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Research Report

Electrophysiological evidence for a natural/artifactual dissociation

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ABSTRACT

The aim of this work was to test whether the differences usually found between the processing of visual stimuli corresponding to natural and artifactual domains reflect the different ways in which these domains are organized in the brain or are rather due to varying task demands. For this purpose, we designed two tasks in which subjects had to classify a series of line drawings. In one task (semantic categorization), the subjects were asked to categorize the stimuli as corresponding either to the natural or the artifactual class, and in the other (gender decision), the subjects had to decide if the names of the stimuli corresponded to either the masculine or the feminine gender. Event-related potentials (ERPs) and reaction times (RTs) were registered during the two tasks. We found both quantitative and topographical differences between ERPs elicited by natural stimuli and those by artifactual stimuli. In the 50- to 200-ms period, ERPs were more positive for the natural stimuli in the categorization task, but more positive for the artifactual stimuli in the gender decision task. In addition, natural stimuli elicited larger P600 and were associated with shorter RTs than artifactual stimuli in the categorization task. These results likely reflect differences concerning the relative difficulty of processing the stimuli of each domain in each task. In the N400 range, in contrast, there were differences between the two domains which were independent of task. In the two tasks, natural and artifactual stimuli elicited ERPs with a different scalp distribution: ERPs were more positive at posterior (parietal and temporal) sites for the natural stimuli and in the frontal areas for the artifactual ones. This finding is consistent with the hypothesis that semantic knowledge associated with natural and artifactual domains is represented in separate subsystems with presumably different anatomical bases.

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1. Introduction

The organization of knowledge and its representation in the brain have been the subject of considerable interest in recent years. It is widely accepted that knowledge is grouped into semantic categories, and the division between the natural and artifactual (or living and nonliving) domains is one of the most

obvious and traditionally studied distinctions. There is evidence suggesting that this distinction is not only cognitive but also has a neurological basis. Data from studies of brain-damaged patients suggest that the two domains are processed, at least partially, in different areas of the brain. For example, patients with lesions in the left frontal area present more problems with images of inanimate objects, whereas

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patients with damage in the temporal lobes tend to present more difficulties with images representing living things (for a review, see Gainotti, 2000). In addition, topographical differences between natural and artificial domains have also been found with neuroimaging techniques. Although there is not complete agreement among all studies, likely due to the variety of tasks and stimuli used by the different investigators, in general, the results indicate that stimuli belonging to the natural class activate predominantly posterior areas of the left hemisphere, whereas those within the artificial domain activate primarily the anterior areas of the left hemisphere (e.g., Dehaene, 1995; Perani et al., 1995; Martin et al., 1996; Grafton et al., 1997; Moore and Price, 1999).

Different hypotheses have been proposed to explain the dissociation observed between the natural and the artificial domain. According to Warrington and colleagues (Warrington and McCarthy, 1983; Warrington and Shallice, 1984), this dissociation is attributable to the differential importance of perceptual and functional semantic attributes for the identification of items belonging to each domain. In their view, visual semantic knowledge is more important for identification of natural objects, whereas functional semantic knowledge is more important for the identification of artificial objects. This difference might explain the greater participation of the visual parieto-occipital areas in processing the first class of object and of the frontal motor areas in processing the second class. The natural/artificial dissociation has also been considered from an evolutionary point of view. Caramazza and Shelton (1998) proposed that this dissociation reflects the discrete organization in the brain of different domains of knowledge. At the neuroanatomical level, this distinction emerges as a function of the roles of natural and artificial objects in the evolution of the human brain: living objects represent food and potential predators, whereas inanimate objects might be manipulated to obtain food or protect against predators. Thus, an understanding of the world in these terms would facilitate individual survival. Although differing in the details, Warrington as well as Caramazza and Shelton agree in the assumption of different subsystems. The key distinction between the two models is that the former further proposes that the semantic system is organized by types of knowledge, visual, or functional, whereas the latter assumes that the system is organized in relation to knowledge about categories of objects. In contrast to these models, other authors defend the existence of a single conceptual system not divided into categories and domains (Tyler and Moss, 2001; Tyler et al., 2003a,b). According to this view, semantic categories and domains emerge as the result of the similarity between the features of the concepts rather than as a result of explicit divisions of conceptual knowledge. Thus, concepts that share features are found close to each other in semantic space. This proposal is somewhat similar to the OUCH model of Caramazza and colleagues (Caramazza et al., 1990; Hillis et al., 1995), in which concepts with common features are likewise neighboring. However, in this case, the different categories or domains do not have independent stores, but, rather, all concepts belong to the same conceptual system. The fact that some patients with brain lesions usually demonstrate increased difficulty with the members of a determined category is interpreted from this perspective as indicating that lesions affect the processing of certain features

shared by members of the category and not necessarily because those objects belong to that category. Another explanation of the natural/artificial differences which do not invoke the existence of different semantic subsystems is that proposed by Humphreys and colleagues (Humphreys and Riddoch, 1987; Lloyd-Jones and Humphreys, 1997a,b). These authors consider that the dissociation occurs at the perceptual level rather than at the semantic level and arises as a consequence of the different requirements of the visual processing of stimuli belonging to the natural and artificial domains. They assume that natural objects are structurally more similar than artificial objects, and that they are therefore more difficult to distinguish one from another since a large number of competitors are simultaneously activated. The greater visual processing required by natural compared to artificial stimuli could account for the greater activation of the posterior areas of the brain in reaction to the former.

Event-related potentials (ERPs) is a technique not yet widely used to study the natural/artificial dissociation but which could provide relevant information. ERPs are recorded from electrodes on the scalp and reflect changes in the electrophysiological activity of a population of neurons time-locked to the processing of external stimulation. Differences in timing and scalp topographies of specific ERP components allow us to identify the timing and the spatial distribution of brain activity associated with a variety of cognitive processes. An important advantage of ERP technique in comparison to RT methods is that it provides information about the entire time course of cognitive processes, with a resolution in the order of milliseconds, and in addition allows us to establish associations between sequential ERP components and the processes that take place between stimulus onset and subject response.

One ERP component that has received a great deal of attention in psycholinguistic studies is the N400. This component is a negative wave with an onset latency between 200 and 250 ms post-stimulus, with maximum amplitude at around 400 ms. This wave has been related to semantic processing, since its amplitude is enhanced with semantic incongruence between word and context (Kutas and Hillyard, 1980; Neville et al., 1986) and decreases in conditions in which the context enables the subject to predict the word (Holcomb and Neville, 1991) or when semantically related stimuli have previously been presented (Bentin, 1987; Bentin et al., 1985; Holcomb, 1988; Kutas and Van Petten, 1988; Holcomb and Neville, 1990; Dominguez et al., 2004; Kiefer, 2005). The presence of the N400 has also been tested in studies in which nonverbal materials are used, and, just as with words, semantic priming in picture processing tasks decreases the amplitude of this component (Barrett and Rugg, 1990; McPherson and Holcomb, 1999).

