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Research report

Electrophysiological evidence of a semantic system commonly accessed by animals and tools categories

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Abstract

Some theoretical perspectives propose a semantic system in which categories are represented in different brain regions. Others assume that distinctions are based rather on differences in the demands placed by different categories on shared processing systems. In this study semantic categorization processes were investigated using the recognition potential (RP), an event-related brain response that reflects semantic processing, peaks at around 250 ms after stimulus onset and originates in areas subserving perceptual-semantic analyses. Results indicate that the RP shows some degree of sensitivity to categorization processes, but that categories assumed to differ markedly in their processing demands share, to a large extent, a common neural generator. This provides support for the non-categorical view on the organization of the semantic system, though introducing subtle variations, and suggesting the existence of a semantic subsystem specializing in the processing of perceptual-semantic features regardless of the semantic category involved. © 2001 Elsevier Science B.V. All rights reserved.

Theme: Neural basis of behavior

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1. Introduction

Neuropsychological literature has reported many patients showing differential impairments in specific semantic categories following brain damage [6,15,18,19,24,47,49,50,54,55]. Various explanations have been developed to deal with these category-specific deficits.

Several authors propose a semantic system in which different categories are represented within different brain areas. This is the case of the domain-specific knowledge hypothesis (DSKH), which assumes a modular perspective in which semantic knowledge is compartmentalized according to category. Evolutionary pressures have resulted in specialized mechanisms that mainly distinguish living and non-living categories. These pressures have also led to a categorical organization of knowledge whereby different semantic categories based upon this dimension would be anatomically segregated in the brain [10]. Some evidence provided by brain lesion data supports this view. In this regard, several patients have been found to present a selective loss of knowledge in specific ‘living things’ categories, such as that of animals [24,28]. These types of impairment are almost invariably associated with particular lesion sites, for example, bilateral inferior temporal lobe damage in the case of living things and left frontal and parietal cortex damage in the case of non-living things [24,47,48].

Another perspective, however, assumes a unitary though distributed semantic categorization system in which several brain areas involved in semantic analysis subserve all categories. Different categories activate to a different

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extent each particular brain area depending on the attributes defining each category. The perceptual–functional theory (PFT) belongs to this perspective. This model supposes that the identification of certain categories depends on their perceptual properties, while the identification of others depends on their functional properties, which would explain why different brain lesions have a different effect on semantic categories according to their position in the perceptual–functional dimension [55,56]. This position has received considerable support from the neuropsychological literature [6,18,35,55], which has revealed the co-occurrence of deficits for certain classes of objects. Thus, patients impaired in the semantic processing of animals tend to be impaired in other semantic categories also distinguished by their perceptual characteristics, such as food [4,21] or cars [18]. Neuroimaging data have provided additional support for this position. It is commonly found that the processing of living things leads to a higher activation of brain areas involved in visual processing, including the posterior regions of the ventral cortex, whereas non-living objects activate to a greater extent those areas related to features of object motion and imagining hands movement, such as the lateral temporal cortex and prefrontal/premotor regions [14,30,36,41].

Also within the perspective assuming a unitary semantic system, the organized unitary content hypothesis (OUCH) focuses on the degree of correlation displayed by the different categories within the same anatomical areas. According to this view, semantic features defining a member belonging to a particular category are highly correlated. With regard to the living/non-living dimension, the degree of correlation and overlapping features would be higher in the living than in the non-living category [9,23,34], as a consequence of the greater perceptual similarity between exemplars in the living things categories [26]. As a result of this higher degree of correlation, the identification of living kinds would be more demanding. Though this claim has not yet been sufficiently developed, some efforts have been made to provide it with empirical support [16,17].

The PFT and OUCH explanations could be considered as complementing one another. In this regard, Bird et al. [6] pointed out that the fact that living things have more features that correlate, and most of them perceptual, might account for the prevalence in the literature of deficits for the living things categories. This suggests that perceptual features have more salience in semantic memory. The approach integrating the PFT and OUCH is also supported by neuroimaging data [36].

