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Highlights

- ERPs to picture pairs of animals, objects, and mixed types were presented
- Participants were asked to decide whether each pair contained pictures belonging to the same category
- C1 and P1 were modulated by same/different supracategory judgments but not by animal vs. object category
- Later N1 and N2 responses were modulated by stimulus semantic category
- Results revealed shared and distinct representations for supra–categorical and categorical knowledge

ERP signs of categorical and supra-categorical processing of visual information

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Key words: ERPs, semantic categories, supra-categorical knowledge, animals, man-made objects, N400, C1, early modulation, P1, selective attention

Abstract

Background The aim of the present study was to investigate to what extent shared and distinct brain mechanisms are possibly subserving the processing of visual supra-categorical and categorical knowledge as observed with event–related potentials of the brain. Access time to these knowledge types was also investigated. Picture pairs of animals, objects, and mixed types were presented. Participants were asked to decide whether each pair contained pictures belonging to the same category (either animals or man–made objects) or to different categories by pressing one of two buttons. Response accuracy and reaction times (RTs) were also recorded.

Results Both ERPs and RTs were grand–averaged separately for the same–different supra–categories and the animal–object categories. Behavioral performance was faster for more endomorphic pairs, i.e., animals vs. objects and same– vs. different–category pairs. For ERPs, a modulation of the earliest C1 and subsequent P1 responses to the same vs. different supra–category pairs, but not to the animal vs. object category pairs, was found. This finding supports the view that early afferent processing in the striate cortex can be boosted as a by-product of attention allocated to the processing of shapes and basic features that are mismatched, but not to their semantic quintessence, during same–different supra–categorical judgment. Most importantly, the fact that this processing accrual occurred independently of a traditional experimental condition requiring selective attention to a stimulus source out of the various sources addressed makes it conceivable that this processing accrual may arise from the attentional demand deriving from the alternate focusing of visual attention within and across stimulus categorical pairs' basic structural features. Additional posterior ERP reflections of the brain more prominently processing animal category and same–category pairs were observed at the N1 and N2 levels, respectively, as well as at a late positive complex level, overall most likely related to different stages of analysis of the greater endomorphy of these shape groups. Conversely, an enhanced fronto–central and fronto–lateral N2 as well as a centro–parietal N400 to man–made objects and different–category pairs were found, possibly indexing processing of these entities' lower endomorphy and isomorphy at the basic features and semantic levels, respectively.

Conclusion Overall, the present ERP results revealed shared and distinct mechanisms of access to supra–categorical and categorical knowledge in the same way in which shared and distinct neural representations underlie the processing of diverse semantic categories. Additionally, they outlined the serial nature of categorical and supra–categorical representations, indicating the sequential steps of access to these separate knowledge types.

1. Introduction

Empirical evidence for distinct cortical loci involved in the recognition of objects belonging to different semantic categories, e.g., natural vs. man-made objects, was initially provided by patient studies, in particular patients with visual agnosia (see Capitani et al. (2003) for a review). Subsequently, hemodynamic neuroimaging studies on healthy participants further investigated these distinctions, reporting involvement of bilateral inferior occipito–temporal regions during the recognition of natural objects and a left-lateralized pattern of activation in response to man–made objects, including the dorsolateral prefrontal cortex (dlPFC) (Perani et al., 1995; Martin, 1996; Cappa et al., 1998). Further, involvement of the left posterior middle temporal gyrus (MTG) was reported in response to tools; this region has been associated with the generation of action words and might therefore code the patterns of visual object movements (Martin et al., 1996; Damasio et al., 1996; Chao et al., 1999).

The neurofunctional mechanisms underpinning the representation of these categories in the brain could not be precisely determined because the specific loci of enhanced activation vary depending on the type of task participants perform and on the specific stimulus features (e.g., Cappa et al., 1998; Moore and Price, 1999; Joseph, 2001). For example, Rogers et al. (Rogers et al., 2005) asked participants to categorize pictures of animals and vehicles according to 3 levels of specificity animal vs. vehicle, bird vs. ship or finch vs. yacht. When participants had to decide whether an animal was a bird and a vehicle was a ship, enhanced activation of the posterolateral fusiform gyrus was found for animals compared to vehicles. Instead, the same region was activated to the same extent by both animals and vehicles when participants performed the more specific categorization task, i.e., deciding whether each animal was a finch and whether each vehicle was a yacht (Rogers et al., 2005). The authors proposed that more perceptual differentiation was needed for animals than vehicles in the former, less-specific task because animal shapes are more homogeneous (i.e., homomorphic) than vehicle shapes; therefore, it is more difficult to categorize an animal as bird than a vehicle as ship because vehicles have greater shape variability. Nevertheless, in the latter task, when it was time to decide whether each animal was a finch and whether each vehicle was a yacht, finer perceptual discrimination among vehicles was needed, and this led to similar processing demands for the two semantic categories. In another study, Proverbio et al. (Proverbio et al., 2007) found faster and more accurate responses to animals than man–made objects in a task requiring selective attention to either semantic category (i.e., respond to either pairs of animals or man–made objects while ignoring the other category and a mixed–type pairs); in this case, the greater shape similarity (i.e., homomorphy) of animals facilitated their direct categorization. The aforementioned studies and some others (e.g., Gerlach et al., 2004; Chao et al., 1999; Moore and Price, 1999; Gerlach et al., 2004) led to the proposal that visual recognition of different object classes depends on the organizational principles of semantic knowledge rather than on semantic category membership *per se* (Tranel et al., 1997a). Organizational principles include shape similarity, i.e., homomorphy, familiarity, value for the perceiver, affordance, characteristic motion, sensory modality of transaction (i.e., vision, touch, or hearing) and age of acquisition (Tranel et al., 1997a).

More recently, empirical evidence from neuroimaging and computational studies has shown that different object categories elicited the activation of distinct brain regions depending on the perceptual or functional features that are specific to each category (Goldberg et al., 2006, O'Toole et al., 2005; Proverbio, 2012).

Therefore, categories that share some features, e.g., fruits and vegetables, which are both characterized by color and shape, will elicit enhanced activation of common, i.e., overlapping, cortical areas (Goldberg et al., 2006; Pulvermüller et al., 2009; Pourtois et al., 2009). In computational terms, object categories are represented by partially distributed activation patterns in which the physical features of the categories are reflected at the level of the ventral temporal cortex; here, different object categories will share a neural substrate when they share common features (O'Toole et al., 2005).

1.1. Time course of semantic categories processing

Because of the high temporal resolution of event–related potentials (ERPs), this technique has been used by researchers to investigate the time course of semantic category processing. In categorization studies investigating ERP discrimination between non-human and non-face-like visual concrete entities of different sorts, the response most consistently reported falls at the N1 level (~150 – 200 ms), a visual ERP component with occipito–temporal scalp distribution that has been shown to be modulated by selective attention. Indeed, the N1 amplitude has been shown to be significantly larger in response to animals compared to fruit/vegetables (Ji et al., 1998) and to animals compared to man–made objects (Kiefer, 2001; Proverbio et al., 2007) during direct categorization tasks, i.e., voluntarily deciding whether either a picture belongs to a specific semantic category or whether two concurrently or subsequently presented pictures belong to the same category.

Studies of face processing with respect to other concrete entities have challenged these findings. Indeed, the literature about ERPs to faces compared to other visual stimulus categories has indicated large variations in face processing onset. In different studies, this onset varied among the N1 (or N170) occipito-temporal component (e.g., Bötzel et al., 1995; Itier and Taylor, 2004; Proverbio et al., 2006), the P1 level (e.g., Herrmann, et al., 2005; Proverbio et al., 2006), and 50 – 80 ms post-stimulus (e.g., Seeck et al., 1997). In trying to resolve these discrepancies in the findings across different studies, some more recent investigations asked samples of volunteers to discriminate between pictures of faces and cars (e.g., Rossion and Caharel, 2011) or faces and houses (e.g., Rousselet et al., 2008), counterbalanced for luminance and other visual features, presented in both their intact and phase–scrambled versions or in their upright or inverted versions, respectively. These studies found a larger P1 to pictures of faces than to cars or houses, independent of shape versions. Conversely, a later N170 component was shown to be larger for faces than cars, but for the intact shape versions only and for both upright and inverted houses. The finding of an early P1 to faces was explained as a brain response to low–level differences in stimuli visual cues, and their N170 effects were explained as a reflection of a face perception or categorization stage. Overall, then, these studies elucidated the idiosyncrasies in the literature and indicated that the N170 (or N1) represents the true ERP signature of the categorization of face–like content of concrete entities as has been found for analogous contrasts between other animate and inanimate categories.

The research has also provided evidence of a larger amplitude for an anteriorly–distributed N2 component (200 – 260 ms) in response to man–made object pairs than to animal pairs (10). In our view, this effect may reflect the allocation of enhanced processing resources for less homomorphic shapes, such as, for instance, the shapes of man–made objects, which are more variable and distinct from each other than are animal shapes. This proposal is at least partly in line with usual reports of this component in picture–matching tasks. More specifically, the N2 has shown a larger amplitude in response to target stimuli that differ from a picture prime compared to either identical targets (Wong et al., 1998) or to both sequentially presented (Wong et al., 2004) or simultaneously presented (Ruiling et al., 2013) picture pairs that differ in one perceptual feature (either shape or color) vs. none. For this reason, it is reasonable to think that this component may index an automatic, pre–semantic detection of feature mismatch in the stimulus material administered (Pritchard et al., 1991; Ruiling et al., 2013).

