classified either correctly (diagonal) or incorrectly (off the diagonal) at the whole-brain level, with respect to the six fine-grained conceptual categories. (*b*) Category-specific sensitivity intersection maps, representing the anatomical regions that consistently allowed us to correctly discriminate each category from the other five categories, in a pairwise fashion. The category-specific intersections are displayed on axial slices (*z*-coordinate levels indicated in mm) of the average anatomical image of all participants (neurological convention). Anatomical region boundaries are displayed for AAL ROIs classified as 'category-invariant hubs' (black colour, LHeG: left Heschl's gyrus; LSTG: left superior temporal gyrus; RFus: right fusiform gyrus; Ver: cerebellar vermis) or 'graded hubs' (grey colour, LMTG: left middle temporal gyrus; LIns: left insula; RPcn: right precuneus).

contextual operator and conceptual representations. Our main intent was to provide a proof of concept for the hypothesis that the neural networks supporting semantic representations are flexibly modulated by the linguistic sentential context [18]. We expanded on two different lines of research: a first line indicating that abstract and concrete concepts, and their respective fine-grained sub-categories, are distinctively encoded in distributed brain networks including categoryinvariant and category-specific nodes [3,4]; and a second line, so far limited to concrete action-related concepts, indicating that sentential negation modulates neural activity of category-specific conceptual representation nodes [14-17]. Our sentence processing fMRI study sought generalization evidence for the modulatory effects of sentential negation by factorial combination of fine-grained abstract and concrete conceptual categories and affirmative/negative polarity.

By applying MVPA across participants, we demonstrated that the fMRI data contained sufficient information to discriminate between affirmative abstract, negative abstract, affirmative concrete and negative concrete sentences resulting from the  $2 \times 2$  concreteness by polarity interaction (CP1). Post hoc classifications showed that affirmative and negative sentences were discriminable also when abstract and concrete conditions were analysed separately. However, when considering a  $6 \times 2$  factorial combination between polarity (affirmative versus negative) and fine-grained abstract (Ms, Em, Ma) and concrete (Mo, Ha, Le) categories (CP2), MVPA failed to accurately discriminate the associated brain activation patterns. Lack of sentential negation modulation on fine-grained semantic categories might be due to methodological aspects. In fact, analyses related to CP2 required separately modelling each of the 12 experimental conditions.

6

This was not the case for CP1, where data were averaged across multiple experimental conditions. It is possible that the number of trials for each experimental condition in our study was not sufficient to ensure fully-fledged category by polarity MVPA separation in CP2. However, this result might also constitute true negative evidence, weakening the conclusions drawn in the present study, and this important limitation needs to be considered. To sum up, the expectations of our proof of concept on negative versus affirmative linguistic contexts were fully met at a level of a simple but conceptually relevant distinction between concrete and abstract sentences, suggesting that the effect of sentential negation is not only limited to concrete actionrelated concepts but also extends to abstract ones. Furthermore, successful classifications were observed when considering the main effects nested in our factorial manipulation. Concerning sentential negation polarity, the MVPA vielded accurate whole-brain classification of the neural patterns associated with affirmative versus negative sentences although classification accuracy in individual searchlights was more successful (CP3). More robust classification accuracy was observed for concreteness (CP4), and fine-grained conceptual category (CP5) main effects.