Several studies using ERP methodology with a focus on the N400 component have revealed wave-form related differences associated with differences in semantic or grammatical category membership or with differences in orthographic properties, distinguishing between concrete versus abstract words (Paz-Caballero and Menor, 1999), nouns versus verbs (Pulvermüller et al., 1999; Kellenbach et al., 2002), items having high versus low numbers of orthographic neighbors (Holcomb et al., 2002). On the specific subject of the natural/artificial dissociation, Kiefer (2001), using a superordinate object categorization task, found that the topographic distribution

of the N400 component varied as a function of domain. Natural stimuli were associated with less negativity in the occipito-temporal and centro-parietal locations of the right hemisphere, whereas artificial stimuli led to diminished N400 in the frontal area of the left hemisphere. He concluded that these domains are processed, at least partially, in different areas of the brain, and that differences occur at the level of semantic processing. Kiefer found a similar category effect on the N400 using words instead of pictures (Kiefer, 2001, 2005), even in a lexical decision task when semantic meaning is only implicitly accessed (Kiefer, 2005). These results support the interpretation that domain-related ERP effects reflect domain-related differences in semantic processing.

Differences in wave-form associated with domain membership have also been found at latencies shorter than that of the N400. In the study of Kiefer (2001), the N1 component in inferior temporal and occipital locations had a significantly larger amplitude in response to pictures of natural stimuli. Differences between natural and artificial visual stimuli with even shorter latencies were observed by Van Rullen and Thorpe (2001). They compared the ERPs elicited by photographs of animals and vehicles in a categorization task and observed a difference between the two categories at 75–80 ms post-stimulus. Kiefer (2001) considered that the early differences between natural and artificial stimuli could be due to the greater visual processing required by the former, as proposed by Humphreys and colleagues (Humphreys and Riddoch, 1987; Lloyd-Jones and Humphreys, 1997a,b). Alternatively, he also suggested that they could be due to the greater informativeness that perceptual features provide for determining superordinate category membership in the natural objects. As Kiefer pointed out, these two interpretations are not mutually exclusive, and there is no evidence to distinguish between them. However, according to the first interpretation, natural stimuli always would produce a greater activation in the visual areas, whereas according to the latter, the natural/artificial differences would be modulated by the specific task requirements. Results from behavioral studies have shown that natural categories are associated with shorter RTs than artificial categories in tasks which require a superordinate categorization, while the opposite is observed when the task is to identify or to name the stimuli (Lloyd-Jones and Humphreys, 1997a,b; Kiefer, 2001). Thus, it would be easier to classify stimuli as natural than as artificial because natural stimuli have more distinguishing features in common. In contrast, when a complete identification is required, it would take longer to differentiate among natural stimuli, precisely because of their greater similarity. The extent to which the differences in brain activation between natural and artificial stimuli may reflect these “difficulty” differences is still a matter of debate. Some evidence supporting the significance of category-related brain activations for semantic memory structure has been found by Kiefer (2005). The results of his work revealed that repetition priming, though affecting in the same way RTs to natural and artificial categories, had ERP effects with different scalp locations for each category. Nevertheless, further investigation is needed to analyze the possible modulator effect of the specific task on the observed natural/artificial dissociation.

Our work was set up to distinguish between perceptual and semantic sources of domain-related effects, as well as to

differentiate domain-related effects from task-related or difficulty effects. To this aim, we analyzed both behavioral responses (RTs) and ERP to pictures of objects belonging to either the natural or the artificial domains in two situations that in principle could be expected to entail an advantage for either the natural or the artificial categories. These two situations were a natural–artificial categorization task and a gender decision task. We chose the latter because, in order to determine the gender of an object, complete identification of the object is required. Thus, the gender decision task necessarily involves naming the stimulus, though this would be done implicitly so that oral production processes would not interfere with the ERPs. The gender decision task is possible in languages, such as Italian and Spanish, that allocate one of two genders (masculine and feminine) to each word. This task has already been used in Italian in an fMRI study by Miceli et al. (2002), who pointed out that the semantic content of a noun bears an arbitrary relationship to its grammatical gender, so that gender effects cannot be ascribed to the organization of knowledge in the brain. We predicted that if natural and artificial domains constitute separate semantic subsystems with different neurological substrates (Warrington and Shallice, 1984; Caramazza and Shelton, 1998), the scalp topography of the ERPs corresponding to each of these domains would differ regardless of the task. Furthermore, according to the multiple subsystems theories, differences between domains would occur in the semantic processing phase and coinciding with the N400 component. Instead, if the differences among stimuli belonging to these two domains are due to the greater perceptual processing required by the natural stimuli (Humphreys and Riddoch, 1987; Lloyd-Jones and Humphreys, 1997a, b), they would be observed from the early perceptual stages and thereby would affect ERP components prior to the N400 which would be enhanced in response to natural stimuli, mainly at visual areas. On the other hand, if the natural/artificial differences are due to the differing difficulty of processing each domain as a function of the tasks requirements, they would be associated with RT differences and should be modulated by the task since the two tasks used imply a greater relative difficulty for either the natural or the artificial stimuli.

2. Results

2.1. Behavioral measures

The number of correct answers was sufficiently high (91.5% \pm 1.17 in the semantic categorization task and 80.4 \pm 1.57 in the gender decision task) to demonstrate an

Table 1 – Mean reaction times and accuracy measures (standard errors in brackets) for natural and artificial stimuli in both task

	Semantic categorization task		Gender decision task	
	RT	Accuracy	RT	Accuracy
Natural	608 (23)	91.7% (1.8)	883 (46)	79.0% (2.2)
Artificial	650 (26)	91.3% (1.2)	860 (37)	81.7% (1.5)

adequate level of attention. In Table 1, the averages and standard errors of the accuracy measures and RTs for each domain in each task are presented. The ANOVA showed significant effects of task on both RTs [$F(1,19) = 48.94, P < 0.001$] and accuracy measures [$F(1,19) = 72.262, P < 0.001$]. RTs were shorter and accuracy levels higher in the categorization task. There was also a task \times domain effect interaction on RTs [$F(1,19) = 6.43, P = 0.02$]. Natural stimuli were associated with shorter RTs than artificial stimuli in the categorization task. In the gender decision task, the opposite trend was observed but did not reach significance.