A later negativity, indexed by the N400 component (~300 – 500 ms), also showed larger amplitude to man–made object pairs than to animal pairs over fronto–central electrodes (Proverbio et al., 2007), to mixed animal–artefact distracters in an attended location over parietal electrodes (Zani and Proverbio, 2012), to tools compared to animals at fronto–centro–parietal sites (Sitnikova et al., 2006) and to semantic intra– and extra–categorical violations (Federmeier and Kutas, 2002). Nevertheless, N400 responses to non–words compared to real words in lexical decision paradigms have also been reported (e. g., Lau et al., 2008). Therefore, its enhanced response to less similar picture pairs resembles that found for lexical deviants processing (see paragraph 1.3 for a more thorough explanation of this similarity). It is probable, then, that this component may index neural processing related to the perceptual awareness of stimulus violation or incongruence with respect to a previous context at a deeper semantic level of analysis, as derived from the previous automatic detection of a mismatch in the incoming stimulus features (Kutas and Hillyard, 1980; Ruiling et al., 2013).

Later–latency positive components also showed effects of semantic categorization. A larger amplitude and higher peak of the P300 component over posterior electrodes (~300 – 400 ms) in response to animals than to fruit/vegetables

(Ji et al., 1998) as well as to pairs of animals than man–made objects (Proverbio et al., 2007) were reported; in addition, the latter contrast also showed a larger amplitude at a still later latency, namely, on the late positive component (LPC; 450 – 520 ms) (Proverbio et al., 2007). These positivities are typically elicited by stimuli that appear with low probability and must be categorized, thus reflecting a process of "context updating;" they also seem to index the evaluation of a stimulus aimed at its categorization and recollection from a mental representation in memory (Donchin and Coles, 1988; Proverbio and Zani, 2003). Their amplitudes and latencies usually correlate with the reaction times in categorization tasks (Proverbio and Zani, 2003; Polich, 2007), i.e., the larger their amplitude and the earlier their latency, the faster the reaction times. In the context of semantic category discrimination, larger positivities to animals may index enhanced processing of more homomorphic and therefore better matching stimuli.

1.2. Early visual processing of semantic categories

In the studies reviewed above, no modulation effects of semantic category for C1 and P1 components – originating in the striate and extra–striate visual cortices, respectively – were reported. These studies compared ERPs to different categories when each one of them was task–relevant, e.g., participants were asked to respond to animals only (ignoring other categories) vs. man–made objects only (Proverbio et al., 2010). Nevertheless, a modulation of C1 and P1 components was recently reported in response to these same stimulus pairs when task–relevant compared to when task–irrelevant, independent of stimulus category (Zani and Proverbio, 2012).

Evidence from previous single unit recordings and recent source reconstruction techniques supports precocious modulation of striate cortex (V1) by spatial and non–spatial attention (e.g., Proverbio et al., 2010; Motter, 1993). Functional magnetic resonance imaging (fMRI) findings further indicated attentional tuning of striate cortex activity (e.g., Ghandi et al., 1999; Kastner et al., 1999) and extended this tuning to the sub-cortical thalamic lateral geniculate nucleus (LGN – O'Connor et al., 2002). Unfortunately, fMRI does not have a temporal resolution sufficient to tell at which time this tuning may occur.

Relatively recently, however, high time-resolution recordings of single cell earliest activity have been obtained showing that besides the primary occipital cortex, spotlight attention modulates neuronal processing of visual information even before it arrives in this area. Indeed, spatial attention boosted the activation of the thalamic LGN and, on the other hand, decreased the activation of the adjacent reticular nucleus (TRN – McLonan et al., 2008). In line with these findings, most recently, evidence has been reported that attention finely tunes neuronal communication of the LGN at the synaptic level by selectively increasing the efficacy of presynaptic input for driving postsynaptic responses (Briggs et al., 2013).

Still, it must be added that a most recent study using a difficult task based on the recognition of perceptually masked objects reported a late ERP modulation of feature-based attention to object shape, starting from "252-502 ms" post-stimulus (Stojanoski and Niemeier, 2014). For truth sake, however, it must be noted that in the "Discussion" the authors argued both that "… earliest sensory processing effects are not inconceivable, even for shapes." and that "… the most likely reason for [our] late effects is that the incompleteness of our stimuli requires the visual system to extract shape information likely based on multiple iterations."

1.3. Same-different judgment and supra-categorical processing

The same/different decision task was first introduced by Posner and coworkers (Posner et al., 1967, 1969) and involved presentation of a series of letter matching-mismatching decisions. By means of this paradigm, these authors discovered the general rule that every match decision is less task demanding than a mismatch decision for our brain. Indeed, “same” reaction times (RTs) have generally been found to be faster than “different” RTs for both mnemonic and discrimination tasks (Posner et al., 1969). Most of the models propose that a fast identity report, perhaps based on template or image matching, underlies “same” responses whereas a slower feature-by-feature comparator is responsible for “different” responses. Indeed a match-mismatch comparison can be carried out at either purely perceptual or semantic level.

In order to make a same/decision task, object stimuli have first to be recognized as belonging to a given semantic category, either on the basis of purely sensory or perceptual features (e.g., presence/absence of legs, presence/ absence of face-like objects, etc.), and/or on the basis of associated information (“a furniture is a non living entity” according to the semantic knowledge). Therefore, the task of deciding whether two objects belong to the same or a different category is however a higher order task, fed by the output of an implicit access to semantic knowledge, but distinct in nature and neural bases.

Therefore, the same/different decision is thought to reflect an higher-order cognitive process not having much to do with visual object processing or access to object semantic processing, the latter being subserved by the ventral stream, and in particular by the inferior and middle temporal cortex. In this sense, supra-categoric and categorical processing should result in anatomically, functionally and temporally segregated patterns.

According to the available ERP literature, the same/different decision for same objects is reflected by P300 component of ERP, whereas for different objects is reflected by N400 response, regardless of stimulus nature and sensory modality. Indeed, this negative-going deflection of ERPs that peaks around 400 milliseconds post-stimulus onset, although it can extend from 250-500 ms, has been found in response to mismatching phonemic stimuli (e.g., syllables; Proverbio et al., 2003), to incongruent action images (e.g., human gestures; Proverbio et al., 2014) and orthographic stimuli (e.g., letters; Palmer et al., 1994), as well as auditory stimuli (e.g., sounds; Aramaki et al., 2010). Therefore, it is thought that the N400 component might represent a supramodal index of conceptual processing reflecting a difficulty in integrating incoming information with previously acquired information (in this case, sensory input and their putative (shared or not shared) semantic domain of belonging. This components is typically maximal over centro-parietal electrode sites and tends to have a small but consistent bias to the right side of the head when visual presentation is used (Kutas et al., 1988; Lau et al., 2008). Also, the surface distribution of N400 to deviance is not related to stimulus material *per se*, since it has been shown for typical visual processing and also for auditory processing, for example of musical sounds (Koelsch et al., 2005)

Some neuroimaging and electromagnetic studies have identified the neural generators of the semantic N400 response to deviance (see a thorough review in Dien et al., 2010). For example, Nobre and McCarthy (1995) and McCarthy et al. (1995) recorded field potentials from isolated non-words and anomalous sentence-ending words using intracranial recordings and found a large negative field potential with a peak latency near 400 ms (N400), which was focally distributed bilaterally in the anterior medial temporal lobe (AMTL). More recent intracranial electroencephalographic studies (Dietl et al., 2008, Fell et al., 2004, Meyer et al., 2005) have identified potential N400 sources in the bilateral AMTL (using auditory and visual sentences). In contrast, MEG studies (Laine et al., 2000, Maess et al., 2006, Mäkelä et al., 2001, Service et al., 2007, Simos et al., 2002) have pointed towards the middle temporal gyrus (MTG)/superior temporal gyrus (STG) region, while some other MEG studies (Helenius et al., 1998, Helenius et al., 1999) have indicated that both the AMTL and the MTG/STG are sources for the N400 semantic incongruence effect.

It has been noted that the N400 tends to have a more anterior distribution when elicited by pictures or actions than when elicited by words. These anterior negativities in the range of the N400 are assumed to reflect action-specific semantic processing (Amoruso et al., 2013). The activation of motor and premotor cortex during action comprehension and motor related-information processing could take into account the frontal distribution of N400 responses to incongruent body patterns or movements actions that have been observed in action processing studies (Proverbio and Riva, 2009).

1.4. Semantic categories processing and features homomorphy

Similarly to the evidence for shared and distinct cortical representations for different semantic categories, higher–order categories (e.g., same vs. different category membership of picture pairs) can also share some features with specific semantic categories. For example, same category picture pairs may overall be more homomorphic than different–category pairs, as animal pairs have shown to be more homomorphic than man–made object pairs. Indeed, findings in the literature indicated that the low–level information characterizing faces, eyes and body parts (mostly the limbs) of animate beings facilitates rapid homomorphic trait detection because of their steeper spatial frequency amplitude spectrum changes than those of inanimate entities (Keil, 2008**),** which in turn, have been noted to be characterized by more rectilinear features **(**Tranel et al., 1997b) and more energy in vertical and horizontal (or 'cardinal') directions compared to animate entities (Torralba and Oliva, 2003) (see Figure 1 for some examples of entities belonging to these categories).