Anatomical localization of condition-specific fMRI activation patterns is not straightforward in MVPA, since decoding is blind to the spatial organization of these patterns [37]. Nevertheless, MVPA localization techniques such as searchlight analysis [30], in combination with independent meta-analytic evidence on the brain functional organization of semantic processing, can provide useful information on the brain regions where contextual sentential negation modulations may occur. In CP1, CP3 and CP4 the searchlight analysis revealed an involvement of regions broadly distributed over both hemispheres, with a high degree of spatial overlap across these three classification problems (figure 1b; electronic supplementary material, tables S2A, S3 and S4). The classification problems CP1 and CP3, which both addressed the manipulation of syntactic polarity, showed overlap in the pars triangularis of the inferior frontal gyrus, the basal ganglia (notably, the left caudate nucleus), and the anterior and middle cingulate cortex. Both the pars triangularis of the inferior frontal gyrus [38,39] and the left caudate nucleus [40,41] have been consistently implicated in syntactic structure processing, that is, word order computation at the sentence level above and beyond the specific issue of sentential negation. Of even greater relevance are previous univariate fMRI studies specifically investigating negation at the syntactic level, independently of the meanings on which it operates, which found an involvement of the basal ganglia [14] and of the left pars triangularis [22], among a set of other brain regions not identified in the present study. However, the inclusion of the anterior and middle cingulate cortex as a region of overlap between CP1 and CP3 prompts another possible functional interpretation. The anterior/middle cingulate and the left pars triangularis are known to be key components of the cognitive control network, also referred to as multiple-demand system, which is recruited by language tasks, including syntactic ones [42]. The left caudate nucleus, in turn, is known to be crucially involved in language monitoring and control [43]. It is therefore possible that these three brain regions jointly contribute to a cognitive control system that may help regulating the contextually-driven modulatory effects of negation on conceptual representations. The syntactic and cognitive control interpretations need not be mutually exclusive: the neural circuit activations underlying syntactic and cognitive control functions may be spatially and temporally distinct, but display the observed spatio-temporal overlap due to the relatively low spatial and temporal resolution of the fMRI data, and to the multivariate analysis technique. Our results may therefore indicate that both syntactic computation and cognitive control are involved in processing negation polarity at the sentence level.

In turn, the classification problems CP1 and CP4, which both addressed the experimental manipulation of semantic concreteness, showed overlap in an extended set of regions, which is more consistent with a semantic functional role. This set included the bilateral anterior temporal lobe, which has been suggested to serve as the main brain's semantic hub [3,44]. But it also included, bilaterally, areas in the ventral posterior and medial temporal cortex (fusiform and parahippocampal gyri), parietal cortex (angular and supramarginal gyri, precuneus), and frontal lobe (inferior frontal gyrus, ventro- and dorsomedial prefrontal cortex), which, together with the anterior temporal lobe, have been postulated to form an extended semantic hub network based on the results of extant metanalyses of fMRI studies [13,45–47].

The broad involvement of brain regions revealed by CP1, CP3 and CP4 searchlight analysis also comprised modality-specific areas, which are thought to contribute to the discrimination of concrete and abstract concepts in embodied and grounded cognition accounts [4,5]. These included areas in sensory-motor systems, such as the visual and auditory cortices, the post-central gyrus, and supplementary motor area, and in the limbic system, particularly the amygdala. These and additional modality-specific brain regions also emerged from the post hoc classification of affirmative and negative sentences, separately for abstract and concrete concepts. For abstract concepts, the discrimination of affirmative versus negative sentences mainly occurred in regions in the limbic system, including the amygdala. A specific modulation of this system by processing abstract sentences is in line with previous evidence showing that abstract concepts do have an emotional connotation. It is possible that sentential negation reduced access to this emotional content, dampening amygdala activation [48]. For concrete concepts, in turn, modality-specific brain regions that contributed most to the discrimination of affirmative versus negative sentences included the post-central gyrus, and the visual cortices (calcarine and lingual gyrus), along with portions of the left posterior middle temporal gyrus previously ascribed to the processing of concrete concepts, such as action-related sentences [49], manipulable objects [50], or manipulation and visual motion features [51]. The modulation of the left posterior middle temporal gyrus by affirmative versus negative concrete sentences confirms previous results on negation of action-related sentences [14], although only partially since in that study polarity modulations extended to the left premotor-parietal action representation system. Altogether, the distinct effects of negation polarity on abstract versus concrete sentences in the present study are largely compatible with our main hypothesis that sentential negation modulates modality-specific semantic brain regions.