These approaches give different answers to the important question of whether there is a general-purpose system for the categorization of objects or separate and specialized areas for categorizing different classes. Most of the evidence supporting these positions has been obtained either from neurological patients, PET or fMRI studies — sources of information that are not free of trade-offs [46]. Event-related potentials (ERPs) showing sensitivity to semantic categorization processes would provide an additional and complementary source of evidence. However, studies on ERPs to semantic categorization are rather scarce. A study by Ji et al. [27] appears to suggest the existence of both common and different brain areas involved in the processing of two different living things categories (animals and fruits/vegetables); another study, by Antal et al. [3], using a heterogeneous category to be compared to the animal category, reported a higher N1 amplitude for non-animals when compared to animals. Accordingly, further ERP research is necessary in order to determine differences in the way the brain processes semantic information when two qualitatively different categories are compared. In this regard, the comparison between the categories of animals and tools would be of particular interest, since animals vs. tools is a frequently documented distinction in the literature on semantic categorization research, referring as it does to categories that clearly differ in terms of both their perceptual and functional properties and of the living/non-living dimension [10,12,19,40,41].

A recently reported ERP response, the recognition potential (RP), may be useful for the purpose of studying processes involved in semantic categorization. The RP peaks between 250 and 300 ms after stimulus onset, and reflects semantic word processing [31,32,43–45]. Its neural generators are located within basal extrastriate areas [25,32]. Neuroimaging studies have consistently shown that these areas participate in semantic processing [5,7,11,52], and more specifically in those aspects related to visual-semantic processing [37,52,53].

Previous findings suggest that the RP shows some degree of sensitivity to semantic categorization, since a pool of animal nouns evoked a higher RP amplitude as compared to that evoked by a pool of nouns belonging to heterogeneous categories [32]. However, no definitive statements can be made on the basis of these findings, since the categories of the pool of heterogeneous nouns were not controlled (as in the Antal et al. [3] study).

In this RP study we present our subjects with nouns belonging to animals and tools categories as stimuli. Its aim is to contribute to semantic categorization research by elucidating whether the sensitivity and topography of the RP varies in response to different semantic categories (animals and tools). Different patterns of results might be expected in accordance with each of the two main theoretical positions described above. The finding of qualitative differences in the topographical distribution of the RP evoked by animals and tools would be in consonance with the DSKH model; on the other hand, the same topographical distribution with differences in the RP amplitude evoked by animals as compared to tools would support the PFT/OUCH perspective.

2. Methods and materials

2.1. Subjects

Thirty native Spanish speakers participated in the experiment (19 of whom were females) ranging in age from 17 to 36 years (mean 22 years). All were right-handed, with average handedness scores [39] of +0.89. All had normal or corrected-to-normal vision. Subjects were paid for participating in this experiment.

2.2. Stimuli

Following procedures detailed elsewhere [31,32], there were pools of Semantically Correct (SC), Orthographically Correct (OC), Random Letters (RL), Control (CN), and Background (BK) stimuli. The pools were of 20 items each, except for the BK pool, which comprised 40 stimuli. The SC stimuli were further divided into two pools of 10 tool nouns (SCt) and 10 animal nouns (SCa).

Both the SCt and the SCa stimuli were two-syllable Spanish words containing 5 (80% of each pool), 4 (10%) or 6 (10%) letters. According to the Alameda and Cueto [1] dictionary of frequencies for Spanish, the pool of SCt stimuli had a mean of 40.4, whilst for Sca it was 19.8. Although the frequency for SCt is double that of SCa, word frequency modulates only RP latency [43], and this study deals with amplitude and topography. In any case, mean frequencies did not statistically differ ($t_{10}=1.1$, $P>0.1$). The OC stimuli consisted of legal pseudowords, following orthographic and phonological rules but devoid of meaning. They were selected on the basis of a previous study with Spanish population [22], and number of letters followed the same percentages as for the SC stimuli. The RL stimuli follow neither orthographic nor phonological rules, and were created by randomizing the letters of the two types of SC words and once again constituting strings of 4, 5, and 6 letters. The CN stimuli were made by cutting the pool of SC words in n portions (n=number of letters that make up a word minus one). The portions were replaced always following this rule: the first piece of the word was placed in the last position of the new stimulus, and vice versa; the penultimate portion was placed in second position, and vice versa; and so on (Fig. 1). Each stimulus obtained in this way had at least two complete letters, but also clearly identifiable non-letters (formed by the joining of different letter fragments). Finally, the pool of BK stimuli was composed of the same 20 CN stimuli, together with a new set of 20 stimuli obtained by replacing the portions randomly.

