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Research Report

Conceptual knowledge in the brain: fMRI evidence for a featural organization

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ABSTRACT

The organization and representation of conceptual knowledge in the brain remains a controversial issue in terms of both neuropsychological and imaging evidence. We report the results of a functional magnetic resonance study in which the role of the most debated dimensions (domain and feature type) was evaluated through a concept–feature verification task. The scope of the task was to eliminate serious methodological concerns that weighed down previous imaging research in this area, and to allow more definitive conclusions regarding the specific contribution of these dimensions. The results show differential patterns of brain activity according to feature type (both motion and visual form/surface features) but not according to concept domain (living vs. nonliving things). These findings are in accord with a modality-specific account of conceptual knowledge organization in the brain, in which specific kinds of features (e.g. form, color, motion, etc) have differential importance for representing different concepts.

1. Introduction

The question of how conceptual knowledge is organized and represented in the brain continues to be widely and controversially debated within the neuroscience research on semantic memory (Barsalou et al., 2003; Caramazza and Mahon, 2003, 2006; Martin and Chao, 2001; Tyler and Moss, 2001). The topic has received considerable attention since patients with category-specific semantic deficits were systematically reported some two decades ago (Warrington and McCarthy, 1983; Warrington and Shallice, 1984). Patients exhibiting impaired knowledge of living things (especially animals), in contrast to preserved artifact knowledge, have been particularly discussed as to their meaning in terms of underlying representation in the brain. For some, the neuropsychological evidence are more in accord with a *domain-specific account* (Caramazza and Shelton, 1998; Shelton et al., 1998). This account proposes that evolutionary pressure has resulted in neuroanatomically and functionally specialized networks for distinguishing evolutionary important categories such as, animals, plant life and artifacts, or, in a more detailed version, animals, plant life, conspecifics and possibly tools (Caramazza and Mahon, 2003, 2006). Others have proposed that the diversity of cases of impairment are best explained by a *modality-specific account* (e.g. Barsalou et al., 2003; Farah and McClelland, 1991; Martin and Chao, 2001; McCarthy and Warrington, 1988; Warrington and McCarthy, 1983; Warrington

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and Shallice, 1984). This account proposes that different kinds of semantic features (e.g. visual, tactile, function, motion, etc) have a varying importance for representing different concepts and domains, resulting in behaviors that are only apparently constrained by categories. A third perspective, the *conceptual structure account*, proposes a unitary amodal system, in which the correlations between features (in particular the correlation between perceptual and functional features) and their degree of distinctiveness are different between domains. Nonliving things possess more distinctive features that are correlated in comparison with living things (Tyler and Moss, 2001; Tyler et al., 2000). This difference, associated with the assumption that

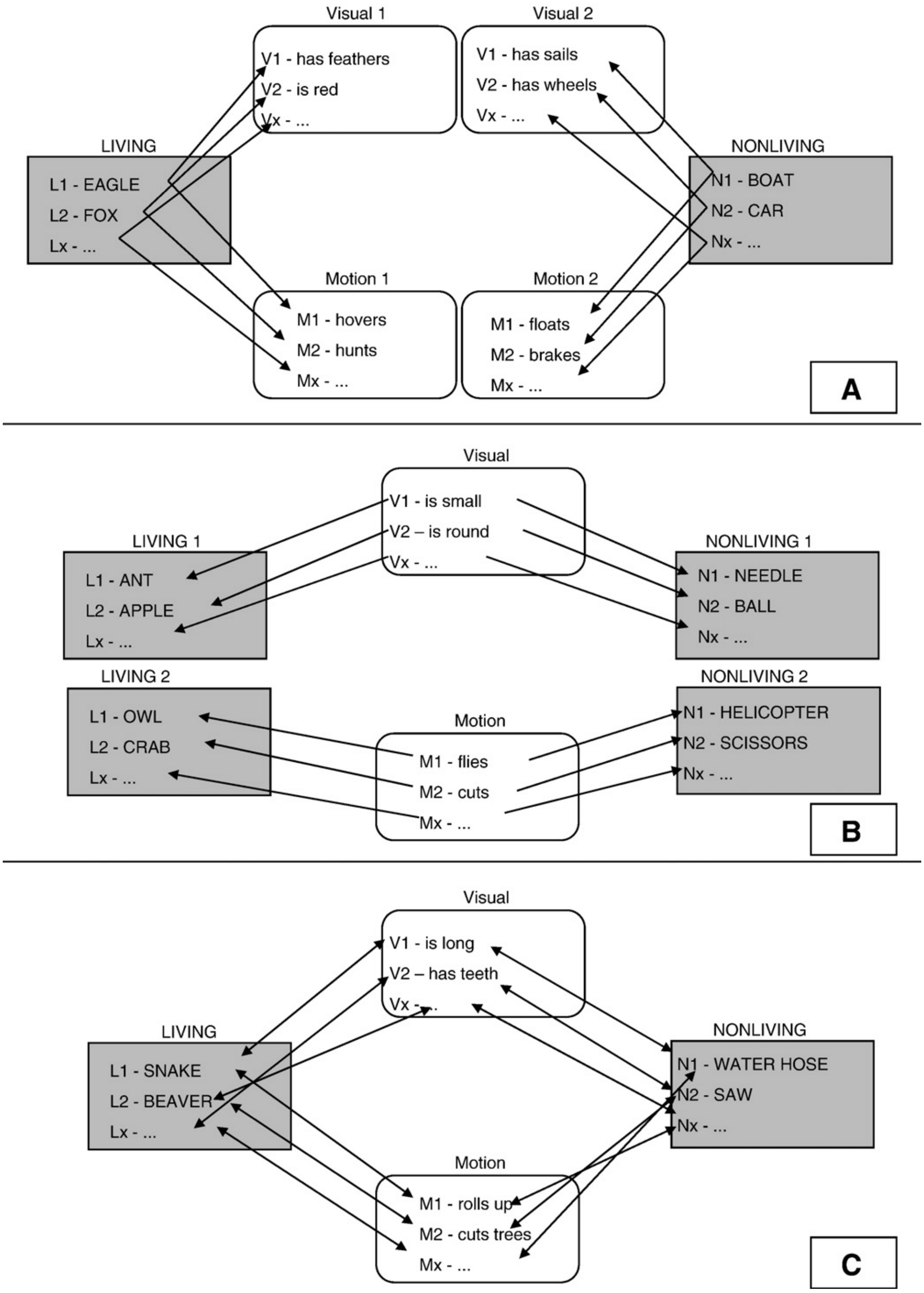

Fig. 1 – Experimental designs and stimuli. Design in top panel (A) is biased by the fact that concepts are compared using different feature sets. Design in middle panel (B) is biased by the fact that features are compared using different concept sets. Design in bottom panel (C) corresponds to the present study. Each feature type (visual/motion) was contrasted on exactly the same exemplars and each category (living/nonliving) was contrasted on exactly the same features. Participants verified simple concept–feature sentences resulting from the combination of feature type, category and status (true vs. false; only true pairs are represented in the figure).

features that are highly correlated with other features are more resistant to brain damage, would explain the disproportionate number of cases in which the living domain seems impaired. The converse deficit (nonliving worse than living) would only occur when damage to the semantic system is severe (Tyler and Moss, 2001; Tyler et al., 2000).