Independent of these experimental findings, it must to be noted that homomorphism can be classified according to different criteria, among which are the mapping of the relationship between the two domains and the nature of the mapping. In this regard, the artefact category is much more varied in the conformance of its elements than the animated elements are, the former varying from a lowest spatial frequency spectrum and highest cardinal conformance (such as, for instance, the case of a 'pen' in the Figure 1a) up to a steeper spatial frequency spectrum and somewhat lower cardinal conformance (such as the case of a 'bicycle' with respect to an 'easy–chair' in Figure 1a). Therefore, the homomorphism of this category to itself (or *endomorphism*) is doubtless lower than that of the animated category, notwithstanding there may be some extreme idiosyncratic examples in the latter category, such as for instance, a snake and a wolf, or a caterpillar and a spider. From this, it follows that it is not easy to provide robust measures of homomorphism because when attempting to map it between the two categories, assigning to each element in the animals domain a hypothetical value with respect to the artefacts codomain, or, in other terms, when performing a 'one–to–one' mapping, the *core* of the homomorphism between these two categories (or *isomorphism*) may change as a function of the set of elements of the former category that are mapped to the identity of the latter category (e.g., the ‘wolf’ with the ‘pen’ or the ‘easy–chair,’ on the one hand, and the ‘cat’ with the ‘bicycle,’ on the other, in Figure 1a). Additionally, it also follows that on the one hand, (1) to some extent, category grouping does not straightforwardly coincide with categorical elements’ homomorphy (or endomorphism; see also (Tranel et al., 1997a)), just as on the other hand, (2) the isomorphism of the different–category pairs is overall lower than that for both the two separate domains (i.e., same–categories), notwithstanding the gross changes in the endomorphism level across the different shape pairs of this supra–category (e.g., the ‘pen–lamb’ pair, on the one hand, and the ‘cat–bicycle’ pair, on the other hand, in Figure 1a).

5. The present study

The main aim of the present study was to explore the time course of access to conceptual knowledge by investigating whether supra—categorical and category–specific knowledge share similar electrophysiological activations or differ in that respect.

We devised an experimental paradigm in which we presented pairs of animals, man–made objects, and mixed pictures, either in the LVF or in the RVF, and asked participants to decide for each pair whether the two pictures belonged to the same semantic category or not by pressing one of two buttons. We hypothesized that to make this decision, attentional resources had to be directly allocated onto the pairs’ supra–categorical representations (i.e., same– vs. different–category pairs) rather than onto the specific semantic category identity representation (i.e., animals vs. man–made objects) within same–pairs.

Given this task, we predicted a faster performance for same–category pairs than for different–category pairs and, similarly, for animals than for man–made objects because of their overall relatively higher endomorphism. Further, we predicted similar patterns of electrophysiological responses for both types of more isomorphic pairs (i.e., same–category and animal pairs), indexing lower processing demand, compared to less isomorphic pairs (i.e., different–category and man–made object pairs).

As long as paying selective attention to relevant compared to irrelevant information was mandatory for the modulation of the earliest sensory activity, we did not expect to find any effects. Conversely, if this selection mode was not necessary, and, as suggested by the literature, attentional allocation demand alone was required for such a modulation, we predicted early ERP components to be tuned only by supra-categorical discrimination. We advanced this prediction because of the voluntary, task–specific allocation of attentional resources for this discrimination but not for the implicit access to category semantic essence.

As for the later conceptual processing, we expected higher N400 responses and lower LPC responses, respectively, for the different–category pairs than for same–category pairs and, similarly, for man–made objects than for animals because of their overall relatively lower endomorphism. Further, we predicted similar patterns of later-latency electrophysiological responses for both types of more isomorphic pairs (i.e., same–category and animal pairs), indexing lower processing demand, compared to less isomorphic pairs (i.e., different–category and man–made object pairs).

2. Methods

2.1 Participants

Twelve young and healthy right–handed adults (5 women and 7 men), 23 to 31 years old (*M* = 26, *SE* = 2.4) with normal or corrected–to–normal vision and no neurological diseases took part in the experiment. Participants did not receive any monetary reward. The study was approved by the ethics committee of the Italian National Research Council (CNR) and was conducted in accordance with APA (American Psychological Association, 1992) ethical standards for the treatment of human experimental volunteers (Helsinki, 1964). Furthermore, the experiments were conducted with the understanding and the written consent of each participant in compliance with the indications of the Declaration of Helsinki (BMJ 1991; 302 1194.)

2.2 Materials

Four hundred forty–eight pairs of black and white pictures representing natural objects (animals) and man–made objects were used. Stimulus pairs included 224 mixed pairs (one animal and one man-made object) and 224 matched-category pairs, half of which were animals and half of which were man–made objects. Within each pair, the two pictures were aligned on the vertical axis (see the lower portion of Figure 1a for some examples of stimulus pairs). Half of the mixed–pairs showed an animal in the upper visual field and a man–made object in the lower visual field and vice versa for the remaining pairs. The brightness of the stimulus pairs was measured in candela/m^2 (mixed pairs M = 17.81; equal pairs M = 17.73; animal pairs M = 17.78; man–made object pairs M = 17.68) and was matched across conditions ($F(1,11)$ = 0.09, p = .77). Furthermore, as

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indicated by Proverbio et al. (2007), shape complexity and familiarity ratings were obtained by administering a 5–point scale questionnaire to a group of 20 college students not involved in the cited ERP study. Ten of the students rated the familiarity of all stimuli (randomly mixed) before rating their complexity, and the remaining 10 rated the complexity of all stimuli before rating their familiarity. Access to verbal or semantic properties of items was not required. For the complexity rating scale, 5 = very complex, 4 = fairly complex, 3 = neither complex nor simple, 2 = fairly simple, and 1 = very simple. For the familiarity rating scale, 5 = very familiar, 4 = fairly familiar, 3 = neither familiar nor unfamiliar, 2 = not very familiar, and 1 = unfamiliar. One–way ANOVA did not yield any difference in the complexity ratings of animals (M = 3.1986) and artifacts (M = 3.1318). Conversely, a separate ANOVA yielded a moderate but significant lower familiarity rating for animals (M = 3.2761) than for artifacts (M = 3.6208; F (1, 19) = 13.548; p < 0.001).

2.3 Procedure

The experiment was conducted at the Cognitive Electrofunctional Imaging Lab of the Institute of Molecular Bioimaging and Physiology, National Research Council, Segrate (Milan), Italy. The InstEP software package (InstEP Inc., Ottawa, Canada), run on a local network made up of a two personal computers (PCs), was used for stimulus presentation and EEG data recording as well as for offline analysis. Participants were seated in an electrically and magnetically shielded room (Faraday cage) in front of a CRT screen at a distance of 3.34 feet (or 114 cm) from the screen. The black–and–white pictures were presented on a white background. They were randomly flashed in the left or right visual hemifields beginning at 2.5 degrees of eccentricity from the vertical meridian, centered on the horizontal meridian. Each picture of the pair began stimulation 1.5 deg above or below the horizontal meridian, so that, overall, each pair subtended 7.5 (Height) x 4.5 (Width) degrees of visual angle (see Figure 1b). Stimulus pairs were presented during 8 runs, each containing 56 stimuli and lasting approximately 1½ minute. The visual hemifield in which the pairs would have appeared, the order of presentation of the pairs, the position of the animal or of the man–made object in the upper visual field for the mixed pairs, and the order of the runs were all randomized across trials and participants. Each stimulus pair was presented for 350 ms with an inter–stimulus interval (ISI) of varying duration between 1000 and 1300 ms. The EEG and electro–oculogram (EOG) signals were continuously recorded during each run.

Participants were instructed to stare at a screen central fixation cross during the recording, to not move and to avoid horizontal eye–movements and blinks. The task consisted of deciding whether each pair contained pictures belonging to the same semantic category (either animals or man–made objects) or to different semantic categories (i.e., mixed pairs) by pressing either a button with the index finger for same–category pairs or another button with the middle finger for different–category pairs. The hand used for the response (right or left) was alternated across runs. To familiarize participants with the task, a few practice runs were presented before the experiment started, each containing 30 stimulus pairs.

2.3.1. EEG recording

Electroencephalograms (EEGs) were continuously recorded from scalp electrodes mounted in a 64-electrode ECI elastic electro–cap. Only 30 electrode scalp-sites were used. The electrodes were located at frontal (Fp1, Fp2, Fz, F3, F4, F7, F8), central (Cz, C3, C4), temporal (T3, T4), posterior temporal (T5, T6), parietal (PZ, P3, P4), and occipital (O1, O2) scalp sites of the 10–20 System devised by Jasper (1958) for the International EEG Federation. Additional electrodes based on the later 10–10

System were placed at an anterior frontal site (AFz), halfway between frontal and central sites (FC1, FC2, FC5, FC6), central and parietal sites (CP5, CP6), parietal and occipital sites (PO3, PO4), and posterior temporal and occipital sites (OL/PO7, OR/PO8). Vertical eye movements were recorded by two electrodes placed below and above the right eye, and horizontal eye movements were recorded by electrodes placed at the outer canthi of the eyes. Linked ears served as the reference lead, whereas an electrode included in the cap between Fp1 and Fp2 but 0.6 inch (1.5 cm) below them was used as a ground site.

The EEGs and EOGs were amplified with a half–amplitude band pass of 0.16–50 Hz or 0.02–50 Hz, respectively. Amplifier gain for the EOG was 0.5 times that for EEG. Electrode impedance was kept below 5 kΩ. Continuous EEGs and EOGs were digitized at a rate of 512 samples/sec. The preparation and experiment lasted 1 hour overall.