2.2. ERPs

Fig. 1 shows the grand averages obtained in the two tasks. As can be seen, the ERPs have very similar morphologies up to 300 ms after stimulus onset. In both tasks, the P100-N150-P230 complex in the posterior areas and the fronto-central component P180 followed by a negative wave N270 can be observed. From 300 ms to the end of the analyzed period, however, the ERPs from both tasks show significant differences (see Table 2). The differences are due to a much greater amplitude of N400 in the gender decision task.

In addition to task differences, the ANOVAs showed significant effects of domain from 50 ms post-stimulus to the end of

the analyzed period (Table 2 and Figs. 2 and 3). In the period from 50 to 200 ms, the effect of domain in the semantic categorization task was opposite to the effect in the gender decision task, and so the domain \times task interaction was significant. In comparison with the artificial stimuli, the natural stimuli evoked greater positivity in the categorization task and less positivity in the gender decision task. These differences were significant only when the anterior electrodes were considered.

In the 250- to 450-ms window, and coinciding with N400, the differences between natural and artificial stimuli were quite similar in both tasks and occurred in interaction with electrode location. This interaction, which will later be analyzed over the rescaled amplitude measures, was due mainly to the greater positivity (or lesser negativity) provoked by the natural stimuli at posterior areas and by the artificial stimuli at frontal and prefrontal areas. In the 300- to 400-ms period, domain emerged as the main factor, natural stimuli eliciting less negativity than artificial stimuli. The two effects described above (50–200 ms and 250–450 ms) are shown in Fig. 4.

Finally, in the 450- to 600-ms period, a significant domain \times task effect was observed. Natural stimuli provoked more positive ERPs than artificial stimuli only in the categorization task.

The results of the ANOVAs performed over rescaled amplitudes showed overall significant domain \times electrode

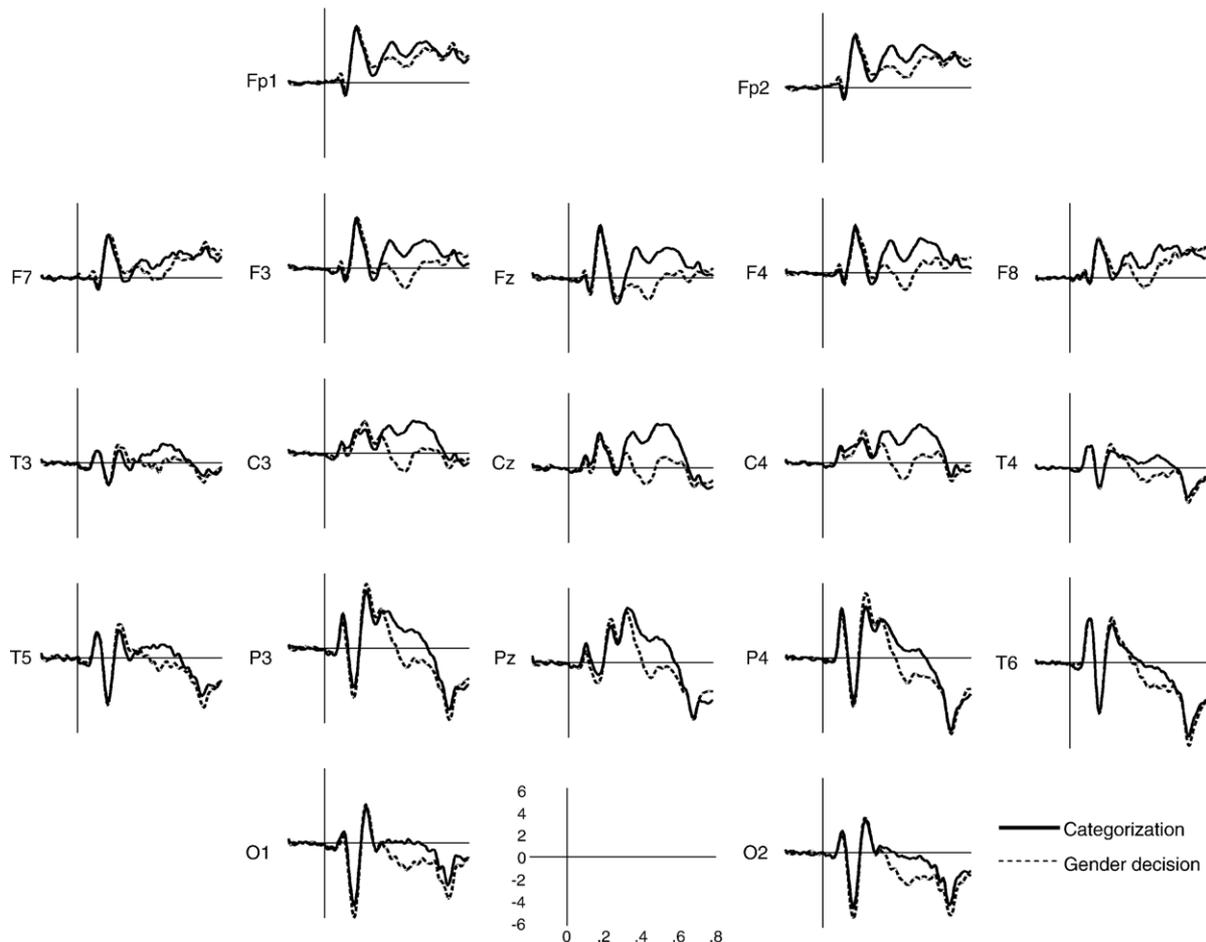


Fig. 1 – Grand average ERPs, averaged over responses to both natural and artificial stimuli, from the semantic categorization and the gender decision task.

Table 2 – Significant effects found in the three-way repeated averages ANOVAs performed over ERP mean amplitudes considering domain, task, and electrode as factors

Time windows	Domain	Task	Domain × Task		Domain × Electrode	Domain × Task × Electrode
			Ant	Post		
50–150			10.206 (1,19) 8.46 (0.005)	(>0.05)		
100–150			6.959 (1,19) 11.97 (0.016)	(>0.05)		
150–200			4.930 (1,19) 13.76 (0.039)	(>0.05)		
200–250					3.253 (2.866, 54.457) 8.06 (0.030)	
250–300					3.058 (3.073, 58.381) 6.85 (0.034)	
300–350	4.853 (1,19) 29.96 (0.040)	10.738 (1,19) 19.17 (0.004)			2.855 (3.041, 57.783) 8.19 (0.044)	2.974 (4.556, 86.562) 3.55 (0.019)
350–400	5.501 (1,19) 32.28 (0.030)	26.454 (1,19) 31.20 (<0.001)			4.274 (3.224, 61.263) 5.97 (0.007)	
400–450		49.970 (1,19) 27.48 (<0.001)				
450–500		36.804 (1,19) 36.32 (<0.001)	4.535 (1,19) 46.01 (0.046)			
500–550		27.320 (1,19) 32.28 (<0.001)	9.443 (1,19) 32.57 (0.006)			
550–600			4.899 (1,19) 38.17 (0.039)			