The increasing number and diversity of category-specific deficits pose difficulties for all three accounts. Some authors have proposed alternative solutions, suggesting that both the domain and feature type (as orthogonal dimensions) would subsume the organization of conceptual knowledge (Caramazza and Mahon, 2003, 2006; Gainotti and Silveri, 1996; Miceli et al., 2001; Powell and Davidoff, 1995). Others have called attention to several methodological concerns that make it difficult to reach decisive conclusions from the available patient evidence (Crawford et al., 2006; Laws, 2005; Laws and Sartori, 2005). In this context, it is crucial to look at the data derived from functional brain imaging. The neuroimaging techniques allow us to study cortical specialization in the normal human brain as a function of these potential dimensions of the organization of conceptual knowledge. The interpretation of the available evidence is however controversial, in some cases raising the question of the comparability of items and tasks (Thompson-Schill, 2003; Devlin et al., 2002). It is thus difficult to evaluate without biases which level of organization – featural or categorical – is more important, or even if it is necessary to consider these two levels.

A majority of studies have used tasks, such as picture naming, viewing, or matching, where exemplars, rather than features, are directly evaluated. The results of these studies are generally explicable in terms of either a domain-specific or a modality-specific account. However, the latter has been preferred, considering that the localization of category-related activations is compatible with the retrieval of information about their underlying modality-specific features stored near the corresponding sensory areas (e.g. Chao et al., 1999; Damasio et al., 1996; Ishai et al., 1999; Martin et al., 1996; Moore and Price, 1999; Perani et al., 1999; Vandenberghe et al., 1996; Beauchamp et al., 2003; Wheatley et al., 2005). Nevertheless, the role of features is not directly tested, but only inferred from the data.

A smaller number of studies have used tasks that involve the processing of featural knowledge (e.g., feature verification, feature generation, questions about feature knowledge), regardless of category or without control of feature information (e.g. Kellenbach et al., 2001; Noppeney et al., 2005). The evidence from these studies seem to be more in accord with a modality-specific account, but in this case the design does not allow an evaluation of the possible contribution of the categorical dimension.

Finally, a small number of studies have manipulated both exemplars and features (e.g. Cappa et al., 1998; Mummery et al., 1998; Lee et al., 2002; Kellenbach et al., 2003; Phillips et al., 2002; Thompson-Schill et al., 1999). This in principle would allow a more adequate evaluation of these dimensions. However, the two types of design that have been used are susceptible to biases that prevent a more definite conclusion. These studies either use different sets of feature decisions for the different categories/domains as shown in Fig. 1A (e.g. Cappa et al., 1998; Kellenbach et al., 2003; Lee et al., 2002; Phillips et al., 2002; Thompson-Schill et al., 1999), or the same feature decisions but with different sets of exemplars within each category (as shown in Fig. 1B) (Mummery et al., 1998; Kellenbach et al., 2003). Both designs have the same consequence. The differential patterns of activation obtained may be biased by factors other than feature type and exemplar's category, such as feature decision difficulty, concept familiarity or feature relevance to concept.

The present study tries to overcome these difficulties by examining the impact of categorical and featural information on brain activity. For this objective, we contrasted the main categories (living things vs. nonliving things) and feature types (visual form/surface vs. motion features) that were discussed in imaging studies of conceptual knowledge with a feature verification task that allows a separation of these two dimensions. We compared the pattern of activation for exactly the same features sets for the two categories. At the same time, we compared exactly the same categories (i.e. the same exemplar sets) for the two feature types, as shown on Fig. 1C. For instance, for each exemplar, we compared the activation for one feature of a single common set within each feature type (e.g. 'is long' (visual form/surface feature) and 'rolls up' (motion feature) for 'SNAKE'; 'has teeth' (visual form/surface feature) and 'cuts trees' (motion feature) for 'SAW'). For each feature, we compared the activation for one exemplar of single common set within each category (e.g. 'long' (visual form/surface feature) for 'SNAKE' and 'WATER HOSE'; 'cuts trees' (motion feature) for 'BEAVER' and 'SAW'). In the end, and in contrast with the previous studies, we can thus evaluate the specific influence of each dimension, concept domain and feature type, with exactly the same materials and task (Fig. 1C).

From a domain-specific perspective, we should expect a main effect of category, corresponding to the idea that this is the most important factor in the organization of conceptual knowledge. In particular, we should expect either a double contrast between animal and artifact activations (Caramazza and Shelton, 1998) or at least a specific activation of animals in relation to nonliving things if the latter is not really a salient representational domain (Caramazza and Mahon, 2003, 2006; Caramazza and Shelton, 1998). In addition, we could also expect a main effect of feature type, as more recent versions of this perspective consider the two dimensions to be orthogonal in the organization of conceptual knowledge (Caramazza and Mahon, 2003, 2006).

Alternatively, from a modality-specific perspective, we should expect a main effect of feature type, corresponding to the idea that specific kinds of features have differential importance for representing different concepts, but no main effect of category (e.g. Barsalou et al., 2003; McCarthy and Warrington, 1988; Martin and Chao, 2001;Warrington and McCarthy, 1983). In addition, a stronger version of this perspective would also predict an interaction between category and feature type (e.g. Farah and McClelland, 1991; Warrington and Shallice, 1984), with more activation of visual form/surface features for living things, and more activation of motion features for nonliving things.

Finally, from a conceptual structure perspective, no main effect should be expected. In fact, in this account semantic memory is amodal, and feature distinctiveness and correlation, rather than category and feature type, are the main organizational factors of conceptual knowledge (Tyler and Moss, 2001; Tyler et al., 2000).

2. Results

The behavioral and imaging results were analyzed by concept domain (living vs. nonliving) and feature type (visual form/surface vs. motion features). Sentence status (true, false) was only considered in the behavioral results. The imaging results regard only true sentences as it can be argued that false sentences may also set off other true conceptual information. As such, we cannot have exact control of the conceptual information that is active.