2.4 Data analysis

Two different statistical designs were used for data analysis one considering the categorical sameness (or supra–categorical processing), in which different–category pairs and same–category pairs were compared, and the other considering the semantic category, in which the pairs of animals vs. pairs of man–made objects were compared (see the upper part of Figure 1a for a rough description of these analysis designs).

2.4.1. EEG averaging. Offline, automated rejection of electrical artifacts was performed before EEG averaging to discard epochs in which eye movements, blinks, or excessive muscle potentials occurred. The artifact rejection criterion was a peak–

to–peak amplitude exceeding +/– 90 µV for EEG signal or +/−120 µV for EOG signal, and the rejection rate was ~3.9 %. ERPs were averaged offline from 200 ms (i.e., 102 digitized points) before stimulus onset to 800 ms (i.e., 410 digitized points) after it. EEG epochs in the averages were synchronized with the onset of stimuli presentation. For each subject, distinct ERP averages were obtained according to stimulus category (i.e., animals and man–made objects) and supra–category (i.e., same–category and different–category). EEG sweeps related to incorrect behavioral responses (i.e., errors, FAs, and omissions, misses) were also discarded from averaged ERPs, amounting, on average, to an overall 17.15 % (*SE* = 1.54) of rejected trials per participant. Average ERPs were then grand–averaged across the participant sample.

No baseline correction across ERP waveforms and no digital filtering were used. Indeed, although the average and grand–average ERP waveforms showed some relatively high–frequency noise, we decided not to apply any offline digital filtering. This because of the reports in the literature identifying the frequencies up to 30 – 35 Hz, most specifically, those frequencies in the alpha (8 – 14 Hz) and beta (15 – 35 Hz) bands, as mechanisms by which visual selective attention is deployed (e.g., Rihs et al., 2009; Capotosto et al., 2009; Banerjee et al., 2011).

ERP components were identified and measured with reference to the baseline voltage averages over the interval from –200 ms to 0 ms relative to stimulus onset. Topographical scalp current density (SCD – i.e., second spatial derivative of the potential) maps were computed from the spherical spline–interpolation of the surface voltage recordings between scalp electrodes at specific latencies. These SCD maps were plotted as rainbow colors scale–coded current density values per square–meter (µV/m^2) over the scalp.

2.4.2. Categorical sameness or supra-categorical processing. Motor response latencies were analyzed by means of repeated-measures ANOVA with 3 factors categorical sameness (same vs. different), visual field (left vs. right) and response hand (H, left vs. right). Reaction times (RTs) exceeding or lagging behind the mean by +/– 3 *SDs* were excluded from the analyses. Errors and omissions, calculated in percentages, were transformed in ϕ (arcsin) degrees and analyzed with two separate repeated–measures ANOVAs with supra–categorical decision as the only factor.

ERP components were analyzed by means of repeated–measures ANOVAs whose factors were categorical sameness (CS: same vs. different), visual field (VF: left vs. right), electrode (E: 2 or more levels, depending on the specific component of interest), and hemisphere (Hem: left vs. right). The latter factor was not present in the case of non–lateralized electrodes. For post–hoc comparisons among means, Tukey’s HSD and Fisher’s LSD tests were used.

After visual inspection of the ERPs and based on the typical scalp distribution of specific ERP components, the time windows between 60 and 90 ms and between 90 and 120 ms were chosen for the measurement of the mean amplitudes of the C1 and P1 components, respectively, over mesial– (O1 and O2) and lateral–occipital sites (OL/PO7, OR/PO8) as well as parietal-occipital (PO3 and PO4), posterior–temporal (T5 and T6) and parietal sites (P3 and P4; see Figure 2) electrode sites. As for the C1 component, it is known that due to the crossed visual field vs. retinotopic organization of early–level visual pathways, this early occipital response can have either a positive– or negative–going polarity as a function of stimulus retinal location across the horizontal meridian of the visual field. Less known is, instead, that this polarity–reversal is also seen as a function of stimulation across the vertical meridian of the visual field, in that it is usually more negative ipsilaterally to the visual stimulation hemifield independent of stimulus lateralization, as indicated by several classical studies. In addition, its amplitude changes as a function of the physical features of visual stimulus patterns, such as for instance, spatial frequency, luminance, and visual stimulation field size. Most importantly, however, this component predominates at midline and mesial–occipital as well as parieto–occipital electrode sites with respect to more lateral occipito–temporal sites. Empirical evidence has also shown that this is true independent of quadrant of stimulation across the horizontal meridian (see, for instance, some classical studies by Lesévre 1982, Bodis-Wollner et al. 1992, or Zani and Proverbio 1997, besides the more recent ones by, for instance, Ales et al., 2010 and Zani and Proverbio 2012), and that often, despite this ipsilaterality, this "elusive" component is largest over the right or left hemispheres as a function of stimulus material utilized (e.g., gratings or checkerboards vs. words). We referred to these indications as support for having soundly identified and measured a true C1 component.

In addition to the earlier C1 and P1 components, the peak amplitude of the longer–latency N1 was automatically measured in the 120-180 ms latency range at the same electrode sites. Furthermore, the peak amplitude of the N2 component was also measured between 230 and 340 ms at these same posterior electrode sites (see Figure 2 again for all these components). Furthermore, the mean amplitude of an N2 and an N400 components was also measured between 230-340 ms and 350-470 ms, respectively, over the centro-parietal midline sites (Cz and Pz; see Figure 5). To investigate any hemispheric asymmetries, the amplitude of these superior scalp components was also measured in the aforementioned latency ranges at the homologous parietal (P3 and P4), central (C3 and C4, dorsolateral prefrontal (F3 and F4) dorsolateral inferior prefrontal (F7 and F8), and frontopolar electrodes (Fp1 and

Fp2; see Figure 5). Again, the mean amplitude of the LPC was measured between 530 and 730 ms over the same electrode sites for investigating scalp distribution and potential hemispheric asymmetries for this late latency processing (see Figure 5 again).

2.4.3. Semantic category processing. The same analyses were carried out for behavioral and ERP data when considering the factor of variability between the semantic categories (animals vs. man–made objects) instead of supra–categorical (same vs. different) processing. Furthermore, the visual field factor was not considered in the analyses of ERP data. The mean amplitudes were computed in the time windows between 60–90 ms and 90–120 ms post-stimulus of category–related ERP averages for the C1 and P1 components at the same electrodes as for the supra–category–related ERPs. Again, N1 peak amplitude and the N2 mean amplitude were measured between 120 and 180 ms and 230-340 ms, respectively at the same posterior electrodes (see Figure 7 for all these components).

Furthermore, the mean amplitudes of the N2 and N400 components were measured at the same parietal–frontopolar homologous electrodes examined for the supra-category–related ERPs (see Figure 9) between 230 and 340 and between 350 and 470 ms, respectively. Finally, the peak amplitude of the LPC was measured in the same 530 and 730 ms latency window at these same parietal–frontopolar electrodes (see Figure 9 again).

ERP measures obtained this way were statistically analyzed by separate repeated–measures ANOVAs. For the earlier C1, P1 and N1 components, as well as the positive-negative complexes, the ANOVAs had semantic category (C: animals vs. objects), hemisphere (Hem: left vs. right) and electrode (E: the same posterior scalp electrodes as those considered for the supra-category processing) as factors.

Conversely, for the N400 amplitude data two further separate ANOVAs were carried out: one for the data obtained at the parietal‒central midline electrodes (i. e., Pz and Cz), with category and electrode as factors, and the other ANOVA with the addition of the hemisphere factor to the category and electrode (i.e., parietal-frontopolar sites) factors.

3. Results

Statistical results of interest for categorical sameness and semantic categorical processing are reported separately for supra-categorical (Same vs. Different) and categorical (Animals vs. Objects) processing.

3.1. Categorical sameness or supra-categorical processing

Motor responses. In all, considering the percentage of errors and misses, volunteers had a rather good supra–categorization performance of 83.67 %. A significant main effect of categorical sameness (F(1,11) = 48.10; p<0.00001) showed faster RTs to same–category pairs (Mean (*M*) = 594 ms; Standard Error (*SE*) = 12 ms) than to different–category pairs (*M* = 653 ms; *SE* = 13 ms). However, a main effect of visual field resulted in slower RTs to stimulus pairs presented in the LVF (*M* = 632 ms; *SE* = 13 ms) than in the RVF (*M* = 615 ms; *SE* = 14 ms), independent of their categorical sameness. No significant differences in either FAs (i.e., same–category pairs judged as belonging to different categories and vice versa) and missed response rates across supra–category pairs were found. Overall, these rates amounted to 15.02% and 3.37%, respectively, for same-category stimulus pairs and 15.44% and 4.76%, respectively, for different-category stimulus pairs.

3.1.1. C1 component. The ANOVA demonstrated a main Electrode factor, in that this earliest negative–positive–going electrical response varied significantly as a function of Electrode site (F(4,44) = 9.76 p < 0.0001). Post-hoc contrasts proved that the negativity was overall more pronounced over mesial–occipital (*M* = 0.42 µV, *SE* = 0.53) and parieto-occipital (*M* = 0.75 µV, *SE* = 0.48) sites than over the lateral–occipital (*M* = 1.28 µV, *SE* = 0.41), the posterior–temporal (*M* = 1.61 µV, *SE* = 0.37) and the parietal sites (*M* = 0.92 µV, *SE* = 0.35; see Figure 2). In addition, in full agreement with the available literature on the polarity inversion across the horizontal and vertical meridians of the visual field, at the mesial-occipital and parietal-occipital electrode sites the negative–going activity was greater over the hemisphere ipsilateral to the stimulus visual field as opposed to the positive–going response being larger contralaterally, independent of stimulus category. This pattern, which can be clearly observed in Figure 3, was supported by a significant three–way interaction between visual field, hemisphere and electrode (F(4,44) = 13.71; p<0.00001).