In each time window, we report *F* (and *df*) values, together with MSE and significance. For the first three time windows, we report the results of separate ANOVAs for anterior and posterior locations.

effects in the 250- to 450-ms period—that is, within the latency range of the N400 component ($F_s \geq 1.966$, $P_s \leq 0.05$). In general, the natural stimuli provoked more positive ERPs in posterior

and right areas, whereas positivity for the artifacts was greater in anterior right areas (see Fig. 5). Significantly greater positivity for the natural stimuli was observed at Pz [Fs

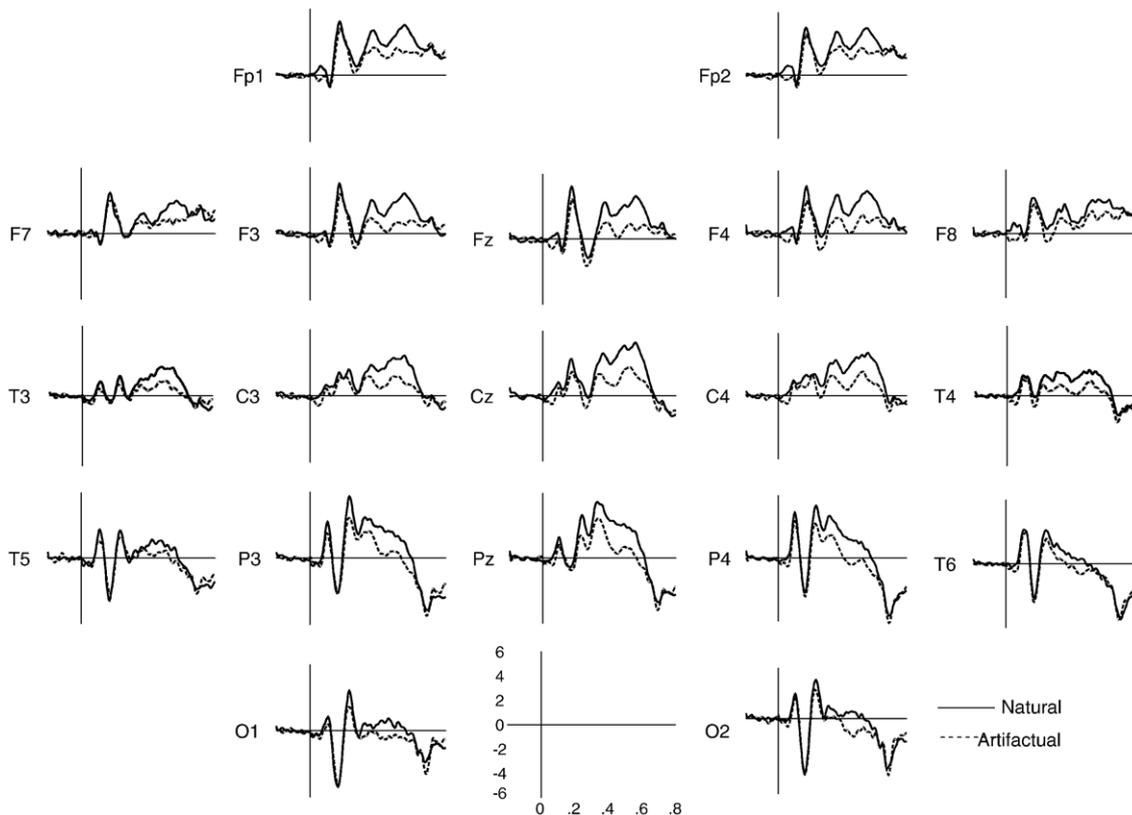


Fig. 2 – Grand average ERPs to natural and artifactual stimuli from the semantic categorization task.

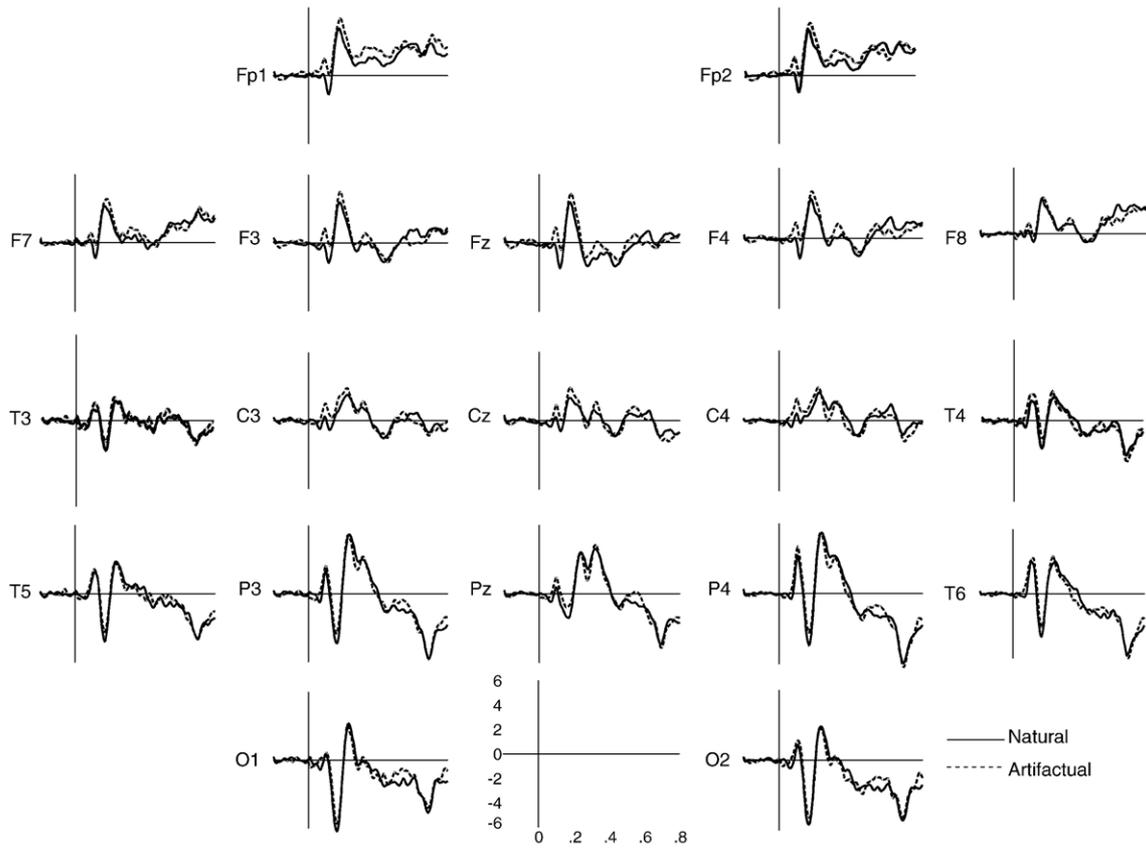


Fig. 3 – Grand average ERPs to natural and artifactual stimuli from the gender decision task.