2.1. *Behavioral results*

Total mean hit rate was 90.5% and only 6 items (i.e. concept-feature pairs; 1.7% of the items) presented a hit rate lower than 50%. When we analyze hit rate by feature type and concept domain (excluding these extreme items) there is only a main effect of feature type ($F_{1,20}=6.85$, $p<0.02$), as indicated in a repeated measures two-way analysis of variance (ANOVA), with motion features presenting a higher hit rate than visual form/surface features (motion mean = 93%; form/surface mean = 90%).

Reactions times were also analyzed by feature and concept domain using a similar ANOVA, after trimming the data for incorrect answers and for outliers, defined as two standard deviations above each subject mean response time (corresponding to the elimination of 12.4% of the data which is within the normal recommended limits; Ratcliff, 1993). In this case, both feature type and concept domain gave main effects (respectively $F_{1,20}=10.05$, $p<0.0005$ for feature type, and $F_{1,20}=59.27$, $p<0.00001$ for concept domain). Motion features

Table 1 – Spatial coordinates of the local maxima in the primary group analysis

Hemisphere	Region of activation (estimated BA)	Cluster extent (voxels)	MNI coordinates			Voxel Z-value
			x	y	z	
Conjunction analysis						
L	Inferior occipital gyrus (18/19)	114	−28	−90	0	>8
R	Inferior occipital gyrus (18/19)	202	32	−88	2	7.56
L	Middle temporal gyrus (21)	136	−56	−48	−2	7.00
L	pre-SMA (6)	125	0	8	60	6.96
L	SMA (6)		−4	−2	60	7.34
L	IFG p. opercularis (44)	303	−52	12	16	>8
L	IFG p. triangularis (45/44)	221	−36	28	0	6.22
L	IFG p. orbitalis (47)		−42	32	−2	5.87
Visual form/surface > Motion						
L	Medial fusiform gyrus (37)	127	−30	−42	−22	4.27
R	Medial fusiform gyrus (37)	59	30	−40	−20	3.97
L	Inferior temporal gyrus (37)	214	−50	−64	−8	5.57
R	Inferior temporal gyrus (37)	118	54	−46	−14	5.74
L	Lingual gyrus/Parahippocampal gyrus	37	−22	−40	−2	4.30
R	Lingual gyrus/Parahippocampal gyrus	53	22	−38	0	3.99
L	Dorsal middle occipital gyrus (19)	1583	−28	−68	36	5.53
L	Caudal intraparietal sulcus (7)		−32	−50	42	4.84
L	Inferior parietal lobule (40)		−40	−38	36	5.02
R	Dorsal middle occipital gyrus (19)	1369	26	−68	48	4.89
R	Caudal intraparietal sulcus (7)		36	−62	52	5.13
R	Inferior parietal lobule (40)		48	−42	50	6.62
L	Precentral gyrus (6)	345	−44	−2	26	3.95
L	IFG p. opercularis (44)		−48	8	30	3.85
L	IFG p. triangularis (45)	96	−46	30	24	3.83
L	Middle frontal gyrus (46)	58	−30	52	20	3.70
R	IFG p. triangularis (45)	892	44	38	14	7.45
R	IFG p. opercularis (44)		50	10	22	5.11
R	Precentral gyrus (44/6)		44	6	30	4.40
L/R	Anterior cingulate cortex (24)		−4	10	30	3.88
L/R	Middle cingulate cortex (32)		6	20	38	4.09
L/R	Superior medial gyrus (6)	384	2	16	42	3.62
Motion > Visual form/surface						
L	Posterior middle temporal gyrus (21)	23	−60	−50	0	4.08
L	Angular gyrus (39)	26	−38	−50	22	5.15

Stereotactic coordinates and Z-values of the foci showing a linear relationship with RTs in the conjunction analysis and the main effects ($p<0.05$ corrected for multiple comparisons with False Discovery Rate) are shown. Coordinates (x, y, and z) are expressed in MNI space adopted by SPM5, in terms of distance in mm from the anterior commissure. L = left, R = right, g = gyrus.

were responded faster to than visual form/surface features (motion mean = 1654 ms; visual form/surface mean = 1692 ms). Living concepts were responded faster to than nonliving concepts (living things mean = 1644 ms; nonliving things mean = 1703 ms). Moreover, the interaction between the two factors was also significant ($F_{1,20}=8.35$, $p<0.001$). Post-hoc analysis (post-hoc Fisher tests between each group) showed that the motion feature advantage was larger and significant only for the nonliving domain. The possible impact of all these differences was taken into account in data analysis by modulation of each event by its reaction time (see Experimental procedures for details).

2.2. *Imaging results*

We first examined the regions activated in all the experimental conditions, independent of both feature type and concept domain, and irrespective of RTs. The conjunction analysis highlighted a network of commonly activated regions, which included: the inferior and middle occipital gyri (BA 18/19) bilaterally, the posterior middle temporal gyrus (BA 21) in the left hemisphere, and the pre-supplementary motor area (pre-SMA) and the SMA proper (BA 6) within the medial wall (Table 1). In addition to these regions, all the experimental conditions activated a wide frontal cluster in the left hemisphere, extending from the precentral gyrus (BA 6) and the middle frontal gyrus (BA 6/9) to the inferior frontal gyrus. Within the latter region, common activations were observed in the pars opercularis (BA 44), pars triangularis (BA 45) and pars orbitalis (BA 47) (Fig. 2A).

Then we examined the effects which were specifically associated with the experimental factors. No interaction between concept domain and feature type was observed, even when lowering the threshold to 0.005 uncorrected for multiple comparisons and an extent threshold of $K=0$ voxels. Thus, we turned to a separate assessment of the main effects of the two factors (Table 1; Fig. 2).