The 'hubs and spokes' organization of conceptual knowledge also emerged from the pattern of results obtained in the analysis of the fine-grained conceptual categories as a main

effect (CP5). CP5 replicated previous studies [23,24] with respect to both the successful discrimination between finegrained conceptual categories, and the anatomical sparseness of the involved brain regions. In particular, we replicated the findings in [24] by showing that category-specific and multicategory spoke regions were sparsely distributed over sensory-motor, limbic and heteromodal cortices. As in [24], however, we didn't observe consistent correspondences between the conceptual categories and the experiential systems in which their representation is thought to be grounded according to grounded cognition accounts (e.g. somatotopically organized motor areas for Mo, Ha and Le action-related sentences). The sensitivity analysis also identified a number of candidate hub brain regions, albeit with the notable exclusion of the ventral anterior temporal lobe, for which the conventional acquisition protocol used in the present study may have lacked signal detection sensitivity, as compared with other studies (e.g. [52]) using an optimized fMRI acquisition protocol [53]. Some of the identified candidate hub regions (i.e. the right fusiform gyrus, the left superior temporal gyrus/Heschl's gyrus, and the cerebellar vermis) presented complete spatial overlap in the voxels that contributed to discriminate between the fine-grained conceptual categories. Based on this characteristic, the 'category-invariant hubs' as we called them (see §2f(ii)), may be assimilated to the class of semantic hubs. This appears quite straightforward in the case of the fusiform gyrus, since it has been identified as part of the 'conceptual hub' network in a meta-analysis of neuroimaging studies of semantic processing [13,45]. Less straightforward, however, is the case of the superior temporal gyrus/Heschl's gyrus, which has been usually considered to play a role in speech perception and phonological rather than semantic processing (but see [45]). As for the cerebellum, there is increasing evidence of its contribution to language functions and, more specifically, to semantic processing tasks, such as predictive processing during language comprehension, lexical-semantic associations and mapping of novel words onto existing concepts [54,55]. However, there is no consensus so far as to what the specific cerebellar contribution to semantic processing might be [55]. Some other candidate hub brain regions (i.e. the left insula, the left anterior middle temporal gyrus, and the right precuneus) contained, in addition to voxels with complete spatial overlap, specific voxels for each of the six categories, thus contributing to discriminate all the categories from each other. These hubs rather conform to the class of 'graded hubs', namely brain regions that present a functionally graded organization, possibly reflecting the varying pattern of connectivity links with category-specific spoke layers [3,24], such as the graded organization for abstract and concrete concepts in the anterior temporal lobe [52].

As discussed so far, the neural code patterns for the interaction between sentential negation polarity and abstract/ concrete semantic categories that emerge from our results appear largely compatible with 'hubs and spokes' accounts of semantic processing. Hub regions highly interconnected with primary and secondary sensory-motor spoke regions may be optimally suited to compute semantic representation by integrating information from different modalities [13,51], and also to combine multiple semantic representations, thus producing semantic meanings at the sentence level [2,13]. The interplay between hubs and spokes might therefore account for the distinction between abstract and concrete concepts, which result from the differential integration of information from multiple modalities (e.g. sensory and motor information for concrete concepts, versus emotional, introspective, social and linguistic information for abstract concepts [5,7-10]). The linguistic context, such as the one investigated here (i.e. sentential negation), might modulate such interplay between hubs and spokes and therefore modulate the representation of abstract and concrete concepts. Still, the exact information processing and coding dynamics occurring between hub and spoke brain regions remain relatively unclear. In one view, the anterior temporal lobe is put forward as the brain's sole semantic hub [3], but with multiple subregions that have been suggested to code for different semantic categories or representational modalities, based on cytoarchitectonic, anatomical and functional connectivity data [3]. In another view, semantic representations are instead served by relatively undifferentiated but multiple hubs [2], including some of the candidate hub regions identified in the present study, such as the medial prefrontal cortex, the anterior and posterior cingulate, the insula, the lateral parietal cortex and the precuneus. Our findings are suggestive of semantic 'hubs and spokes' dynamics that incorporate features from both views. On the one hand, we found multiple hub brain regions located in the frontal, temporal and parietal lobes. On the other hand, while some of the multiple hub regions were undifferentiated (i.e. category-invariant hubs), some others presented with category-specific subregions for all types of abstract and concrete concepts included in our study (i.e. graded hubs). Our results indicate that combinatorial meaning specificities produced by the interaction between linguistic context and conceptual category emerge from activation patterns across multiple voxels distributed in unimodal spokes, as well as in undifferentiated and graded hubs.