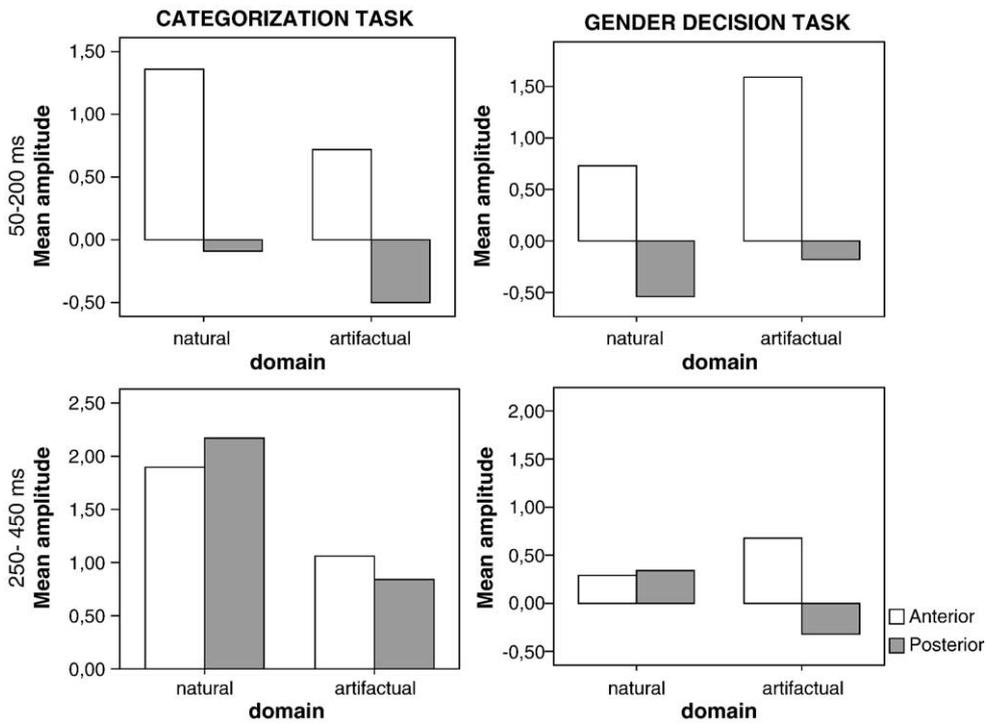


Fig. 4 – Mean ERP amplitudes associated with natural and artifactual stimuli of each task in the anterior (mean of Fp1, Fp2, Fz, F3, F4, F7, and F8) and posterior (mean of O1, O2, Pz, P3, P4, T5, and T6) electrodes. Means have been obtained for the 50-200-ms and the 250-450-ms time windows.

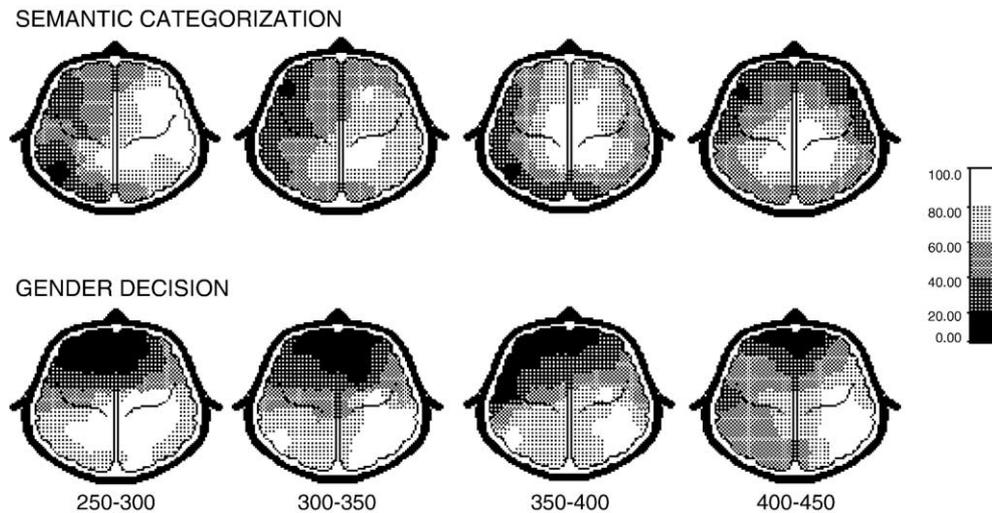


Fig. 5 – Scalp distribution of the natural-artifactual differences in the 50-ms time windows from 250 to 450 ms. Differences are shown on a percent scale.

(1,19) ≥ 5.12 , $P_s \leq 0.036$], P4 [$F_s(1,19) \geq 9.23$, $P_s \leq 0.007$], and C4 [$F_s(1,19) \geq 7.66$, $P_s \leq 0.012$] in all of the 50-ms windows between 250 and 450 ms. On the other hand, the artifactual stimuli provoked more positivity at Fp2 [$F(1,19) = 8.20$, $P = 0.010$] and F8 [$F(1,19) = 7.96$, $P = 0.011$] in the 400- to 450-ms period. Differences in scalp distribution of natural and artifactual stimuli were more evident in the gender decision task, although not significantly so (see Fig. 5).

In the time window of 350–400 ms, the domain \times electrode interaction was different for each task [$F(5.61,107.76) = 2.658$, $P < 0.001$]. Thus, in the semantic categorization task, the natural stimuli again elicited a larger positivity than the artifactual ones did in both the C4 [$F(1,19) = 9.19$, $P = 0.007$] and P4 [$F(1,19) = 4.51$, $P = 0.047$] electrodes. In contrast, in the gender decision task, differences between categories were also present in the left hemisphere. Thus, the greater positivity of the natural stimuli was located at the P4 [$F(1,19) = 5.75$, $P = 0.027$] and T5 [$F(1,19) = 15.24$, $P = 0.001$] sites, whereas the artifacts elicited more positivity at Fp2 [$F(1,19) = 6.34$, $P = 0.021$] and F7 [$F(1,19) = 7.15$, $P = 0.015$].