The retrieval of visual form/surface features compared to motion features (independently of concept domain) activated a bilateral network of areas (Fig. 2B). These included the inferior temporal and the medial fusiform gyrus (BA 37), and a region located at the border between the rostral lingual gyrus and the parahippocampal gyrus. A wide region extending from the dorsal portion of the middle occipital gyrus (BA 19), through the caudal portion of the intraparietal sulcus (BA 7), to the rostral portion of the inferior parietal lobule (40) was also activated. In the frontal lobe, activations extended bilaterally from the precentral gyrus (BA 6) to the pars opercularis (BA 44) and triangularis (BA 45/46) in the inferior frontal gyrus. Both parietal and frontal activations were bilateral, but with a right hemispheric prevalence. A further cluster of activation was observed in the left middle frontal gyrus (BA 46). Within the medial wall, the retrieval of visual, compared to motion,

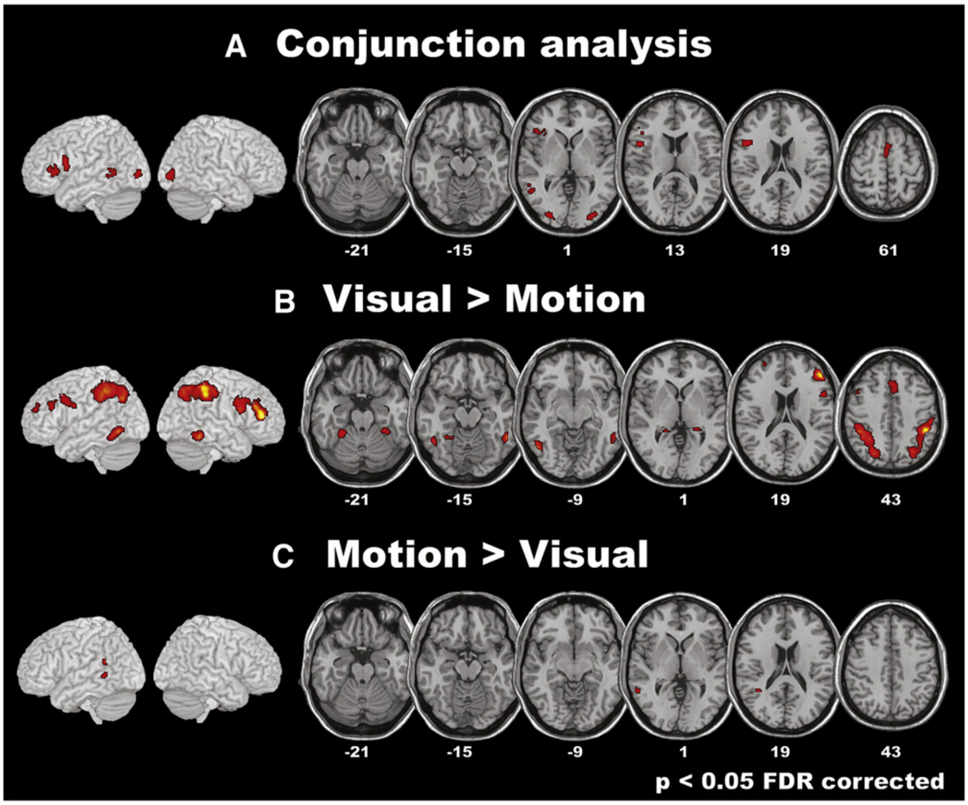

Fig. 2 – Imaging results. From top to bottom: A, the cerebral regions which were activated in all the experimental conditions (conjunction analysis); B, the cerebral regions which were more strongly activated by retrieval of visual form/surface vs. motion features; and C, the cerebral regions which were more strongly activated by retrieval of motion vs. visual form/surface features ($p<0.05$ corrected with False Discovery Rate). Areas of increased activation were superimposed onto a 3D rendering of the MNI template (left) and on six representative slices of the same brain (right). Coordinates of the transverse sections (distance in mm from the AC-PC plane) are given.

features activated the anterior and middle cingulate cortex (BA 24 and 32) and the superior medial gyrus (BA 6).

The opposite comparison revealed the cerebral regions which were more strongly activated by motion compared with visual form/surface features (Fig. 2C). These were located in the temporo-parietal junction, including the posterior portion of the middle temporal and the angular gyri (BA 39) in the left hemisphere.

Then, we examined the main effect of concept domain (independent of the effect of feature type). No region was more strongly activated by living vs. nonliving items or vice-versa.

Finally, the effects of reaction time on domain- and on feature-specific semantic processing failed to reach significance.

3. Discussion

We evaluated the role of concept domain and feature type information on the cerebral organization of conceptual knowledge by means of a feature verification task based on the same items. This allowed us to evaluate the contribution of the two dimensions, and to test the predictions of three different theoretical perspectives on exactly the same materials.

The results revealed a common, left-lateralized large-scale network dedicated to semantic processing (McDermott et al., 2003). More importantly, they highlighted that feature type, rather than concept domain is the main organizational factor of the brain representation of conceptual knowledge. The overall pattern of activations, and especially the activations associated to feature type, are more in accord with a modality-specific account of semantic memory, in which different kinds of semantic features have a varying importance for representing different concepts (Barsalou et al., 2003; Farah and McClelland, 1991; Martin and Chao, 2001; McCarthy and Warrington, 1988; Warrington and McCarthy, 1983; Warrington and Shallice, 1984). However, we did not find an interaction between feature type and concept domain as proposed by the strong version of the modality-specific account (e.g. Farah and McClelland, 1991; Warrington and Shallice, 1984). This does not undermine claims about domain differences in terms of feature proportion but it does indicate that the differential importance of feature type to the representation and processing of conceptual knowledge does not seem to apply at a general domain level. This aspect needs to be investigated at a more specific subordinate category level (McCarthy and Warrington, 1988).

Regions specifically associated to the retrieval of visual form/surface features, compared to motion ones and irrespective of domain, were located in both hemispheres but with a right hemispheric prevalence. These included areas involved in high-order visuo-perceptual processing, such as the inferior temporal and fusiform gyri in the temporal lobe and a wide occipito-parietal region extending from the dorsal middle occipital gyrus to the inferior parietal lobule. Several other studies have related activations in these areas to this particular class of featural information (Cappa et al., 1998; Kellenbach et al., 2001; Lee et al., 2002; Thompson-Schill et al., 1999; Moore and Price, 1999; Vandenbulke et al., 2006; Wheatley et al., 2005). A similar interpretation has been proposed for the parahippocampal activation that was also observed in the present study (Cabeza, Rao, Wagner, Mayer and Schacter, 2001). In addition, we also found prefrontal activations, extending from the precentral (BA 6) to the inferior frontal gyrus (BAs 44, 45) that have been associated to the retrieval of semantic representations stored elsewhere (Gabrieli et al., 1998; Wagner, 1999). The fact that these frontal regions were more active for visual form/surface than for motion information may be related to the more specific nature of the former features which may have demanded additional processing. This hypothesis is supported by the longer RT observed for these items.