Most importantly for our comparison of categorical sameness, however, this negative–positive activation of posterior scalp sites was demonstrated to be robustly affected by the interaction of this factor with the hemisphere and electrode ones (F(4,44) = 4.62; p < 0.005). Indeed, post-hoc analyses showed a greater negative–going activation in response to same–category pairs compared to different–category pairs at the mesial-occipital (Same: *M* = 0.10 µV, *SE* = 0.33; Different: *M* = 1.25 µV, *SE* = 0.29), parietal-occipital (Same: *M* = 0.64 µV, *SE* = 0.47; Different: *M* = 1.12 µV, *SE* = 0.38) and lateral-occipital sites (Same: *M* = 1.43 µV, *SE* = 0.43;

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Different: *M* = 1.89 μV, *SE* = 0.40), but not at the posterior-temporal and parietal electrode sites, over the right hemisphere. This findings were also supported by the series of scalp current density (SCD) difference maps computed every 5 ms during the 60-90 ms temporal window plotted in Figure 4.

3.1.2. P1 component. The ANOVA yielded a significant interaction between supra-category processing, hemisphere and electrode (F(4,44) = 3.77; p< 0.025) in this latency range. Tukey post-hoc tests showed that the amplitudes of this relatively long–latency positivity for both the different–category and same–category pairs obtained over the left-sided mesial-occipital (Different category: 0.90 μV, SE = 0.81; Same category: *M* = 0.41 μV, *SE* = 0.99, respectively; see Figure 2) and parietal–occipital sites (Different category: 1.72 μV, SE = 0.91; Same category: *M* = 0.91 μV, *SE* = 0.99, respectively; see Figure 2 again) were significantly larger than those recorded over the right-sided homologous mesial-occipital sites (Different category: 0.71 μV, SE = 0.91; Same category: *M* = 0.55 μV, *SE* = 0.97, respectively), and parieto-occipital sites (Different category: 0.71 μV, SE = 0.91; Same category: *M* = 0.55 μV, *SE* = 0.99; p<0.025 and p<0.001, respectively). This was supported by SCD time-series maps plotted every 5 ms during the latency range of this component shown in Figure 4. This finding might potentially be related to the persistence in this latency range of the earlier, parallel negative–going activation in response to the supra-category pairs, which intermingled with, as well as partly cancelled, the more lateralized volume–conducted positive–going activity at these more mesially-located scalp sites over the right hemisphere.

3.1.3. N1 component. Although the peak of this component proved to be significantly higher over the right (*M* = –1.77, *SE* = 1.01) than the left hemisphere (*M* = –0.82, *SE* = 0.53), as demonstrated by the significant effect of the main Hemisphere factor ($F(1,11) = 9.73$, $p < 0.01$), the ANOVA did not yield any significant main supra–categorical effect.

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3.1.4. Posterior N2 component. The categorical sameness factor significantly interacted with both the hemisphere and electrode factors ($F(4,44) = 3.16$; $p < 0.025$), pointing out an overall greater amplitude of the N2 at the parietal, mesial-occipital, and parietal-occipital electrodes than at the lateral-occipital and posterior-temporal electrode sites. More importantly, the Tukey's HSD post-hoc contrasts for this three-way interaction also revealed that, with the exception of the left parietal location, all the other left-sided electrode sites showed a greater negativity to the same–category pairs than to the different–category pairs (Mesial-occipital: Same, *M* = –1.43 µV, *SE* = 0.71 // Different: *M* = –0.62 µV, *SE* = 0.79; Parietal-occipital: Same, *M* = –0.32 µV, *SE* = 0.71 // Different: *M* = 0.96 µV, *SE* = 0.79; Lateral-occipital: Same, *M* = 0.32 µV, *SE* = 0.89 // Different: *M* = 1.32 µV, *SE* = 0.79; Posterior-temporal: Same, *M* = 0.64µV, *SE* = 0.87 // Different: *M* = 1.92 µV, *SE* = 0.79). Conversely, these findings revealed to be not true for none of the right-sided electrode locations (see Figure 2).

3.1.5. Anterior N2 component.

3.1.5.1. N2 at midline Cz and Pz electrodes. The category sameness factor interacted with the electrode factor ($F(1,11) = 6.91$; $p < 0.025$). Post-hoc contrasts showed that the different shape -pairs elicited larger N2 than the same shape-pairs at the Cz ($p < 0.01$) but not at the Pz electrode site.

3.1.5.2. N2 at lateral homologous electrodes. Besides other findings, a significant interaction of supra-categorical processing factor with the electrode factor (F(4,44) = 3.18; $p < 0.05$) was found, indicating an overall greater amplitude of the N2 to the different- than to the same-category pairs at the fronto-lateral (Same: *M* = –1.53 µV, *SE* = 0.79; Different: *M* = –0. 99, *SE* = 0.83), and central electrode sites (Same: *M* = –2.42 µV, *SE* = 0.83; Different: *M* = –1. 39, *SE* = 0.98), but not at the other scalp sites.

3.1.6. N400 component.

3.1.6.1. N400 at midline Cz and Pz electrodes. The ANOVA carried out on the data measured at the midline electrodes, yielded a significant main Electrode factor (F(4,44) = 3.39; $p < 0.025$), in that this component was significantly greater over the Cz site (*M* = –6.02 µV, *SE* = 0.99) than the Pz (*M* = –2.23 µV, *SE* = 0.86) site as can be seen in the ERP waveforms displayed in Figure 5. There was also a main effect of category sameness (F(1,11) = 5.01; $p <0.05$) indicating that different–pairs (*M* = –4.59 µV, *SE* = 0.76) reached a larger amplitude than the same–category pairs (*M* = –3.85 µV, *SE* = 0.75). However, there was an interaction effect between category sameness and visual field (F(1,11) = 6.05; $p < 0.05$) and post-hoc Tukey contrasts revealed that a higher N400 to different–category pairs (*M* = –4.26 µV, *SE* = 0.98) than to same–category pairs (*M* = –2.64 µV, *SE* = 0.86) was present for the LVF (Tukey's HSD, $p < 0.025$) but not for the RVF (Different category *M* = –2.75 µV, *SE* = 1.23; Same category *M* = –2.61 µV, SE = 0.72).

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3.1.6.2. N400 at lateral homologous electrodes. The ANOVA carried out on the lateral electrodes showed that there was a significant supra-categorical effect (F(1,11) = 6.78; $p < 0.025$) in that the amplitude of the N400 was larger for the different pairs (*M* = –4.16 μV, *SE* = 0.89) than for the same pairs (*M* = –2.36 μV, *SE* = 0.71). As for the analysis for the midline centro-parietal sites, there was also a significant interaction between the category sameness and the visual field of pairs presentation (F(1,11) = 5.18; $p < 0.05$). Post-hoc analysis showed that the amplitude of N400 for the different–category pairs was larger than for the same–category pairs for both the LVF (Different category, *M* = –3.89 μV, *SE* = 0.54; Same category, *M* = –1.92 μV, *SE* = 0.75; Tukey's HSD, $p < 0.01$) and the RVF (Different category, *M* = –3.19 μV, *SE* = 0.98; Same category *M* = –2.23 μV, SE = 0.78; Tukey's HSD, $p < 0.05$). However, the post-hoc analyses also showed that the amplitude of the N400 to the different pairs was larger for the LVF than for the RVF (Tukey HSD, $p < 0.01$), whereas the amplitude to the same pairs was not. Most interestingly, the hemisphere and electrode factors interacted significantly (F(4,44) = 4.89; $p < 0.005$). Post-hoc analyses revealed that the amplitude of this component was significantly larger for the different category than for the same category at the left-sided central (C3) electrode (Different category, *M* = –4.52 μV, *SE* = 0.87; Same category, *M* = –2.77 μV, *SE* = 0.95; Tukey's HSD, $p < 0.01$), whereas this same difference was significantly prominent at the right-sided parietal (P4) scalp location (Different category, *M* = –3.90 μV, *SE* = 0.91; Same category, *M* = –1.77 μV, *SE* = 0.65; Tukey's HSD, $p < 0.01$; see Figure 5 again). The time series topographical SCD maps support this distribution focused in the central-parietal scalp areas (Figure 6) and progressively spreading from the left-sided central areas toward the midline central-parietal areas, and, again, toward the right-sided parietal scalp region.

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3.1.7. LPC.

3.1.7.1. LPC at midline Cz and Pz electrodes. A main categorical sameness effect was obtained (F(1,1) = 9.71; p < 0.01) reflecting the generally greater late positivity to different shape pairs (*M* = 2.57 µV; *SE* = 0.77) than to same shape pairs (*M* = 1.61 µV; *SE* = 0.82). In addition, a main effect of electrode sites was found (F(1,11) = 6.93; p < 0.025), which was associated with the fact that both the different– and same category–pairs elicited larger LPC amplitudes at the central (*M* = 4.10 µV; *SE* = 0.69) than at the parietal electrode site (*M* = 2.45 µV; *SE* = 0.74).