### 5. Conclusion

The overall picture emerging from this set of results is largely compatible with the view that sentential negation polarity operates by modulating the neural activation patterns coding for concepts, to an extent that is sufficient to make the processing of affirmative and negative sentences with either an abstract or concrete content distinguishable by means of MVPA. We suggest that the negation polarity modulation occurs in distributed representational semantic networks, through the functional mediation of syntactic and cognitive control systems.

Ethics. The study was approved by the Ethics Committee of the San Raffaele Scientific Institute, Milan, Italy. Subjects gave written consent for their participation in the study.

Data accessibility. The data and code that support the findings of this study are publicly available at https://doi.org/10.6084/m9. figshare.5492698.v2.

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Authors' contributions. M.G., M.M.V. and M.T. conceived and designed the experiments; M.G., M.M.V. and M.T. performed the experiments; M.G., K.H. and M.T. analysed the data; M.G., K.H., M.M.V. and M.T. wrote the manuscript. All authors approved the final version of the manuscript.

# References

- Hoffman P. 2016 The meaning of 'life' and other abstract words: insights from neuropsychology. *J. Neuropsychol.* **10**, 317–343. (doi:10.1111/jnp. 12065)
- Binder JR, Desai RH. 2011 The neurobiology of semantic memory. *Trends Cogn. Sci.* 15, 527-536. (doi:10.1016/j.tics.2011.10.001)
- Lambon Ralph MA, Jefferies E, Patterson K, Rogers TT. 2017 The neural and computational bases of semantic cognition. *Nat. Rev. Neurosci.* 18, 42–55. (doi:10.1038/nrn.2016.150)
- Meteyard L, Cuadrado SR, Bahrami B, Vigliocco G. 2012 Coming of age: a review of embodiment and the neuroscience of semantics. *Cortex* 48, 788–804. (doi:10.1016/j.cortex.2010.11.002)
- Borghi AM, Binkofski F, Castelfranchi C, Cimatti F, Scorolli C, Tummolini L. 2017 The challenge of abstract concepts. *Psychol. Bull.* 143, 263–292. (doi:10.1037/bul0000089)
- Kiefer M, Barsalou LW. 2013 Grounding the human conceptual system in perception, action, and internal states. In *Action science* (eds W Prinz, M Beisert, A Herwig), pp. 381–407. Cambridge, MA: MIT Press.
- Crutch SJ, Troche J, Reilly J, Ridgway GR. 2013 Abstract conceptual feature ratings: the role of emotion, magnitude, and other cognitive domains in the organization of abstract conceptual knowledge. *Front. Hum. Neurosci.* 7, 186. (doi:10. 3389/fnhum.2013.00186)
- Crutch SJ, Williams P, Ridgway GR, Borgenicht L. 2012 The role of polarity in antonym and synonym conceptual knowledge: evidence from stroke aphasia and multidimensional ratings of abstract words. *Neuropsychologia* 50, 2636 – 2644. (doi:10. 1016/j.neuropsychologia.2012.07.015)
- Ghio M, Vaghi MMS, Tettamanti M. 2013 Finegrained semantic categorization across the abstract and concrete domains. *PLoS ONE* 8, e67090. (doi:10. 1371/journal.pone.0067090)
- Troche J, Crutch S, Reilly J. 2014 Clustering, hierarchical organization, and the topography of abstract and concrete nouns. *Front. Psychol.* 5, 360. (doi:10.3389/fpsyg.2014.00360)
- Schwanenflugel PJ, Harnishfeger KK, Stowe RW. 1988 Context availability and lexical decisions for abstract and concrete words. *J. Mem. Lang.* 27, 499–520. (doi:10.1016/0749-596X(88)90022-8)
- Hoffman P, Lambon Ralph MA, Rogers TT. 2013 Semantic diversity: a measure of semantic ambiguity based on variability in the contextual usage of words. *Behav. Res. Methods* 45, 718–730. (doi:10.3758/s13428-012-0278-x)
- Binder JR. 2016 In defense of abstract conceptual representations. *Psychon. Bull. Rev.* 23, 1096–1108. (doi:10.3758/s13423-015-0909-1)
- Tettamanti M, Manenti R, Della Rosa P, Falini A, Perani D, Cappa SF, Moro A. 2008 Negation in the brain: modulating action representations.