Regions specifically associated with the retrieval of motion information were left-lateralized. Activations were located in the temporo-parietal junction and included portions of the posterior middle temporal and angular gyri that previous studies have related to the retrieval and integration of motion information (Cappa et al., 1998; Chao et al., 1999; Mummery et al., 1998; Perani et al., 1999; Phillips et al., 2002; Beauchamp et al., 2003; Kellenbach et al., 2003). Several imaging studies have provided a detailed view on the specificity of the lateral temporal cortex for processing different types of complex visual motions (e.g. Beauchamp et al., 2002, 2003). The results have shown an increasing degree of abstraction and convergence when moving from its ventral (MT area, associated with the analysis of "pure" motion) to dorsal (posterior middle and superior-temporal areas, involved in the analysis of object and biological-motion, respectively) sub-regions. Consistent with this view, it has been also reported that its dorsal-most portion, located in the proximity of our dorsal focus of activation, is specifically involved in the integration of different types of information both within and across modalities (Beauchamp, 2005). The fact that the specific activations for motion information were less extended in comparison with those for visual form/surface features may reflect their partial overlap, due to the visual nature of motion and action features (Cree and McRae, 2003).

The lack of significant effects of concept domain are inconsistent with the accounts that posit this dimension as the main factor for the organization of conceptual knowledge, either exclusively (Caramazza and Shelton, 1998; Shelton et al., 1998) or as the primary organizational constraint in relation to featural information (Caramazza and Mahon, 2003, 2006). It could be argued that the present study does not allow the evaluation of all of the salient domains proposed by this approach (i.e. plant life, conspecifics and tools). However, the fact that the present results failed to find a distinction between animals and other categories as explicitly predicted (Caramazza and Shelton, 1998) is clearly inconsistent with a domain perspective. Nevertheless, the possibility that an orthogonal dimension of domain can coexist with modality cannot be ruled out on the basis of the present null findings (Caramazza and Mahon, 2003, 2006).

The present results are also inconsistent with a conceptual structure account of semantic memory (Tyler and Moss, 2001; Tyler et al., 2000). This account does not consider concept domain and feature type as relevant organizational factors of conceptual knowledge and, as such, would predict no significant effects of the two dimensions. Also in this case, however, the present findings do not exclude that the factors considered by this model, such as feature correlation and distinctiveness, contribute to the neural organization of semantic memory. In fact, there is indication that feature distinctiveness (as a component of semantic relevance) is an important modulator of category activation in the medial fusiform gyrus (Mechelli et al., 2005).

The present fMRI evidence in support of the modality-specific account are strengthened by the fact that the different models were all explicitly evaluated on exactly the same materials (concepts and features). The study is thus not biased by any of the previous design limitations (e.g. testing only exemplars or only features; evaluating different features for different categories; evaluating the same features but with different exemplars), which may result in a insufficient or unfair test for some models, or in evidence that are compatible with different models.

In conclusion, the present results give a clear contribution to the present dispute regarding the organization of conceptual knowledge. They support the comprehensive view that, at least, visual form/surface features and motion features are important channels through which conceptual knowledge is organized in the brain. As such, it is in accord with a general modality-specific account. The neural implementation of the modality-specific account has focused on visual/form and motion dimensions (e.g. Chao et al., 1999; Martin and Chao, 2001). However, this perspective also considers that other sensory and associative features, such as function information (what an object is used for) are important dimensions of conceptual organization (e.g. McCarthy and Warrington, 1988; Warrington and McCarthy, 1983; Warrington and Shallice, 1984). While it could be argued that functional information may include a motion or action component, different behavioral and imaging studies have shown that, although related, these are different feature dimensions (e.g. Cree and McRae, 2003; Kellenbach et al., 2003; Canessa et al., in press). The contribution of other sensory and associative features within this comprehensive perspective should thus be evaluated following the same principles of unbiased design used in the present study. Other featural and conceptual dimensions (e.g. feature correlation, concept familiarity) may also constrain this general model of cortical specialization for semantic memory. This hypothesis remains to be tested with other experimental designs and with both normal and patient populations.

4. Experimental procedures

4.1. *Participants*

Twenty-one healthy (neurologically normal) participants, native speakers of Italian (9 males, 12 females; mean age = 26.09 years, SD = 1.89, range = 24–29) took part in the study. Participants gave informed written consent to the experimental procedure, which was approved by the local Ethics Committee.

4.2. *Experimental design*

The experiment involved a 2×2×2 within-subjects factorial design, corresponding to the variables feature type (visual form/surface, motion), concept domain (living, nonliving) and sentence (true, false). Visual form/surface features included form, color, size and part information, while motion features corresponded to information about motor actions made by the concept. Living concepts corresponded to animals (e.g. bee, donkey, whale; 42 concepts), while nonliving concepts included tools and small manipulable objects (e.g. hammer, needle, bottle; 22 concepts), vehicles (e.g. sledge, train; 15 concepts), furniture (blinds, chair, wardrobe; 3 concepts) and clothing (pants, skirt; 2 concepts). For the experimental conditions, 42 different features and 42 different concepts were considered, respectively, for each feature type and for each concept domain. The final list of stimuli included 336 items (i.e. concept–feature pairs), half of which were true statements and half false; and 42 items for each of the 8 concept domain × feature type × response status combination (and 84 for the concept domain × feature type combination). All materials were in Italian. Each item was embedded in a simple sentence (e.g.'The airplane lands') that appeared on screen for 2800 ms; the participant had to decide if the statement presented was true or false, and press the corresponding button with their left hand (left finger for true, right finger for false). A baseline condition was added to the experimental conditions. This corresponded to 42 strings of '+' (e.g., +++ +++++ +++ +++++) that appeared on screen for 2800 ms; the participant had to press a button (left finger) for each presented string. The study was composed of seven scanning periods lasting about 6 min 40 s each, that begun with a 500 ms ready sign ("Ready"). Each scanning period was composed of 6 concept–feature pair sentences that were randomly selected from each of the 8 experimental conditions, plus the baseline (total of 54 items per scanning period). The order of presentation of both conditions and stimuli within each scanning period and the order of presentation of the seven scanning periods were completely randomized for each subject. Successive trials were separated by a variable inter-stimulus interval. In order to optimize statistical efficiency, inter-stimulus intervals between successive trials within a block were presented in different ("jittered") durations across trials (2850, 5850 and 7850 ms, in proportion of 4:2:1) (Dale, 1999). Stimulus pairs were viewed via a back-projection screen located in front of the scanner and a mirror placed on the head coil. Stimulus pairs were presented, and subjects' answers and experimental timing information were recorded, using the software Presentation 9.13 (http://nbs.neuro-bs.com). The final list of stimuli was selected from a larger database of 838 concept–feature pairs that were rated on 4-point rating scale by 83 participants that otherwise did not participate in the study; each concept–feature pair was rated by a mean of 18 participants on how the feature described was more or less relevant for the concept (from always false to always true of the concept). A first behavioral pilot of this list showed that some of the selected false features were ambiguous in terms of their false/true status and were interchanged between concepts, totaling 29 new concept–feature pairs that were not further rated in terms of relevance.