All stimuli were 1.3 cm high and 3.5 cm wide, and were equated in overall physical attributes. Images were 1.14° high and 3° wide in their visual angles. Subjects' eyes were 65 cm from the screen. All stimuli were presented white-on-black on a computer monitor.

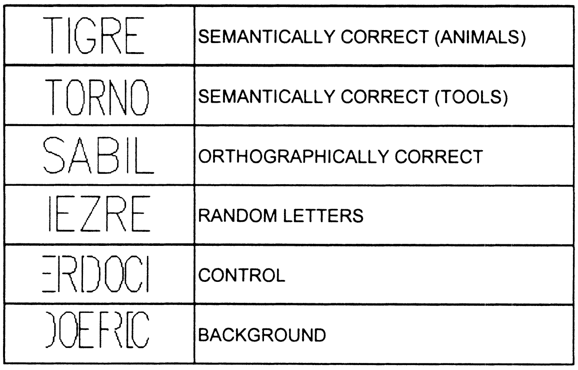

Fig. 1. Examples of the images for each type stimulus.

2.3. Procedure

Rapid stream stimulation [42] was used for presenting stimuli. Accordingly, stimulation was organized in sequences. Stimuli were displayed with a SOA of 257 ms. The computer displayed mostly BK stimuli. Periodically (after either six or seven BK), a test stimulus instead of a background one was presented. The test stimulus could be SCt, SCa, OC, RL or CN. A random process determined the type of stimulus presented, and no more than two of the same type occurred in succession.

A total of 16 sequences were presented to each subject. Each sequence contained five SCt, five SCa, five OC, five RL and five CN stimuli, together with the proportional amount of background stimuli. Half of the subjects were instructed to press a button every time they detected an animal name (animals as target subgroup), while the other half were instructed to press a button when a tool name was detected (tools as target subgroup). Each subject was presented with all of the stimuli from the pools. Subjects were explicitly told to respond as rapidly as possible every time they detected a target stimulus. At the beginning of each sequence subjects pushed the button, and a message appeared on the screen telling them to blink as much as they wanted (they were told to avoid blinking as much as possible during stimulus presentation) and push again to start the sequence. At the end of each sequence, subjects were provided with feedback about their performance.

2.4. Electrophysiological recordings

The EEG was recorded with 59 tin electrodes (electro-Cap International) from Fp1, Fpz, Fp2, AF3, AF4, F7, F5, F3, F1, Fz, F2, F4, F6, F8, FC5, FC3, FC1, FCz, FC2, FC4, FC6, T7, C5, C3, C1, Cz, C2, C4, C6, T8, TP7, CP5, CP3, CP1, CPz, CP2, CP4, CP6, TP8, P7, P5, P3, P1, Pz, P2, P4, P6, P8, PO7, PO3, PO1, POz, PO2, PO4, PO8, O1, Oz, O2 and left mastoid, all referenced to the right mastoid. These labels correspond to the revised 10/20 International System [2], plus two additional electrodes, PO1 and PO2, located halfway between POz and PO3 and between POz and PO4, respectively. A bipolar horizontal and vertical electrooculogram (EOG) was recorded for artifact rejection purposes. Electrode impedances were kept below 3 kΩ. The signals were recorded continuously with a bandpass between 0.3 and 100 Hz (3 dB points for −6 dB/octave roll-off), and were digitized at a sampling rate of 250 Hz.

2.5. Data analysis

The continuous recording was divided into 1024-ms epochs, starting from the onset of each SCt, SCa, OC, RL and CN type stimulus. Artifacts were automatically rejected by eliminating those epochs that exceeded ±65 μV. Additionally, a visual inspection was performed, and trials in which there were no responses to target stimuli, or containing false alarms, were excluded. Trials in which RT was not between 200 and 800 ms were also excluded. ERP averages were categorized according to each type of stimulus.

Originally M2-referenced data were algebraically re-referenced off-line using the average reference method [29], which has proved to be the best way of obtaining the RP [32]. Both the latency and amplitude, together with the topography of the RP, were measured from average waveforms in the interval 160–417 ms after test image onset, following criteria outlined elsewhere [43].

3. Results

3.1. Performance

Of the 8000 trials, 1.4% were excluded because of eye blinks. Also excluded were those trials with omissions, false alarms, and premature or late responses, which represented 3%, 1.8% and 1.2%, respectively. Mean reaction time was 575 ms for SCt and 538 ms for SCa, this difference failing to reach statistical significance (t_{28}= 0.09; $P>0.1$).