3.1.7.2. LPC at lateral homologous electrodes. A significant main effect of categorical sameness (F(1,11) = 6.64; p < 0.05) showed larger amplitudes of this late–latency brain activation for different–category (*M* = 3.36 µV; *SE* = 0.85) than for same–category (*M* = 1.57 µV; *SE* = 0.63) pairs (see Figure 5). Most importantly, post–hoc comparisons for a significant four–way interaction between categorical sameness, visual field, hemisphere and electrode (F(4,44) = 2.94; p < 0.05) clearly indicated a larger response to ipsilateral than to contralateral stimuli, which was much more pronounced at the left fronto–polar and frontal-inferior electrode sites, for the different–category pairs only.

3.2. Semantic categories processing

We report in this and the following paragraphs the results for the analyses relative to the processing of implicitly accessed knowledge of stimulus pairs' semantic category for behavioral and brain electrophysiological indices.

Motor responses. The subdivision of the percentage of correct same–category decisions as a function of the two shape categories revealed faster RTs to animal pairs (*M* = 564 ms, *SE* = 13) than to man–made object pairs (*M* = 626 ms, *SE* = 19; F(1,11) = 61.09; p< 0.00001). This perceptual advantage for the animate category was further supported by performance accuracy data showing a significantly lower amount of both decision errors (F1,11) = 57.34; p < 0.00001) and misses (F(1,11) = 5.12; p< 0.05) for that category (*M* = 7.7%, *SE* = 1.58 and *M* = 0.9 %, *SE* = 1.13, respectively) than for man–made object pairs (*M* = 24.2 %, *SE* = 2.43 and *M* = 2.11 %, *SE* = 1.52, respectively).

3.2.1. C1 component. Notwithstanding the lower positive amplitude shown at mesial–occipital electrodes than at the other electrodes, as supported by the ANOVA's significant electrode factor (F(4,44) = 7.22; p< 0.001), brain activation in the latency range of this component did not statistically differ between semantic categories (Figure 7). The topographical SCD maps computed on the animals minus objects categories difference-waveform strongly support the lack of any difference in the activation level between these categories in this latency range (Figure 8).

3.2.2. P1 component. Also for this component, the ANOVA did not yield any significant difference between the semantic categories. Also in this case, the topographical SCD maps computed on the animals minus objects categories difference-waveform did not show any different activation in this latency range between the two categories (Figure 8). Unlike for the C1 component, however, its amplitude was higher at both the lateral–occipital and parietal-occipital sites than at the mesial–occipital, posterior-temporal and parietal electrodes (see Figure 7 again). In addition, a significant hemisphere x electrode interaction was obtained (F(4,44) = 2.83; p< 0.05), the amplitude of this component being larger at the RH than at the LH at the lateral-occipital (RH: *M* = 3.20, *SE* = 1.01; LH: *M* = 2.48, *SE* = 1.13, respectively; Tukey's $p < 0.025$) and posterior-temporal sites (RH: *M* = 2.91, *SE* = 1.01; LH: *M* = 1.72, *SE* = 0.99, respectively; Tukey's $p < 0.01$).

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3.2.3. N1 component. Consistent with behavioral data, this component showed a significantly higher peak in response to animals (*M* = –2.27 μV, *SE* = 0.89) than to man–made objects (*M* = –1.27 μV, *SE* = 0.94), as pointed out by a main effect of the category factor ($F(1,11) = 6.81$; $p < 0.01$) and as can be seen in Figure 7. However, there was a 3-way interaction of category x hemisphere x electrode ($F(4,44) = 3.27$; $p < 0.025$). Post-hoc analyses showed that this interaction was produced by the fact that, unlike the objects category, the animals category produced a greater N1 response over the RH that the LH at all the posterior electrodes but the parietal one (see Figure 7 again).

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3.2.4. Posterior N2 component. A significant interaction of categorical processing factor with the electrode factor ($F(4,44) = 2.88$; $p < 0.05$) was found, pointing out an overall greater amplitude of the N2 at the parietal, parietal-occipital and lateral-occipital electrodes than at the mesial-occipital and posterior-temporal electrode sites. More importantly, the Tukey's HSD post-hoc contrasts for this interaction revealed that, with the exception of the posterior-temporal locations, all the other electrode sites showed a greater negativity to the object-category pairs than to the animal–category pairs (see Figure 7).

3.2.5. Anterior N2 component.

3.2.5.1. N2 at midline Cz and Pz electrodes. The ANOVA yielded a significant main categorical processing effect (F(1,11) = 4.90; $p < 0.05$). **A**s can be seen in the ERP waveforms displayed in Figure 9, this component was significantly greater for the object-pairs (*M* = –6.46 μV, *SE* = 0.77) than for the animal-pairs (*M* = –3.79 μV, *SE* = 0.86).

3.2.5.2. N2 at lateral homologous electrodes. The ANOVA showed a highly significant categorical effect (F(1,11) = 10.14; $p < 0.01$) in that the amplitude of the N2 was greater for the object pairs (*M* = –5.98 μV, *SE* = 0.69) than for the animal pairs (*M* = –3.78 μV, *SE* = 0.72). In addition, there was an interaction of the categorical processing with the electrode factor (F(4,44) = 3.92; $p < 0.01$). Post-hoc contrasts showed that, overall, the amplitude of N2 to objects was larger than that to animals at all the electrode sites but the fronto-polar ones (Figure 9 again). Furthermore,

these contrasts indicated that the N2 was overall larger over fronto-lateral, central and parietal sites than inferior-frontal and fronto-polar sites.

3.2.6. N400 component.

3.2.6.1. N400 at midline Cz and Pz electrodes. The ANOVA yielded a significant main categorical processing effect (F(1,11) = 4.90; $p < 0.05$). **A**s can be seen in the ERP waveforms displayed in Figure 9, this component was significantly greater for the object-pairs (*M* = –6.03μV, *SE* = 0.81) than for the animal-pairs (*M* = –3.92 μV, *SE* = 0.79).

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3.2.6.2. N400 at lateral homologous electrodes. The ANOVA revealed a highly significant categorical effect (F(1,11) = 10.14; $p < 0.01$) in that the amplitude of the N400 was greater for the object pairs (*M* = –5.21 μV, *SE* = 0.79) than for the animal pairs (*M* = –3.136 μV, *SE* = 0.88). A significant main effect of electrode was also obtained (F(4,44) = 3.92; $p < 0.01$). Post-hoc contrasts showed that, overall, the amplitude of N400 obtained at the fronto-lateral, central and parietal electrodes was larger than that obtained at the inferior frontal (F7, F8), fronto-polar (Fp1, Fp2), and parietal electrodes (P3, P4; see Figure 9 again). The scalp distribution for this component is also supported by the SCD maps plotted in Figure 10, which show a focus centered in the lateral-frontal scalp areas that progressively spreads bilaterally towards the central scalp regions, and, still more backwards, toward the parietal ones.

3.2.7. LPC component.

3.2.7.1. LPC at midline Cz and Pz electrodes. A main categorical processing effect was obtained (F(1,11) = 9.74; $p < 0.01$), reflecting the generally greater positivity to the animal-pairs (*M* = 4.05 μV, *SE* = 0.91) than to the object-pairs (*M* = 2.98 μV, *SE* = 0.89), as can be seen in the ERP waveforms displayed in Figure 9. In addition, a significant main effect of electrode (F(1,11) = 6.72; $p < 0.025$) was found indicating a greater amplitude of LPC at the Cz electrode site (*M* = 5.27 μV, *SE* = 0.88) than the Pz site (*M* = 4.01 μV, *SE* = 0.84).

3.2.7.2. LPC at lateral homologous electrodes. A significant categorical processing x electrode interaction revealed to be highly significant (F(4,44) = 6.27; $p < 0.001$). This interaction was produced by the fact that, overall, animals attained a larger LPC than artifacts, and the response to these categories at central (Animals: *M*

= 5.64 μV, *SE* = 0.59; Objects: *M* = 3.31 μV, *SE* = 0.68) and lateral-frontal sites (Animals: *M* = 5.63 μV, *SE* = 0.63; Objects: *M* = 4.42 μV, *SE* = 0.72) was higher than that shown by the inferior-frontal (Animals: *M* = 4.22 μV, *SE* = 0.66; Objects: *M* = 3.11 μV, *SE* = 0.72) and fronto-polar sites (Animals: *M* = 3.61 μV, *SE* = 0.75; Objects: *M* = 2.21 μV, *SE* = 0.69), besides the parietal sites (Animals: *M* = 4.82 μV, *SE* = 0.71; Objects: *M* = 2.81 μV, *SE* = 0.80), as clearly visible in the ERP grand–average waveforms plotted in Figure 9. Categorical processing ($F(1,11) = 7.02$; $p< 0.025$) and Electrode main effects ($F(4,44) = 4.87$; $p < 0.01$) were also found.

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4. Discussion

The aim of the present study was to examine the time course of brain activation during direct access to supra–categorical and indirect category–specific conceptual knowledge. In this way, no overt selective attention to the specific semantic category was required; hence, any discrimination between animals and man–made objects would index implicit access to conceptual knowledge. Given the category–matching task used, we expected to find that more isomorphic and endomorphic pairs (shapes with more similar features; i.e., same–category pairs and animals) were easier to categorize than less isomorphic and endomorphic pairs (i.e., different–category pairs and man–made objects with less similar characteristics). As predicted, it turned out that more endomorphic picture pairs were more easily and accurately categorized, as reflected by faster reaction times to same–category than to different–category pairs and by faster reaction times and lower omissions and errors to animals than to man–made objects. We believe that in some way, this pattern of results provides support to the supposed greater endomorphy and isomorphy of the same–category with respect to the different–category shape pairs as well as for the animate and inanimate pairs. Again, it is important to consider here that although categorical knowledge discrimination was not directly measured in the present study, the obtained pattern of results for indirect categorical knowledge access was consistent not only with that found by our group in a previous study, where, conversely, the access to this knowledge was dealt with directly (see Proverbio et al., 2007), but also with that reported by other studies (Ji et al., 1998; Kiefer, 2001).