*Neuroimage* **43**, 358–367. (doi:10.1016/j. neuroimage.2008.08.004)

- Tomasino B, Weiss PH, Fink GR. 2010 To move or not to move: imperatives modulate action-related verb processing in the motor system. *Neuroscience* 169, 246–258. (doi:10.1016/j.neuroscience.2010. 04.039)
- de Vega M, Morera Y, León I, Beltrán D, Casado P, Martín-Loeches M. 2016 Sentential negation might share neurophysiological mechanisms with action inhibition. Evidence from frontal theta rhythm. *J. Neurosci.* 36, 6002–6010. (doi:10.1523/ JNEUROSCI.3736-15.2016)
- Liuzza MT, Candidi M, Aglioti SM. 2011 Do not resonate with actions: sentence polarity modulates cortico-spinal excitability during action-related sentence reading. *PLoS ONE* 6, e16855. (doi:10. 1371/journal.pone.0016855)
- Ghio M, Tettamanti M. 2016 Grounding sentence processing in the sensory-motor system. In *Neurobiology of language* (eds LS Small, G Hickok), pp. 647–657. Amsterdam, The Netherlands: Elsevier.
- Haynes JD, Rees G. 2006 Decoding mental states from brain activity in humans. *Nat. Rev. Neurosci.* 7, 523–534. (doi:10.1038/nrn1931)
- O'Toole AJ, Jiang F, Abdi H, Pénard N, Dunlop JP, Parent MA. 2007 Theoretical, statistical, and practical perspectives on pattern-based classification approaches to the analysis of functional neuroimaging data. *J. Cogn. Neurosci.* **19**, 1735–1752. (doi:10.1162/jocn.2007.19.11. 1735)
- Wang J, Baucom LB, Shinkareva SV. 2013 Decoding abstract and concrete concept representations based on single-trial fMRI data. *Hum. Brain Mapp.* 34, 1133 – 1147. (doi:10.1002/hbm.21498)
- Bahlmann J, Mueller JL, Makuuchi M, Friederici AD. 2011 Perisylvian functional connectivity during processing of sentential negation. *Front. Psychol.* 2, 104. (doi:10.3389/fpsyg.2011.00104)
- Anderson AJ, Murphy B, Poesio M. 2014 Discriminating taxonomic categories and domains in mental simulations of concepts of varying concreteness. *J. Cogn. Neurosci.* 26, 658–681. (doi:10.1162/jocn\_a\_00508)
- Ghio M, Vaghi MMS, Perani D, Tettamanti M. 2016 Decoding the neural representation of fine-grained conceptual categories. *Neuroimage* **132**, 93–103. (doi:10.1016/j.neuroimage.2016.02.009)
- Belin P, Zatorre RJ, Hoge R, Evans AC, Pike B. 1999 Event-related fMRI of the auditory cortex. *Neuroimage* 10, 417–429. (doi:10.1006/nimg.1999. 0480)
- Hall DA, Haggard MP, Akeroyd MA, Palmer AR, Summerfield AQ, Elliott MR, Gurney EM, Bowtell RW. 1999 'Sparse' temporal sampling in auditory fMRI. *Hum. Brain Mapp.* 7, 213–223. (doi:10.1002/ (SICI)1097-0193(1999)7:3<213::AID-HBM5>3.0. CO;2-N)