3.2. Electrophysiology

After subtracting the responses for control trials from each of those elicited by SCt, SCa, OC, and RL stimuli trials, in order to eliminate driving and enhance language-related factors, a negative wave peaking maximally at PO7 was obtained. Amplitude and peak latency values were −3.7 μV and 260 ms for SCt, −4.3 μV and 256 ms for SCa, −2.8 μV and 256 ms for OC, and 1.8 μV and 244 ms in the case of RL stimuli. Grand-mean average waves corresponding to each type of stimulus after subtracting the responses for control trials are shown in Fig. 2 for PO7 and PO8 electrodes.

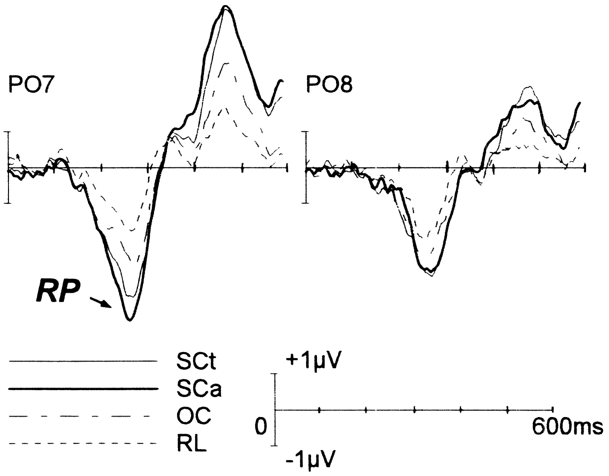

Fig. 2. Absolute grand average waveforms after subtracting control trials from each of the waveforms for each type of stimulus at PO7 and PO8 electrodes. A clear recognition potential (RP) can be identified for tool and animal nouns (SCt and SCa, respectively), being higher in the case of animal nouns. Orthographically correct (OC) and random letter (RL) stimuli also displayed an low RP. RP amplitude was maximum at PO7. Latency was around 252 ms.

An analysis of variance (ANOVA) comparing RP peak latencies at PO7 electrode with Type of stimulus as repeated-measures factor (four levels: SCt, SCa, OC, RL) and Target as between-subjects factor (two levels: Tools as target, Animals as target) yielded non-significant results (Type of stimulus by target; $F_{3,84}=1.7$, $P>0.1$). Therefore, the same peak latency could be assumed across types of stimulus, and regardless of the semantic category that constituted the target. With regard to type of stimulus, a narrow window was established centered on the overall mean peak amplitude (about 252 ms) for all types of stimulus, with the purpose of measuring amplitude for statistical analysis. This window extended from 224 to 280 ms (around mean ±28 ms) after stimulus onset.

Maps of the average referenced activity in the 224–280 ms period for SCt and SCa stimuli after subtracting activity evoked by CN stimuli are shown in Fig. 3. The two maps show a very similar topography, which basically consists in a left-lateralized inferior parieto-occipital negativity, together with a positive activity of lower intensity over frontal regions.

Statistical analyses were carried out on the amplitude of a selected sample of 30 electrodes, with the aim of avoiding an unacceptable degree of loss of statistical power due to the use of the high number of electrodes [38]. These 30 selected electrodes were: Fp1, Fp2, AF3, AF4, F5, F1, F2, F6, FC5, FC1, FC2, FC6, C5, C1, C2, C6, CP5, CP1, CP2, CP6, P5, P1, P2, P6, PO7, PO1, PO2, PO8, O1, and O2. A three-way ANOVA was performed on the mean amplitude along the 224–280 ms window with three repeated-measures factors (Type of stimulus, with five levels: SCt, SCa, OC, RL, or CN; Electrode, with 15 levels; and Hemisphere, with two levels) and one between-