Considering the semantic component of the task used, stimuli were equated in terms of age of acquisition (AoA) at concept level and in terms of feature relevance at feature level. In fact, these two dimensions have far more consistent effects than others in behavioral tasks in which mapping operations involve the semantic component (see for example, Juhasz, 2005, for AoA; and Sartori et al., 2005 for feature relevance) and have also consistent specific brain activation effects (see for example for Ellis et al., 2006, for AoA; and Mechelli et al., 2005, for feature relevance). Regarding AoA, stimuli were equated in terms of concept domain for both subjective AoA (combined

AoA 9-point scale norms from Dell'Acqua et al., 2000; Nisi et al., 2000) and objective AoA (from Caselli and Casadio, 1995), with no significant differences between domains [$F(1,60)=.35$, MSE=.92 $p<.56$ for Objective AoA but data only for 74% of the items; and $F(1,82)=.16$, MSE=617.93, $p<.69$, all items]. Regarding feature relevance, the stimuli (only data for 307 items) were equated in terms of relevance for both feature type and concept domain (as relevance values refer to concept–feature pairs), with no significant differences between sets [$F(1,303)=.07$, MSE=1.12, $p<.79$ for Domain; $F(1,303)=.92$, MSE=1.12, $p<.34$; $F(1,303)=.36$, MSE=1.12, $p<.55$ for Domain × Feature].

Considering the nature of the Italian language (i.e. shallow orthography and very regular letter-to-sound mappings), stimuli (data for the 336 items) were further equated in terms of written word frequency and word length, the main factors that affect Italian word naming time (e.g. Barca et al., 2002; Burani et al., 2007). For the latter we considered the number of characters, which were equated between domains at concept level [$F(1,82)=3.02$, MSE=7.64, $p<.09$], and between feature types at feature level [$F(1,82)=1.34$, MSE=23.13, $p<.25$]. Furthermore, considering sentence length (i.e. number of characters for concept plus feature of the different concept–feature pair combinations), the interaction between concept domain and feature type was also non significant [$F(1,332)=.001$, MSE=29.87, $p<.98$]. Finally, in terms of written word frequency (i.e. logarithmic of written word frequency taken from Bertinetto et al., 2005) stimuli were equated between domains at concept level [$F(1,82)=1.20$, MSE=2.10, $p<.28$] and between feature types at feature level [$F(1,82)=1.32$, MSE=3.80, $p<.25$], in the latter case considering the corresponding verb form or adjective that defined the feature (e.g. frequency of 'lands'; or 'white' for 'is white').

4.3. *Data acquisition and analysis*

Anatomical T1-weighted and functional T2*-weighted MR images were acquired with a 3 Tesla Philips Intera scanner (Philips Medical Systems, Best, NL), using an 8-channels Sense head coil (sense reduction factor=2). Functional images were acquired using a T2*-weighted gradient-echo, echo-planar (EPI) pulse sequence (30 interleaved slices parallel to the AC-PC line, covering the whole brain, TR=2000 ms, TE=30 ms, flip angle=85°, FOV=240 mm×240 mm, no gap, slice thickness=4 mm, in-plane resolution 2 mm×2 mm). Each scanning sequence comprised 200 sequential volumes. Immediately after the functional scanning a high-resolution T1-weighted anatomical scan (3D, SPGR sequence, 124 slices, TR=600 ms, TE=20 ms, slice thickness=1 mm, in-plane resolution 1 mm×1 mm) was acquired for each subject.

Image pre-processing and statistical analysis were performed using SPM5 (Wellcome Department of Cognitive Neurology, http://www.fil.ion.ucl.ac.uk/spm), implemented in Matlab v7.0.4 (Mathworks, Inc., Sherborn, MA). The first 5 volumes of each subject were discarded to allow for T1 equilibration effects. EPI images were realigned temporally to acquisition of the middle-slice, spatially realigned and unwarped. The anatomical T1-weighted image, coregistered to the mean of the realigned EPI images, was segmented into grey and white matter, and the grey-matter image was spatially normalized (voxel size: 2 mm×2 mm×2 mm) to a grey-matter template (http://www.loni.ucla.edu/ICBM/ICBM_TissueProb.html.). The resulting deformation parameters were then applied to all the realigned and unwarped functional images, which were finally spatially smoothed (FWHM Gaussian kernel: 6 mm×6 mm×6 mm) and globally scaled to 100. The resulting time-series across each voxel were then high-pass filtered to 1/128 Hz, and serial autocorrelations were modeled as an AR(1) process.

Statistical maps were generated using a random-effect model (Friston et al., 1999), implemented in a two-level procedure. At the first level, single-subject fMRI responses, synchronized with the acquisition of the middle-slice, were modeled by a design-matrix comprising the middle point between the onset of the stimulus and the motor true/false response for each trial of all experimental conditions. Only those trials in which subjects gave a correct response were modeled as belonging to a given task, while all the other trials, independently of the experimental condition, were modeled in a separate regressor. Any possible influence of the length of the semantic processing on cerebral activation was discounted by modeling a linear parametric modulation of the height of the delta function in each event by its reaction time. Regressors modeling events were convolved with a canonical Haemodynamic Response Function (HRF), along with its temporal and dispersion derivatives, and parameter estimates for all regressors were obtained by maximum-likelihood estimation.

At the second level, random-effects group analyses across the 21 subjects were computed by means of a factorial design which incorporated the HRF parameter estimates corresponding to the true sentence-conditions only (corrected for non-sphericity using a restricted maximum-likelihood (reML) procedure (Friston et al., 2002). This allowed testing for the main effects of the two factors (category and feature type), and for the interactions between them. In order to ensure that the observed activations did not result from relative deactivations, the statistical maps of the main effects were inclusively masked at $p<0.05$ by those associated with the conditions of interest minus the baseline task. The statistical maps were thresholded at $p<0.05$ corrected for multiple comparisons with False Discovery Rate (FDR; Genovese et al., 2002), and only clusters larger than 20 voxels were considered. To test for common activations across the four experimental conditions (living-visual, living-motion, nonliving-visual, nonliving-motion), the corresponding statistical maps were used to perform a conjunction analysis by means of inclusive masking.

In a supplementary analysis, the effect of reaction time on domain- and on feature-specific semantic processing was investigated by examining the regressors that modeled a linear parametric modulation of the canonical HRF by the reaction time in each event and in each subject. This allowed to explore those regions in which a linear relationship between cerebral activity and reaction time was specific for living vs. nonliving domains or visual form/surface vs. motion features.