ERP data showed a difference in the way different–category and same–category pairs were processed at the earliest C1 sensory level and early sensory–perceptual P1 level (i.e., starting as early as 60 ms post-stimulus). Indeed, the higher positivities found in the latency ranges of these components in response to different–category than to same–category pairs suggests a task–related, top–down modulation of visual sensory–perceptual processing. This modulation is most likely related to the overall increase of attentional resources demanded by the comparison of the low–level structural features of the pairs belonging to different categories that were more difficult to categorize because of both their low endomorphism and isomorphism.

Modulation of the C1 and P1 components by attentional resource deployment to supra–categories is a novel finding and adds to previous evidence of modulation of these same components by the selective deployment of attentional resources onto relevant semantic categories (independent of their animate or inanimate content) compared to when semantic category is irrelevant in an overall less attention–demanding task (Zani and Proverbio, 2012). The present finding is also supported by recent connectivity studies showing the integration of information from distant locations in the visual field at the striate cortex level through enhancement by visual selective attention of cortico-cortical functional coherence between otherwise functionally separate areas (Haynes et al., 2005). However, the present findings are dissimilar to Zani and Proverbio's (2012) findings of more negative amplitudes of C1 and P1 for visual entity categories (independent of their animate or inanimate content) when task–relevant compared to when task–irrelevant. It must be considered, however, that unlike in Zani and Proverbio's (2012) study based on a space–category conjoined attentional selection where targets were a single–category–based small portion of the trials, the present study adopted a more attention–demanding task in which all trials were targets that required a decision–making and a motor response.

We believe that the finding that the visual system may show signs of distinguishing between pairs' supra–categories at an early 60–90 ms processing latency does not mean that it has reached the complete recognition of the shape-pair's different categories at a semantic level. Indeed, this result may simply indicate that the system has begun the selective processing of shapes pairs' shallow information at an entry level required as a prerequisite for identifying and attributing them to a same or different category by means of later latency perceptual decisions, the latter being most likely based on diverse, successive degrees of accumulation of salient information and different time scales. In our view, this proposal is supported by the findings of early latency face ERPs reported in the literature (e.g., Itier and Taylor, 2004; Proverbio et al., 2006; Herrmann et al., 2005; Seeck et al., 1997; Rossion and Caarel, 2011; Rousselet et al., 2008) besides by our present findings. This would be consistent with both the views that basic–level categorization at a shallow physical–code level is an entry level of processing that precedes stages of categorization at a deeper semantic–code level (Grill-Spector and Kanwisher, 2005) and that conscious perception is possible only with recurrent processing of stimulus inputs (Roelfsema et al., 2002).

Most importantly, however, the aforementioned processing mechanisms, together with those accumulated by parallel lines of research on perceptual and attentional mechanisms, may explain how the same–different judgment may be efficiently performed before the processing of a stimulus–pair's semantic category. Indeed, counter to traditional views of object detection and categorization, research over the past few years has shown that stimulus material manipulations, such as image degradation and stimulus inversion, impair categorization at a more basic level but not object detection (e.g., Mack et al., 2008). In addition, other studies have also shown that objects can often be successfully detected without being successfully categorized (e.g., de la Rosa et al., 2011). In addition, and most fascinatingly, several recent studies have also demonstrated effects of feature–based attention on the processing of stimuli of which the participants were not at all aware (e.g., Schmidt and Schmidt, 2010), in line with the view proposed by different sources that different neurophysiological processes underlie perception, attention and awareness (e.g., Lamme, 2005).

The lack of any finding of significant differences at these earliest processing stages for the animate (animal) and inanimate (objects) categorical contrasts seems also to suggest that notwithstanding the acknowledged low–level endomorphic and isomorphic differences characterizing these two categories (e.g., Keil, 2008; Tranel et al., 1997b; Torralba and Oliva, 2003), the visual system does effortlessly process this different low–level information at a similar level as the physical–code is concerned. It is only when enough visual information has been extracted that the shape pairs are attributed to the separate categories to which they belong at the longer N1 latency.

Most importantly, however, the lack of any differences either at the earliest C1 or at the later P1 stages showed that at these shallow levels of processing, the animate entities category may elicit patterns of neural processing differing from those elicited by a face-specific category, most likely because the low–level features of the former category are somehow less endomorphous and have a less steep spatial frequency spectrum than do those of the latter category *per se*. In support of this viewpoint, there are no findings in the literature of ERPs discriminating between animate and various types of inanimate entities earlier than the N1 component (e.g., Proverbio et al., 2007; Ji et al., 1998; Kiefer, 2001), as conversely reported for face processing (e.g., Itier and Taylor, 2004; Proverbio et al., 2006; Seeck et al., 1997; Rossion and Caharel, 2011; Rousselet et al., 2008).

A further relevant finding concerns the enhanced implicit response to the animate compared to the inanimate category between 120 and 180 ms, as reflected by the N1 accentuation. This response would index a relatively early discrimination of semantic categories based on access to conceptual knowledge, with this access apparently being facilitated for the biologically salient category, namely, animals. This result replicates Kiefer's (Kiefer, 2001) findings as well as previous findings by Proverbio et al. (2007) and Ji et al. (1998), who directly compared pictures of animals with pictures of fruits and vegetables.

Overall, our findings extend the aforementioned results by suggesting that at this stage of processing (i.e., N1), animate and inanimate category discrimination may be somehow achieved independently of explicit full processing of their semantic representations, even in the absence of selective attention voluntarily paid to a specific category.

A similar enhanced response was found over posterior occipito-temporal sites at a later N2 processing stage. Indeed, this component had a larger amplitude in response to same–category pairs compared to different–category pairs. This difference was significant over the LH only, and, apparently, mainly involved the aforementioned scalp regions of this hemisphere. This might very probably reflect a greater activation of the LH ventral stream. This latter result seems to be fully consistent with the findings by Proverbio et al. (2004), who identified the posterior occipito-temporal regions of the left hemisphere as the possible locus of processing of conjoined knowledge about perceptual entities' canonical attributes, such as for instance, color (e.g., yellow) and shape (e.g., a banana).

When compared to the finding of greater N1 to animal pairs at the posterior scalp, our N2 result at this same scalp area seems to suggest the existence of distinct mechanisms of access to supra–categorical information as a function of analysis levels. Indeed, at a shallow level of sensory analysis, the emergence of an entry–knowledge of supra–category would occur at the earliest processing stages (i.e., C1), the reason for this being, most likely, the allocation of further attentional resources onto the perceptual discrepancy at this level. Conversely, at a deeper level of processing, the access to the conscious knowledge of the semantic identity of the shapes belonging to different categories – or to a supra–category – would occur at a later latency (i.e., N2) than that found for discerning the identity of a same semantic category (i.e., N1). This might be due either to the higher relevance of category–matching visual exemplars (Wang et al., 1998) or to the fact that supra–categorical concepts are created ad–hoc during the task depending on the specific semantic categories involved, rather than being based on relatively stable memory representations or neuronal networks (as is the case for specific semantic categories) ang et al., 2007).

Following these electrophysiological responses of the posterior brain, two divergent processing streams for both same vs. different and animal vs. man–made object discriminations were identified (1) a sequence of ERP components with negative polarity, including fronto–central N2 and N400, with larger amplitudes to man–made objects than to animals, as well as a centro–parietal N400 component with larger amplitude for different–category pairs than for same–category pairs as well as a frontal LPC with a larger amplitude for same-category pairs than for different–category pairs. It might be possible that these two streams reflect some neurofunctionally distinct mechanisms. On the one hand, the negative components may in sequence reflect an automatic, pre–semantic detection of basic features' relative incongruence or mismatch (i.e., N2), and the perceptual awareness of stimulus material incongruence at a deeper semantic level of shape pairs analysis (i.e., N400). This would support the view that man–made objects as well as different–category pairs are more functionally and perceptually distinct compared to more endomorphic animals and, in general, members of same–category pairs. Consistent with this interpretation is the fact that the N400 indexes semantic intra– and extra–categorical violations (e. g., Federmeier and Kutas, 2002; Aramaki et al., 2010) and difficulty in integrating incoming semantic information that is incongruent with the individual's general semantic knowledge (e. g., Kutas and Hillyard, 1980; Lau et al., 2008; Proverbio and Riva, 2009; Amoruso et al., 2013; Proverbio et al., 2014) as well as the processing of a match–mismatch judgment as a possible logical output of stimulus mismatch detection (e. g., Palmer et al., 1994; Ruiling et al., 2013). On the other hand, the positive components may index an enhanced conscious processing of the endomorphous similarities, presumably aimed at a task–related updating and amelioration of shape pairs categorical and supra–categorical memory schematas or representations. A substantial body of literature associates the LPC as well as P300 responses with matching of expectations (Polich, 2007; Dien et al., 2004) or predictions (Dien et al., 2004) as well as enhanced processing of more salient, emotional information (Dien et al., 2004; Delplanque et al., 2004, 2006; Jiang et al., 2007). Data have also been provided indicating that this P300–LPC-enhanced processing of emotionally salient stimuli would be affected by individuals’ gender and biological and cultural statuses, independently of their socio–economic statuses (Proverbio et al., 2006).