3. Discussion

The present work was aimed at analyzing the extent to which the differences in brain activation usually found between natural and artifactual categories reflect the different ways in which these categories are organized in semantic memory or are due rather to the differing perceptual processing required in each task. We have compared ERPs elicited by pictures of natural and artifactual objects in two tasks demanding different processing levels: a natural/artifactual categorization task and a gender decision task, the last involving a complete identification of the objects. We predicted that specific semantic domain effects must be identical in the two tasks, and that the existence of multiple semantic subsystems must be associated with a different scalp location of the ERPs corresponding to natural and artifactual objects. Consistent

with this prediction, pictures from natural and artifactual categories were found to elicit ERPs with different scalp distribution in the 250- to 450-ms period independent of task (i.e., there were similar domain-related differences in scalp topography in the two tasks). In addition to these domain specific effects, we observed natural/artifactual differences which were task dependent. Thus, our results support the assumption of different semantic subsystems with different neuroanatomical substrates, although they point to the need to control task-related effects that could explain some observations of the natural/artifactual dissociation.

Based on the perceptual explanation of domain effects (Humphreys and Riddoch, 1987; Lloyd-Jones and Humphreys, 1997a,b), we predicted that it would be easier to correctly categorize a stimulus as natural than as artifactual due to the greater perceptual similarity of natural stimuli. But precisely because of this greater perceptual similarity, items belonging to natural categories might be identified more slowly than item belonging to artifactual categories in tasks requiring finely graded distinctions between competing alternatives, as is the case in the gender decision task. Our performance data are in agreement with these predictions. RTs to natural stimuli were shorter than RTs to artifactual stimuli when the subjects performed a semantic categorization task. In contrast, no significant natural/artifactual differences in RTs were displayed in the gender decision task, though we observed a tendency for RTs to be longer for responses to natural stimuli. Some previous studies have likewise reported shorter RTs for natural compared to artifactual stimuli in superordinate categorization tasks (Price and Humphreys, 1989; Kiefer, 2001) but longer RTs in tasks demanding object naming or discrimination between very similar categories (Lloyd-Jones and Humphreys, 1997a,b).

In relation to the effect of domain on the ERPs, our results reveal difficulty-related and semantic effects. The first effects were task-dependent and consisted of quantitative (amplitude) differences between the wave-forms elicited by stimuli belonging to natural categories and those belonging to

artificial categories. Such differences were observed at very short latencies (50–200 ms) in the two tasks as well as in the pre-response period (450–600) in the categorization task. The first (early) differences were greater at anterior locations and affected the P180 component. In addition, the natural stimuli evoked wave-forms of greater amplitude than the artificial stimuli in the categorization task, whereas the opposite occurred in the gender decision task. These early differences seem to reflect an initial process of discrimination based on the physical features of the stimuli. In line with this possibility, it is known that stimuli with different contours provoke differences in the early components of visual ERPs, and that these differences are much more marked when contour constitutes a distinctive feature of the categories to be discriminated (Paz-Caballero and García-Austt, 1992). It is worth noting that the natural objects generally have more irregular and rounded contours than do artificial objects, and hence, natural objects share common physical features that make them distinguishable from artificial objects in the first perceptual stages of processing. In agreement with our findings, other authors have reported domain effects in the first 100 or 200 ms post-stimulus. As already mentioned, Van Rullen and Thorpe (2001) found a short latency (75–80 ms) difference between two semantic categories (vehicles and animals). Kiefer (2001) also found differences between natural and artificial categories in the 160–200 ms post-stimulus period, natural stimuli eliciting a larger N1 component at posterior electrodes. Unlike Kiefer, we found that natural stimuli elicited a larger P180 component at anterior locations, but such differences in polarity and scalp distribution may be attributed to the fact that we used a linked-mastoids reference, whereas Kiefer performed an average-reference transformation. Kiefer considered that the enhancement of the N1 component may occur, either because natural objects produce a greater activation of visual areas or because perceptual information plays a more important role in the processing of natural categories than in the processing of artificial categories when a superordinate categorization is required. The second interpretation seems to better fit our findings and could explain why the early differences between natural and artificial categories run in opposite directions in the categorization task and the gender decision task. Thus, the domain \times task interaction in our ERP findings, congruent with that found in our RT data, would reflect the different role that perceptual information plays in each task, visual features of natural stimuli being more informative than those of artifacts in the categorization task but less informative in the gender decision task. It should be noted that these early ERP differences between domains cannot be attributed to factors such as familiarity (which was the same for both domains) or visual complexity. Although the natural categories were visually somewhat more complex than the artificial categories, the influence of complexity on the domain effect found in ERPs of 50–200 ms was ruled out because the effect of domain in the gender decision task was in the opposite direction to that observed in the categorization task. The differences found seem to be due rather to the different demands of each task. Besides these early perceptual differences between domains, other difficulty-related effects with longer latency were observed in the categorization task. In the

pre-response period (450–600 ms), the stimuli from the natural domain elicited a significantly larger amplitude than those from the artificial domain that enhances the amplitude of the P600 component. This increase in the amplitude of P600 along with the significant decrease in the RTs associated with the natural stimuli may again reflect a lesser difficulty in the categorization of such stimuli as compared to the artificial stimuli.

Along with the quantitative differences between ERPs, there were differences in ERP scalp distribution between natural and artificial domains. These qualitative differences occurred between 250 and 450 ms, thus modulating the amplitude of N400, and they were generally independent of the task performed. Furthermore, as also found in the work of Kiefer (2005), such differences did not relate to performance differences. In both tasks, natural objects provoked greater positivity (that is, smaller N400) in parietal areas, whereas artifacts provoked more positive ERPs in frontal areas. This scalp distribution is consistent with that observed in previous works, including ERP studies (Kiefer, 2001), reports of patients with brain lesions (e.g., Warrington and McCarthy, 1983; Warrington and Shallice, 1984), and studies using neuroimaging techniques (e.g., Perani et al., 1995; Martin et al., 1996; Grafton et al., 1997; Moore and Price, 1999). Therefore, all available evidence strongly suggests that the natural and artificial domains have different neuroanatomical substrates. However, the laterality of domain effects we observed (mainly located in the right side) was, in part, different to that reported in previous studies. Generally, whereas brain activation associated with natural stimuli seems to be bilateral or right lateralized (e.g. Tranel et al., 1997; Kiefer, 2001, 2005) activity associated with the processing of artifacts is rather left lateralized (Gainotti, 2000). In our work, left hemispheric differences between the two domains were observed only in the gender decision task and in the 350- to 400-ms period, natural stimuli eliciting greater positivity at left posterior temporal sites and artifacts, in the left fronto-inferior area. The different scalp distributions of the effect of semantic domain for the semantic categorization and gender decision tasks in the 350- to 400-ms period could possibly be explained by the greater involvement of brain areas supporting language in the latter task, since gender decision entails lexical processes that are not necessarily involved in semantic categorization (Miceli et al., 2002). Using an object-naming task, Martin et al. (1996) also found that naming animals produced greater activity than naming of tools in the parieto-temporal areas of the left hemisphere. Another tentative explanation for the different hemispheric locations of brain activation for natural and artificial stimuli between tasks could be that suggested by Moore and Price (1999). According to these authors, differences in brain activation between natural and artificial stimuli in the right hemisphere could be produced by either a difference in semantic organization or a difference in processing difficulty. In the left hemisphere, however, the differences would be more consistent with functional specialization within the semantic system. This could explain the fact that, in the present work, natural/artificial differences occurred mainly in the right hemisphere in the semantic categorization task, in which significant differences in the RT measures, and hence differences in

difficulty levels, were also obtained between the stimuli in both domains.