- Misaki M, Luh WM, Bandettini PA. 2013 The effect of spatial smoothing on fMRI decoding of columnar-level organization with linear support vector machine. J. Neurosci. Methods 212, 355–361. (doi:10.1016/j.jneumeth.2012.11.004)
- Misaki M, Kim Y, Bandettini PA, Kriegeskorte N. 2010 Comparison of multivariate classifiers and response normalizations for pattern-information fMRI. *Neuroimage* **759**, 103–118. (doi:10.1016/j. neuroimage.2010.05.051)
- Hanke M, Halchenko YO, Sederberg PB, Hanson SJ, Haxby JV, Pollmann S. 2009 PyMVPA: a Python toolbox for multivariate pattern analysis of fMRI data. *Neuroinformatics* 7, 37-53. (doi:10.1007/ s12021-008-9041-y)
- Kriegeskorte N, Goebel R, Bandettini P. 2006 Information-based functional brain mapping. *Proc. Natl Acad. Sci. USA* **103**, 3863–3868. (doi:10.1073/ pnas.0600244103)
- Raizada RD, Lee YS. 2013 Smoothness without smoothing: why Gaussian naive Bayes is not naive for multi-subject searchlight studies. *PLoS ONE* 8, e69566. (doi:10.1371/journal.pone.0069566)
- Stelzer J, Chen Y, Turner R. 2013 Statistical inference and multiple testing correction in classificationbased multi-voxel pattern analysis (MVPA): random permutations and cluster size control. *Neuroimage* 65, 69–82. (doi:10.1016/j.neuroimage.2012.09. 063)
- Hanson SJ, Halchenko YO. 2008 Brain reading using full brain support vector machines for object recognition: there is no 'face' identification area. *Neural. Comput.* 20, 486–503. (doi:10.1162/neco. 2007.09-06-340)
- Tzourio-Mazoyer N, Landeau B, Papathanassiou D, Crivello F, Etard O, Delcroix N, Mazoyer B, Joliot M. 2002 Automated anatomical labeling of activations in SPM using a macroscopic anatomical parcellation of the MNI MRI single-subject brain. *Neuroimage* 15, 273–289. (doi:10.1006/nimg.2001.0978)
- Fry J. 1997 Negative polarity licensing at the syntax semantics interface. In Proc. 8th Conf. European Chapter of the Association for Computational Linguistics, Madrid, Spain, 7 – 12 July 1997 (eds PR Cohen, W Wahlster), pp. 144–150. Stroudsburg, PA: Association for Computational Linguistics.
- Horn LR. 1989 A natural history of negation. Chicago, IL: University of Chicago Press.
- Naselaris T, Kay KN. 2015 Resolving ambiguities of MVPA using explicit models of representation. *Trends Cogn. Sci.* 19, 551–554. (doi:10.1016/j.tics. 2015.07.005)
- Musso M, Moro A, Glauche V, Rijntjes M, Reichenbach J, Buchel C, Weiller C. 2003 Broca's area and the language instinct. *Nat. Neurosci.* 6, 774–781. (doi:10.1038/nn1077)
- Pallier C, Devauchelle AD, Dehaene S. 2011 Cortical representation of the constituent structure of sentences. *Proc. Natl Acad. Sci. USA* 108, 2522–2527. (doi:10.1073/pnas.1018711108)