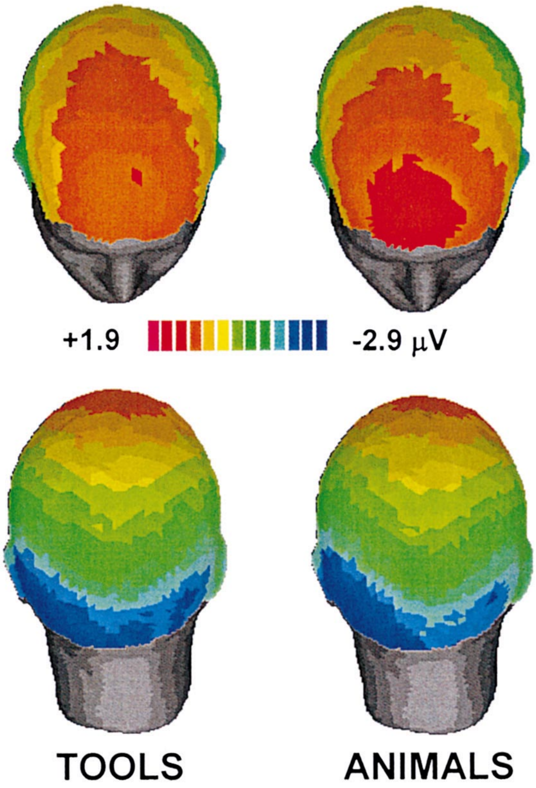

Fig. 3. Topographic maps of RP distribution across the total array of 60 cephalic electrodes. These maps represent mean values for the period 224–280 ms. Activity to control stimuli has again been subtracted from each of the waveforms to make the maps. The topography of the two maps is notably similar, and mainly consists in a slightly left-lateralized inferior parieto-occipital negativity. A lower-amplitude positivity over frontal regions can also be observed.

subjects factor (Target, with two levels: Tools as target, Animals as target).

Significant results were obtained for Type of stimulus ($F_{4,112}=20$; $P<0.0001$), Electrode ($F_{14,392}=105.3$; $P<0.0001$); Hemisphere ($F_{1,28}=13.5$; $P<0.01$), and the interactions Type of stimulus by Electrode ($F_{56,1568}=33.2$; $P<0.0001$), Type of stimulus by Hemisphere ($F_{4,112}=7.6$; $P<0.01$), Electrode by Hemisphere ($F_{14,392}=3.1$; $P<0.05$), and Type of stimulus by Electrode by Hemisphere ($F_{56,1568}=2.9$; $P<0.05$).

Post hoc analyses with the Bonferroni correction were then carried out at the PO7 electrode, which showed the maximum RP values. The comparison between SCt and SCa gave only a statistical trend ($F_{1,29}=3.5$; $P=0.07$). Also, types of stimulus differed significantly when compared to one another ($103.7>F_{1,29}>10.9$; $P<0.0001$ in all cases, with the exception of SCt vs. OC; $P<0.05$). Thus, statistical analyses supported the existence of amplitude differences across types of stimulus at the PO7 electrode, with the exception of tool compared to animal nouns, these differences being independent of whether or not a specific category was used as target.

In order to elucidate whether the topographic distribution of the evoked RP was the same for either type of stimulus, a profile analysis was performed [33]. Mean amplitudes in the 224–280-ms window were scaled for each subject across all electrodes, with average distance from the grand mean ERPs as denominator. An ANOVA was performed on these scaled data with Type of stimulus (two levels, SCt and SCa) and Electrode (30 levels). Only the two semantic categories were used in this case, in order to enhance the statistical power of the profile analysis, since the comparison of these categories was the purpose of the present study. No significant differences were obtained in the Type of stimulus by Electrode interaction ($F_{29,841}=0.7$; $P>0.1$). Hence, the same neural generators could be assumed for the two types of stimulus.

4. Discussion

The present data show a negative ERP response peaking at about 250 ms (the RP) evoked by both animals and tools, as compared to non-meaningful stimuli, including pseudowords and strings of random letters. Some differences in the pattern of activation exist, however, since animals evoked a slightly higher activation than tools. Nevertheless, our results cannot strongly support a clear distinction between the activity evoked by animals and that evoked by tools within the brain regions and at the time when the RP occurs, despite the fact that the stimuli presented in this experiment clearly differed in their perceptual–functional properties and in the living/non-living dimension.