Finally, it is important, in comparing our results with those of other authors, that we included in our study a number of different categories in each semantic domain. This is consistent with the procedure used by Kiefer (2001), but it contrasts with other previous work concerned with the natural/artificial dissociation in which only one of two categories of each domain have been included (e.g., animals versus tools, animals versus vehicles). The inclusion of several categories within each domain might well have resulted in a decrease or even an elimination of the differences between the two domains, since evidence from neuropsychological and neuroimaging studies suggests that natural and artificial domains are not homogeneous and can even overlap. In a review carried out by Gainotti (2000) involving 47 brain-damaged patients, some the patients who presented problems with natural categories also had problems with the category of musical instruments, and others, for whom artificial categories were compromised, had problems naming human body parts. Furthermore, Tyler et al. (2003a,b) found differences in cortical activation even between animals and other natural categories, such as fruits and plants, the activation of the latter being undifferentiated from that of artifacts. In general, those studies that have provided evidence in favor of a neurological dissociation between natural and artificial stimuli involved comparisons of only one natural category (specifically, animals) with one artificial category. Therefore, by using several categories within each of the two semantic domains, the results of the present study confirm and extend the neurological dissociation between natural and artificial stimuli previously demonstrated and argue for the existence of a semantic system organized according to different types of knowledge.

4. Experimental procedure

4.1. Participants

Twenty-four undergraduate students (12 men and 12 women) from the University of Oviedo, 18 to 27 years of age, participated in the experiment. The data of four subjects (one man and three women) were not considered because they did not meet the criteria for inclusion (see below). All the subjects were right-handed and had normal or corrected-to-normal vision.

4.2. Materials

The stimuli consisted of 120 line drawings taken from the Snodgrass and Vanderwart (1980) norms, half the pictures were drawings of natural objects (animals, plants, fruits, and human body parts), and the other half were of artificial, or man-made, objects (vehicles, tools, furniture, and musical instruments). Stimuli from natural and artificial domains were matched as closely as possible in relation to familiarity (mean \pm SD: 5.78 \pm 0.76 and 5.88 \pm 0.70, respectively) and word frequency (22.1 \pm 33.5 and 25.8 \pm 37.1, respectively), although the drawings of the natural objects were more visually complex than those of the artificial ones (2.97 \pm 0.9 and 2.39 \pm 0.8, respectively, $t_{111} = 3.55$, $P = 0.001$). Familiarity ratings were taken from the LEXESP database (Sebastian et al., 2000). Groups of subjects were asked to judge the degree to which they come in contact with or think about the object

represented by the word. A 7-point scale was used, on which 1 indicated “very unfamiliar” and 7 “very familiar”. Word frequency values, counted as occurrences per million words, were also taken from the LEXESP database and are based on usage in a corpus of written texts comprising five million words. Visual complexity values were taken from Sanfeliú and Fernández (1996), in which 59 subjects rated each drawing for its complexity on a scale from 1 (very simple) to 5 (very complex). Familiarity, word frequency, and complexity values for all the stimuli are reported in the Appendix.

The 120 stimuli were divided into two lists (List A and List B) of 60 drawings each. In each list, half the drawings were of natural objects, and the other half were of artifacts. Also, within each category, half the drawings had masculine names, and the other half had feminine ones. There were no between-list differences between the natural and artificial categories in familiarity or in word frequency. The pictures were presented in the center of the monitor screen, inside a virtual white frame measuring 10 \times 10 cm on a dark background. Each picture subtended 7.6° of horizontal and 7.6° of vertical visual angle. The presentation time of each stimulus was 200 ms, and the interval between the onsets of consecutive stimuli was 2200 ms.

4.3. Design

A 2 \times 2 factorial design was used, with repeated measures in the two factors. The factors were stimulus domain (natural versus artificial) and task (semantic categorization versus gender decision).

4.4. Procedure

The experiment was performed in an acoustically isolated chamber. The participants were seated comfortably at a distance of 80 cm from a computer screen with the forefingers of left and right hands placed on the “z” and “m” keys of the keyboard, respectively. They were asked to respond as quickly as possible with one of the two keys to classify drawings as a function of the demands of the task. In the semantic categorization task, they had to classify each of 60 drawings as either natural or artificial. In the gender decision task, the participants saw an additional 60 drawings and had to indicate whether the dominant name for the object was masculine or feminine. Half the participants were shown List A for the categorization task and List B for the gender decision task, the other half of the participant sample saw List B items for the categorization task and List A items for the gender decision task. The order in which tasks were administered was counterbalanced across participants, and the association between response type and response keys (hence the hand used for each response) was counterbalanced across tasks. Prior to the critical trials in each task, participants carried out several practice runs.

4.5. ERP recording

The EEG activity was recorded using an elastic cap with 19 electrodes placed on 19 leads (10/20 International System): Fz, Cz, Pz, Fp1/2, F3/4, C3/4, P3/4, O1/2, F7/8, T3/4, and T5/6. All were referenced to the left mastoid during recording; the right mastoid was also recorded, referenced to the left. The vertical electrooculogram (EOG) was recorded from the electrodes positioned between the left mastoid and the outer canthus of the left eye. The horizontal EOG was recorded from electrodes placed at the outer canthus of each eye. Impedance was kept below 10 K Ω .

The EEG and EOG signals were amplified by a 34-channel Medecid Neuronic polygraph and filtered between 0.05 and 30 Hz. An additional notch filter was used for 50 Hz. EEGs and EOGs were continuously digitized at 250 Hz per channel and stored on a Hewlett Packard Vectra VE (Pentium MMX, 200 MHz). For the acquisition and subsequent analyses of EEG and EOG signals, the

Track Walker (2.0) program was used. Data were re-referenced to the algebraic mean of the left and right mastoids. The recording epoch was 1000 ms (200 ms before and 800 ms after the stimulus). Each EEG segment was visually inspected off-line, and those with movement or ocular artifacts were eliminated. After the ERPs were obtained, reliability coefficients were obtained for each recording (via the two-half procedure). A minimum value of 0.75 was required. Four subjects who did not achieve this value were not included in the analyses.