The location of the activation foci in terms of Brodmann areas was determined using the nomenclature given by Talairach and Tournoux (1988), after correcting for differences between the MNI and Talairach coordinate systems by means of a nonlinear transformation (see http://www.mrc-cbu.cam.ac.uk/Imaging/Common/mnispace.shtml). Those cerebral regions for which maps were provided were also localized with reference to cytoarchitectonical probabilistic maps of the human brain, using the

SPM-Anatomy toolbox (Eickhoff et al., 2005). For visualization purposes, the activated foci were superimposed on 3D renderings created with MRIcro (Rorden and Brett, 2000).

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REFERENCES

Barca, P., Burani, C., Arduino, L., 2002. Word naming times and psycholinguistic norms for Italian nouns. Beh. Res. Met., Inst. and Comp. 34, 424–434.

Barsalou, L.W., Simmons, W.K., Barbey, A.K., Wilson, C.D., 2003. Grounding conceptual knowledge in modality-specific systems. Trends Cogn. Sci. 7, 84–91.

Beauchamp, M.S., 2005. See me, hear me, touch me: multisensory integration in lateral occipital–temporal cortex. Curr. Opin. Neurobiol. 15, 145–153.

Beauchamp, M.S., Lee, K.E., Haxby, J.V., Martin, A., 2002. Parallel visual motion processing streams for manipulable objects and human movements. Neuron 34, 149–159.

Beauchamp, M.S., Lee, K.E., Haxby, J.V., Martin, A., 2003. fMRI responses to video and point-light displays of moving humans and manipulable objects. J. Cogn. Neurosci. 10, 991–1001.

Bertinetto, P.M., Burani, C., Laudanna, A., Marconi, L., Ratti, D., Rolando, C., Thornton, A.M. 2005. *Corpus e lessico di frequenza dell'Italiano scritto (CoLFIS)*. [Corpus and Frequency Lexicon of Written Italian] Retrieved January 9, 2006, from http://www.istc.cnr.it/material/database/colfis/.

Burani, C., Arduino, L.S, Barca, L., 2007. Frequency, not age of acquisition, affects Italian word naming. Eur. J. of Cog. Psy. 19, 828–886.

Cabeza, R., Rao, S.M., Wagner, A.D., Mayer, A.R., Schacter, D.L., 2001. Can medial temporal lobe regions distinguish true from false? An event-related functional MRI study of veridical and illusory recognition memory. Proc. Natl. Acad. Sci. U. S. A. 98, 4805–4810.

Canessa, N., Borgo, F., Cappa, S.F., Perani, D., Falini, A., Buccino, G., Tettamanti, M., Shallice, T. in press. The different neural correlates of action and functional knowledge in semantic memory: an fMRI study. Cerebral cortex.

Cappa, S.F., Perani, D., Schnur, T., Tettamanti, M., Fazio, F., 1998. The effects of semantic category and knowledge type on lexical-semantic access: a PET study. Neuroimage 8, 350–359.

Caramazza, A., Mahon, B.Z., 2003. The organization of conceptual knowledge: evidence from category-specific semantic deficits. Trends Cogn. Sci. 7, 354–361.

Caramazza, A., Mahon, B.Z., 2006. The organization of conceptual knowledge in the brain: the future's past and some future directions. Cogn. Neuropsychol. 23, 13–38.

Caramazza, A., Shelton, J.R., 1998. Domain-specific knowledge systems in the brain: the animate–inanimate distinction. J. Cogn. Neurosci. 10, 1–34.

Caselli, M.C., Casadio, P., 1995. *Il primo vocabolario del bambino: Guida all'uso del questionario MacArthur per la valutazione della comunicazione e del linguaggio nei primi anni di vita* [The Child's First Words: Guide to the Use of the MacArthur Questionnaire for Assessing Communication and Language in the First Years of Life]. Franco Angeli, Milan.

Chao, L.L., Haxby, J.V., Martin, A., 1999. Attribute-based neural substrates in temporal cortex for perceiving and knowing about objects. Nat. Neurosci. 2, 913–919.

Crawford, J.R., Garthwaite, P.H., Azzalini, A., Howell, D.C., Laws, K.R., 2006. Testing for a deficit in single-case studies: effects of departures from normality. Neuropsychologia 44, 666–677.

Cree, G.S., McRae, K., 2003. Analyzing the factors underlying the structure and computation of the meaning of chipmunk, cherry, chisel, cheese, and cello (and many other such concrete nouns). J. Exp. Psychol. Gen. 132, 163–201.

Dale, A.M., 1999. Optimal experimental design for event-related fMRI. Hum. Brain Mapp. 8, 109–114.

Damasio, H., Grabowski, T.J., Tranel, D., Hichwa, R.D., Damasio, A.R., 1996. A neural basis for lexical retrieval. Nature 380, 499–505.

Dell'Acqua, R., Lotto, L., Job, R., 2000. Naming time and standardized norms for the Italian PD/DPSS set of 266 pictures: direct comparisons with American, English, French, and Spanish published databases. Behav. Res. Meth., Ins. Comp. 32, 588–612.

Devlin, J.T., Russell, R.P., Davis, M.H., Price, C.J., Moss, H.E., Fadili, M.J., Tyler, L.K., 2002. Is there an anatomical basis for category-specificity? Semantic memory studies in PET and fMRI. Neuropsychologia 40, 54–75.

Eickhoff, S., Stephan, K.E., Mohlberg, H., Grefkes, C., Fink, G.R., Amunts, K., Zilles, K., 2005. A new SPM toolbox for combining probabilistic cytoarchitectonic maps and functional imaging data. NeuroImage 25, 1325–1335.

Ellis, A.W., Burani, C., Izura, C., Bromiley, A., Venneri, A., 2006. Traces of vocabulary acquisition in the brain: evidence from covert object naming. NeuroImage 33, 958–968.

Farah, M.J., McClelland, J.L., 1991. A computational model of semantic memory impairment: modality specificity and emergent category specificity. J. Exp. Psychol. Gen. 120, 339–357.

Friston, K.J., Holmes, A.P., Worsley, K.J., 1999. How many subjects constitute a study? Neuroimage 10, 1–5.

Friston, K.J., Penny, W., Phillips, C., Kiebel, S., Hinton, G., Ashburner, J., 2002. Classical and Bayesian inference in neuroimaging: theory. Neuroimage 16, 465–483.

Gabrieli, J.D.E., Poldrack, R.A., Desmond, J.E., 1998. The role of left prefrontal cortex in language and memory. Proc. Natl. Acad. Sci. U. S. A. 95, 906–913.