A more robust and important finding of the present study is the absence of topographical differences when comparing animals and tools in the RP, which indicates that these semantic categories share the brain regions involved in its generation. These areas are within the fusiform/lingual gyri, as previous research on RP has revealed [25,32]. The absence of such topographical differences can be taken as evidence against a semantic system organized exclusively by category, in which animals and tools categories would be allotted to separate cerebral areas, as proposed by the DSKH. The same conclusion has been drawn by recent neuroimaging research indicating that object knowledge is more probably stored as a distributed network in the brain, and that the location of the sites involved in categorization processes mirrors the organization of sensory and motor systems [8,12,36,41]. In fact, brain damage studies supporting the DSKH have recently been criticized for failing to control in a consistent and careful way certain experimental variables [47]. With regard to this question, two studies have shown how an apparently selective deficit for living things disappeared when materials were matched for familiarity and visual complexity [20,51]. In any case, and on the basis of the present findings, we cannot totally rule out the possibility of the existence of other brain areas different from those generating the RP but exclusively specialized in the processing of either animals or tools. Rather, our findings indicate that there are semantic processing areas within the brain that subserve the two semantic categories in a similar way.

Our data might be better understood in the light of the PFT/OUCH perspective, even though they introduce subtle variations on these models. As the PFT/OUCH view postulates, semantic knowledge would be distributed in non-categorically organized subsystems. In line with this, our data indicate several brain areas devoted to processing semantic information, and which are jointly accessed by different categories (e.g. animals and tools).

Included among these areas would be the fusiform/lingual gyri, which generate the RP [25,32]. The involvement of the fusiform/lingual gyri in the processing of visual-semantic aspects — rather than their being related merely to basic perceptual processes — has recently been emphasized [37,52,53]. Accordingly, it appears that the areas activated by both semantic categories are most probably dealing with visual-semantic processing, that is, a semantic processing based on the perceptual attributes of objects.

However, tools belong to a non-living category mainly defined by functional properties, but activate those brain areas dealing with visual-semantic processing to a similar extent to animals, a category defined by perceptual attributes, according to PFT/OUCH. This perspective would therefore predict a higher activation evoked by animals, as compared to tools, in those areas related to visual-semantic processing, a prediction that would hold true for either the PFT model (in which this activation would be due to the greater dependence on perceptual knowledge of animals) or the OUCH model (which would propose higher demands on these areas for animals than for tools). However, the differences in activation of the areas generating the RP were extremely slight, supported only by a statistical trend, and these differences were negligible when compared to the differences between the animals and tools categories and non-meaningful stimuli. It could thus be concluded that the areas generating the RP subserve the analysis of visual attributes for both animals and tools, supporting the existence of a semantic subsystem specializing in the processing of perceptual features, regardless of the semantic category involved. Accordingly, at least part of the semantic system appears to be non-categorically organized, and is similarly accessed by categories differing in their perceptual–functional properties and in terms of the living/non-living dimension.

De Renzi and Lucchelli [15] reported a patient following herpes encephalitis that showed impairment in the retrieval of the perceptual features of several living things categories, including animals, vegetables and flowers. This patient had no problem with man-made objects, except that he could not recall their perceptual properties, thus providing evidence of a visual-semantic system accessed by several different living and non-living categories.

In a study using fMRI, Thompson-Schill et al. [53] presented yes/no questions about visual and non-visual properties of living and non-living things to subjects participating in their experiment. These authors found an increase in the activity of the left fusiform gyrus for non-living, as well as for living things, in response to questions related to their visual properties. This increase in activation was taken as an index of visual retrieval, leading the authors to propose that the semantic system is functionally segregated into anatomically discrete, but highly interactive, modality-specific brain regions.

Finally, Coltheart et al. [13] described a patient that was unable to access visual semantic attributes but could access semantic attributes relevant to other sensory modalities and non-perceptual semantic attributes, regardless of the category tested. These authors took this finding as evidence of the existence of a semantic subsystem for the processing of visual attributes, resulting in similar conclusions to those proposed by De Renzi and Lucchelli [15], Thompson-Schill et al. [53] and the present study.

In conclusion, the question of whether the brain's semantic categorization system is anatomically segregated by category or is made up of subsystems in which different categories involve different demands according to their properties still deserves more research. In this regard, there are other ERP components related to semantic processing, such as the N400, whose role in semantic categorization remains unexplored. In any case, we provide here further evidence of an ERP response peaking around 250 ms after stimulus onset, originating within the fusiform/lingual gyri, and reflecting visual-semantic processing. This would indicate that part of the semantic system is non-categorically organized and equally accessed by categories that differ widely in their perceptual–functional properties and in terms of the living/non-living dimension.

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