- Ni W, Constable RT, Mencl WE, Pugh KR, Fulbright RK, Shaywitz SE, Shaywitz BA, Gore JC, Shankweiler D. 2000 An event-related neuroimaging study distinguishing form and content in sentence processing. *J. Cogn. Neurosci.* **12**, 120–133. (doi:10. 1162/08989290051137648)
- Moro A, Tettamanti M, Perani D, Donati C, Cappa SF, Fazio F. 2001 Syntax and the brain: disentangling grammar by selective anomalies. *Neuroimage* 13, 110–118. (doi:10.1006/nimg. 2000.0668)
- Fedorenko E. 2014 The role of domain-general cognitive control in language comprehension. *Front. Psychol.* 5, 1–17. (doi:10.3389/fpsyg.2014.00335)
- Crinion J *et al.* 2006 Language control in the bilingual brain. *Science* **312**, 1537–1540. (doi:10. 1126/science.1127761)
- Patterson K, Nestor PJ, Rogers TT. 2007 Where do you know what you know? The representation of semantic knowledge in the human brain. *Nat. Rev. Neurosci.* 8, 976–987. (doi:10.1038/nrn2277)
- Binder JR, Desai RH, Graves WW, Conant LL. 2009 Where is the semantic system? A critical review and meta-analysis of 120 functional neuroimaging

studies. *Cereb. Cortex* **19**, 2767–2796. (doi:10.1093/ cercor/bhp055)

- Price CJ. 2010 The anatomy of language: a review of 100 fMRI studies published in 2009. *Ann. N Y Acad. Sci.* **1191**, 62–88. (doi:10.1111/j.1749-6632. 2010.05444.x)
- 47. Van Den Heuvel MP, Sporns O. 2011 Rich-club organization of the human connectome. *J. Neurosci.* 31, 15 775 15 786. (doi:10.1523/JNEUROSCI.3539-11.2011)
- Vigliocco G, Kousta ST, Della Rosa PA, Vinson DP, Tettamanti M, Devlin JT, Cappa SF. 2013 The neural representation of abstract words: the role of emotion. *Cereb. Cortex* 24, 1767–1777. (doi:10. 1093/cercor/bht025)
- Tettamanti M *et al.* 2005 Listening to action-related sentences activates fronto-parietal motor circuits. *J. Cogn. Neurosci.* 17, 273–281. (doi:10.1162/ 0898929053124965)
- Ishibashi R, Pobric G, Saito S, Lambon Ralph MA.
   2016 The neural network for tool-related cognition: an activation likelihood estimation meta-analysis of 70 neuroimaging contrasts. *Cogn. Neuropsychol.* 33, 241–256. (doi:10.1080%2F02643294.2016.1188798)

- Fernandino L, Binder JR, Desai RH, Pendl SL, Humphries CJ, Gross WL, Conant LL, Seidenberg MS. 2015 Concept representation reflects multimodal abstraction: a framework for embodied semantics. *Cereb. Cortex* 26, 2018–2034. (doi:10.1093/cercor/ bhv020)
- Hoffman P, Binney RJ, Lambon Ralph MA. 2015 Differing contributions of inferior prefrontal and anterior temporal cortex to concrete and abstract conceptual knowledge. *Cortex* 63, 250–266. (doi:10.1016/j.cortex.2014.09.001)
- Embleton KV, Haroon HA, Morris DM, Lambon Ralph MA, Parker GJ. 2010 Distortion correction for diffusion-weighted MRI tractography and fMRI in the temporal lobes. *Hum. Brain Mapp.* 31, 1570–1587. (doi:10.1002/hbm.20959)
- Lesage E, Nailer EL, Miall RC. 2016 Cerebellar BOLD signal during the acquisition of a new lexicon predicts its early consolidation. *Brain Lang.* 161, 33-44. (doi:10.1016/j.bandl.2015.07.005)
- Sokolov AA, Miall RC, Ivry RB. 2017 The cerebellum: adaptive prediction for movement and cognition. *Trends Cogn. Sci.* 21, 313–332. (doi:10.1016/j.tics. 2017.02.005)