Gainotti, G., Silveri, M.C., 1996. Cognitive and anatomical locus of lesion in a patient with a category-specific impairment for living beings. Cogn. Neuropsychol. 13, 357–389.

Genovese, C.R., Lazar, N., Nichols, T.E., 2002. Thresholding of statistical maps in functional neuroimaging using the false discovery rate. Neuroimage 15, 870–878.

Ishai, A., Ungerleider, L.G., Martin, A., Schouten, J.L., Haxby, J.V., 1999. Distributed representation of object form in the human ventral visual pathway. Proc. Natl. Acad. Sci. U. S. A. 96, 9379–9384.

Juhasz, B.J., 2005. Age-of-acquisition effects in word and picture identification. Psych. Bull. 131, 684–712.

Kellenbach, M.L., Brett, M., Patterson, K., 2001. Large, colourful, or noisy? Attribute- and modality-specific activations during retrieval of perceptual attribute knowledge. Cogn. Affect. Behav. Neurosci. 1, 207–221.

Kellenbach, M.L., Brett, M., Patterson, K., 2003. Actions speaker louder than functions: the importance of manipulability and action in tool representation. J. Cogn. Neurosci. 15, 30–46.

Laws, K.R., 2005. "Illusions of normality": a methodology critique of category-specific naming. Cortex 41, 842–851.

Laws, K.R., Sartori, G., 2005. Category deficits and paradoxical dissociations in Alzheimer's disease and herpes simplex encephalitis. J. Cogn. Neurosci. 17, 1453–1459.

Lee, A.C.H., Graham, K.S., Simons, J.S., Hodges, J.R., Owen, A.M., Patterson, K., 2002. Regional brain activations differ for semantic features but not categories. Neuroreport 13, 1497–1501.

Martin, A., Chao, L.L., 2001. Semantic memory and the brain: structure and process. Curr. Opin. Neurobiol. 11, 194–201.

Martin, A., Wiggs, C.L., Ungerleider, L.G., Haxby, J.V., 1996. Neural correlates of category-specific knowledge. Nature 379, 649–652.

McCarthy, R.A., Warrington, E.K., 1988. Evidence for modality-specific meaning systems in the brain. Nature 334, 428–430.

McDermott, K.B., Petersen, S.E., Watson, J.M., Ojemann, J.G., 2003. A procedure for identifying regions preferentially activated by attention to semantic and phonological relations using functional magnetic resonance imaging. Neuropsychologia 41, 293–303.

Mechelli, A., Sartori, G., Orlandi, P., Price, C.J., 2005. Semantic relevance explains category effects in medial fusiform gyri. Neuroimage 30, 992–1002.

Miceli, G., Fouch, E., Capasso, R., Shelton, J.R., Tomaiuolo, F., Caramazza, A., 2001. The dissociation of color from form and function knowledge. Nat. Neurosci. 4, 662–667.

Moore, C.J., Price, C.J., 1999. A functional neuroimaging study of the variables that generate category-specific object processing differences. Brain 122, 943–962.

Mummery, C.J., Patterson, K., Hodges, J.R., Price, C.J., 1998. Functional neuroanatomy of the semantic system: divisible by what? J. Cogn. Neurosci. 10, 766–777.

Nisi, M., Longoni, A.M., Snodgrass, J.G., 2000. Misure italiane per l'accordo sul nome, familiarità, ed età di acquisizione per le 260 figure di Snodgrass e Vanderwart (1980). [Italian measures of name agreement, familiarity and age of acquisition for the 260 pictures of the Snodgrass and Vanderwart (1980) picture set]. Giornale Italiano di Psicologia 27, 205–218.

Noppeney, U., Josephs, O., Kiebel, S., Friston, K.J., Price, C.J., 2005. Action selectivity in parietal and temporal cortex. Cog. Brain Res. 25, 641–649.

Perani, D., Schnur, T., Tettamanti, M., Gorno-Tempini, M., Cappa, S.F., Fazio, F., 1999. Word and picture matching: a PET study of semantic category effects. Neuropsychologia 37, 293–306.

Phillips, J.A., Noppeney, U., Humphreys, G.W., Price, C.J., 2002. Can segregation within the semantic system account for category-specific deficits? Brain 125, 2067–2080.

Powell, J., Davidoff, J., 1995. Selective impairments of object knowledge in a case of acquired color blindness. Memory 3, 435–461.

Ratcliff, R., 1993. Methods for dealing with reaction time outliers. Psyc. Bull. 114, 510–532.

Rorden, C., Brett, M., 2000. Stereotaxic display of brain lesions. Behav. Neurol. 12, 191–200.

Sartori, G., Lombardi, L., Mattiuzzi, L., 2005. Semantic relevance best predicts normal and abnormal name retrieval. Neuropsychologia 43, 754–770.

Shelton, J.R., Fouch, E., Caramazza, A., 1998. The selective sparing of body part knowledge: a case study. Neurocase 4, 339–352.

Talairach, J., Tournoux, P., 1988. Co-planar Stereotactic Atlas of the Human Brain. Thieme, Stuttgart.

Thompson-Schill, S.L., 2003. Neuroimaging studies of semantic memory: inferring "how" from "where". Neuropsychologia 41, 280–292.

Thompson-Schill, S.L., Aguirre, G.K., D'Esposito, M., Farah, M.J., 1999. A neural basis for category and modality specificity of semantic knowledge. Neuropsychologia 37, 671–676.

Tyler, L.K., Moss, H.E., 2001. Towards a distributed account of conceptual knowledge. Trends Cogn. Sci. 5, 244–252.

Tyler, L.K., Moss, H.E., Durrant-Peatfield, M., Levy, J., 2000. Conceptual structure and the structure of concepts. Brain Lang. 75, 195–231.

Vandenberghe, R., Price, C.J., Wise, R., Josephs, O., Frackowiak, R.S. J., 1996. Functional anatomy of a common semantic system for words or pictures. Nature 383, 254–256.

Vandenbulke, M., Peeters, R., Fannes, K., Vandenberghe, R., 2006. Knowledge of visual attributes in the right hemisphere. Nat. Neurosci. 9, 964–970.

Wagner, A.D., 1999. Working memory contributions to human learning and memory. Neuron 22, 19–22.

Warrington, E.K., McCarthy, R.A., 1983. Category-specific access dysphasia. Brain 106, 859–878.

Warrington, E.K., Shallice, T., 1984. Category-specific impairment. Brain 107, 829–853.

Wheatley, T., Weisberg, J., Beauchamp, M.S., Martin, A., 2005. Automatic priming of semantically related words reduces activity in the fusiform gyrus. J. Cogn. Neurosci. 17, 1871–1885.