4.6. Data analysis

The average amplitudes of the ERPs were obtained from the stimulus onset every 50 ms for each electrode and each domain of each task. These amplitudes were submitted to three-way repeated-averages ANOVAs with task, domain, and electrode as factors. The domain \times electrode interaction was analyzed after the linear transformation of the ERP amplitudes to a 0–1 scale was made (McCarthy and Wood, 1985), using deviation contrasts and the Greenhouse–Geisser correction. Because the early ERP components were different in the anterior and posterior locations, for windows prior to 200 ms separate ANOVAs were performed for posterior (O1, O2, P3, P4, T5, T6, Pz) and anterior (Fp1, Fp2, F3, F4, F7, F8, Fz, C3, C4, Cz, T3, T4) electrodes.

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Appendix A

Stimuli used and their scores on word frequency, familiarity, and visual complexity. Frequency and familiarity scores were taken from the LEXESP database (Sebastian et al., 2000). Scores on visual complexity were obtained from Sanfeliu and Fernández (Sanfeliú and Fernández, 1996).

Stimuli	Frequency	Familiarity	Visual complexity
Artichoke	1.0	4.64	3.120
Tree	55.0	6.67	3.950
Arm	95.5	6.64	2.20
Donkey	18.0	6.24	3.510
Horse	93.5	5.65	3.630
Goat	10.5	5.94	3.140
Gourd	3.0	5.41	2.120
Kangaroo	1.0	5.48	3.860
Snail	11.0	4.98	2.660
Onion	17.5	6.77	2.360
Zebra	2.5	4.6	*
Swan	5.0	5.42	3.070
Finger	65.5	6.36	2.390
Elephant	9.0	5.81	4.150
Star	47.5	5.66	1.190
Seal	5.0	5.85	2.860
Hen	18.5	6.23	3.410
Rooster	16.5	6.11	3.760
Gorilla	3.5	5.45	3.690
Worm	6.0	5.97	3.420
Ant	4.0	5.91	3.690

Appendix A (continued)

Stimuli	Frequency	Familiarity	Visual complexity
Giraffe	1.0	4.39	4.420
Lettuce	6.0	6.6	3.360
Lion	27.5	4.85	3.80
Lemon	5.5	6.45	1.370
Moon	79.5	5.88	1.140
Maize	14.0	6.14	3.470
Apple	11.5	6.5	1.540
Raccoon	0.5	4.29	4.250
Butterfly	7.5	5.95	3.530
Peach	1.0	6.14	1.490
Skunk	0.5	4.61	4.410
Monkey	24.0	5.85	3.710
Mountain	35.0	6.38	2.610
Fly	15.5	5.94	4.0
Orange	16.5	6.44	1.580
Nose	70.5	6.5	1.140
Nut	7.0	5.17	*
Eye	96.0	7	3.0
Ear	34.5	6.46	2.710
Bear	24.0	5.41	3.530
Sheep	5.0	5.88	3.460
Banana	3.0	6.36	1.340
Peacock	0.5	5.51	4.470
Clown	5.5	6.1	2.390
Fish	29.5	5.14	3.340
Foot	193.0	6.44	2.170
Leg	38.5	6.41	2.150
Pineapple	3.0	5.9	3.950
Thumb	13.0	5.7	1.970
Frog	5.0	5.78	2.150
Mouse	17.5	5.96	2.90
Rhinoceros	1.0	4.42	3.0
Grasshopper	1.5	5.67	2.240
Watermelon	1.0	5.77	4.390
Serpent	17.5	2.99	1.810
Mushroom	0.5	5.89	3.710
Tortoise	9.0	6.26	*
Cow	12.0	6.09	2.970
Fox	6.0	5.68	3.490
Mean	22.1	5.778	2.967
SD	33.5	0.7	0.9
Coat	39.5	5.55	2.540
Accordion	4.0	4.15	4.250
Needle	15.5	6	1.220
Ring	20.0	6.12	1.640
Harp	2.0	3.51	4.080
Bank	51.5	6.35	*
Bat	2.0	4.74	1.20
Pen	4.5	6.68	2.170
Button	25.0	6.49	1.460
Chain	60.0	6.55	2.310
Box	60.0	6.53	1.190
Bed	206.0	6.41	2.690
Truck	12.5	6.26	*
Bell	17.0	6.18	2.310
Brush	8.0	6.85	1.920
Basket	7.0	5.76	3.710
Tie	25.5	5.44	2.320
Knife	23.5	6.31	1.490
Thimble	0.5	5.35	2.220
Stairs	65.0	6.5	2.080
Broom	4.5	6.15	2.290
Flute	5.5	5.33	2.580
Guitar	18.5	5.67	2.780

Appendix A (continued)			
Stimuli	Frequency	Familiarity	Visual complexity
Helicopter	2.0	5.14	2.850
Jersey	10.0	6.42	2.730
Lamp	27.0	6.15	1.690
Pencil	10.0	6.16	1.680
Lime	0.5	5.32	1.980
Key	44.0	6.71	2.190
Gauntlet	0.5	5.25	2.030
Rocking chair	4.0	5.15	3.780
Meter	27.0	5.41	*
Wrist	16.0	6.25	3.850
Trousers	30.5	6.14	1.980
Umbrella	17.5	6.49	2.850
Ball	22.0	6.29	1.920
Hanger	6.5	4.63	1.170
Pimient	3.0	4.86	2.050
Pistol	25.0	5.37	3.170
Handle	2.5	5.33	2.240
Well	24.0	6.09	*
Cigar	66.0	5	2.850
Racket	2.0	6.76	3.190
Watering-can	0.5	5.55	3.310
Clock	71.0	5.93	2.120
Roller	1.5	6.44	4.020
Frying pan	4.0	6.1	3.120
Semaphore	6.0	5.69	*
On	0.5	6.19	2.190
Drum	11.0	6.39	2.220
Tart	8.0	6.94	2.250
Cup	23.0	5.38	2.420
Telephone	93.0	5.78	1.590
Tea-pot	2.0	6.76	2.20
Screw	2.5	5.32	1.660
Train	55.0	6.3	3.050
Nut	0.5	5.78	*
Glass	59.5	6.77	1.950
Candle	27.0	5.86	1.530
Window	162.5	6.1	2.920
Mean	25.8	5.885	2.393
SD	37.1	0.7	0.8

* Value not available.

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