Overall, the present results strongly support the view that access to supra–categorical and category–specific knowledge may share some common electrophysiological responses. In addition, they also suggest that distinct responses to supra–categorical and category–specific knowledge may arise when the two types of knowledge are accessed by means of different task–related cognitive strategies, namely, the allocation of a demanding load of processing resources mostly onto shape pairs’ low-level structural-features vs. an implicit categorization, the former reflected by the modulation of occipitally and parietally–occipitally focused C1 and P1, and the latter observed at the later, temporal–related, N1 level. This pattern of results is in line with extant literature showing that features shared by different categories activate overlapping brain regions and features that are unique to each category activate distinct cortical loci (Goldberg et al., 2006; Portois et al., 2009). Most importantly, our results possibly lend hemodynamic studies precious knowledge of access time to supra–categorical conceptual knowledge.

4.1. Conclusions

The present study investigated the time course of access to supra–categorical and category-specific conceptual knowledge. Response speed and accuracy were higher for more similar pairs, i.e., same–category vs. different–category pairs and animals vs. man–made objects. ERPs showed common and distinct effects for the two contrasts an earlier response to perceptual salience or relevance for animals than for man–made objects, reflected in the N1 component, and for same–category than for different–category pairs in the N2; a sequence of later negative components with enhanced amplitude for less homomorphic pairs, reflecting detection of differences; and a sequence of later positive components with enhanced amplitude for more homomorphic pairs, indexing enhanced processing of similarities. Finally, this study showed the modulation of the C1 and P1 components by attentional processing load subserving supra-categories' discrimination and further confirmed no such modulation during implicit access to category-specific knowledge.

Conflict of interests

The authors declare that they have no financial or non-financial conflicts of real or perceived interests.

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Figure captions

Figure 1. (**1a**). A single example of pictures–pair is reported for the animal and object categories. Conversely, for a mixed category, two samples are drawn, one with the animal shape falling below and the other with the animal above the visual–field horizontal meridian. In the upper portion of the Figure, a rough indication is also provided of the separate supra–categorical (i.e., same– vs. different–category) and categorical (i.e., animals vs. man–made objects) processing modes compared in the study. (**1b**) Graphical depiction of the presentation parameters of a pictures pair on the remote PC monitor in front of the observer.

Figure 2. *Supra-categorical processing*: grand–average ERP waveforms elicited by same–category and different–category pairs at the posterior scalp electrodes. The C1 component recorded over the mesial–occipital (O1, O2), parietal-occipital (PO3, PO4) and lateral occipital (OL/PO7, OR/PO8) electrodes shows a larger positivity for different–category pairs compared to the same–category pairs. Noteworthy, P1 amplitude was overall larger for different– than for same–category pairs over the left-sided than the right-sided mesial–occipital and parietal-occipital electrodes. Conversely, the N1 did not show any consistent difference in the response to the same and different pairs, whereas N2 amplitude was greater for same–category than for different–category pairs.

Figure 3. *Supra-categorical processing*: Histograms showing the mean amplitudes of the C1 component for the three-way interaction between visual field, hemisphere and electrode. Noteworthy is that this component shows an overall significant difference in polarity between ipsi– and contra–lateral stimuli at the mesial-occipital and

parietal-occipital scalp electrodes. Namely, the former stimuli produced a greater ipsilateral negative–going response, whereas the latter stimuli produced a greater contralateral positive–going response. Error bars represent mean standard errors (SE).

Figure 4. *Supra-categorical processing*: Scalp current density (SCD) difference maps for shapes' supra-categorical processing effects (different category pairs – same category pairs). Temporal series of scalp current density difference maps were obtained by subtracting brain activity related to same–category shape pairs from activity related to different–category shape pairs every 5 ms during the C1 (60 – 90 ms) and P1 (90 – 120 ms) responses, respectively, in the 60 – 120 ms post–stimulus interval.

Figure 5. *Supra-categorical processing*: grand–average ERP waveforms elicited by same–category and different–category pairs as recorded from midline central (Cz) and parietal (Pz) electrodes as well as parietal (P3, P4), central (C3, C4), lateral-frontal (F3, F4), inferior-frontal (F7, F8) and fronto-polar (Fp1, Fp2) homologous electrodes. ERPs are plotted with a full time–scale going from –a 200 to 0 ms pre-stimulus span up to 800 ms post it, where tick–marks indicate 100-ms time spans. Worth of note is that the amplitude of the N400 was much larger in response to the different–category pairs than to same–category pairs. RT indicates the reaction times distribution, reported in percentage values, grand–averaged across trials and participants as a function of supra–categorical same–different decisions.

Figure 6. *Supra-categorical processing*: Temporal series of scalp current density (SCD) difference maps for shapes' supra-categorical processing effects (different

category pairs – same category pairs), obtained by subtracting brain activity related to same–category shape pairs from activity related to different–category shape pairs, plotted every 5 ms during the N400 (350 – 470 ms) post-stimulus latency range.

Figure 7. *Categorical processing at posterior scalp*: grand–average ERPs elicited by animal and man–made object pairs at posterior mesial–occipital, parietal-occipital, lateral–occipital, posterior–temporal and parietal electrodes. Unlike for the same-different contrast, ERPs discriminated animal from objects starting at N1 level processing only. Indeed, the amplitude of this component was overall greater for animals than for man–made objects. RT: Consistent with the trend shown by different–category pairs in Figure 5, man–made objects showed a more delayed distribution of RT percentages than did animals.

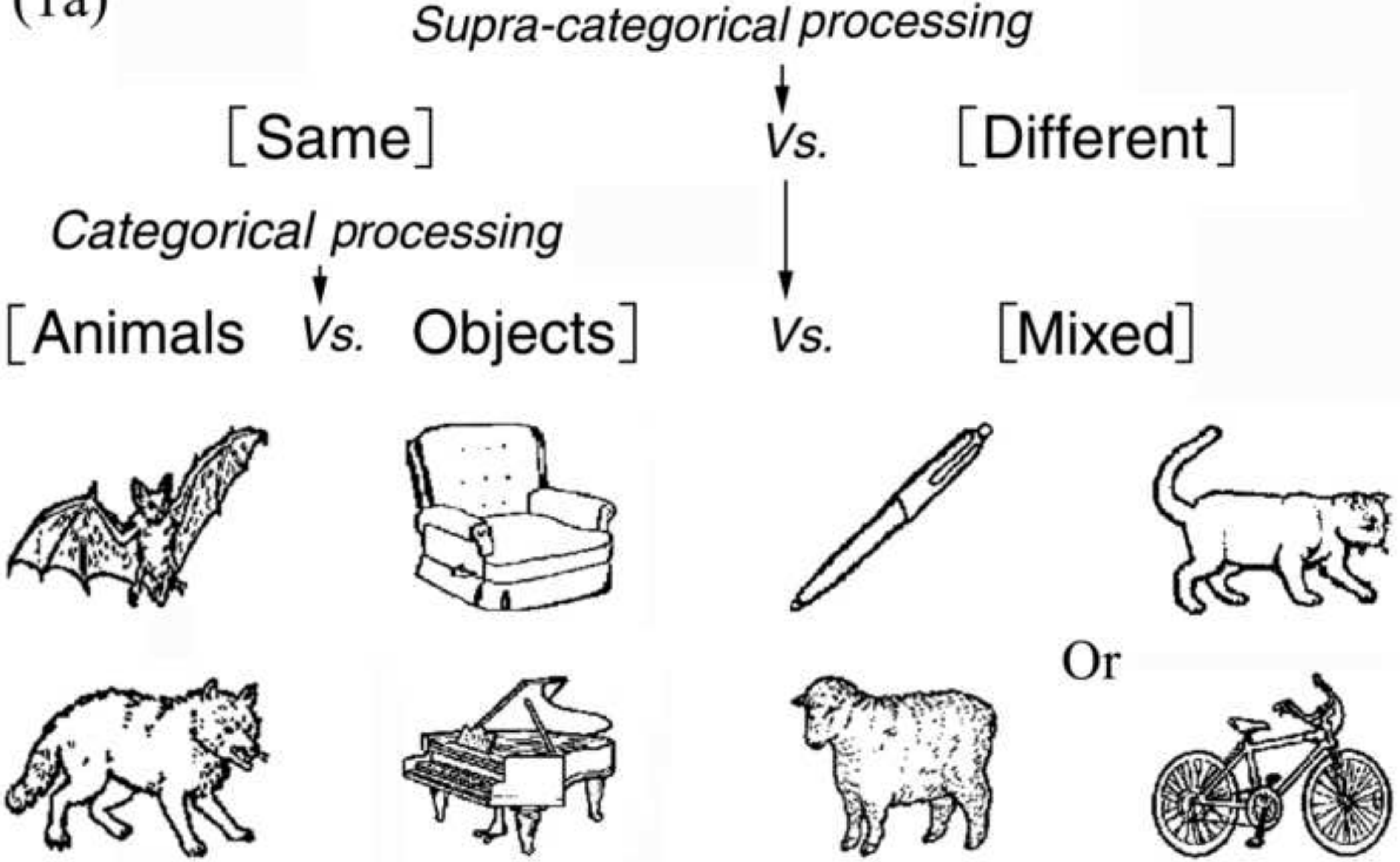
Figure 8. *Categorical processing*: Temporal series of scalp current density (SCD) difference maps obtained by subtracting brain activity related to object shape pairs from activity related to animal–category shape pairs every 5 ms during the C1 (60 – 90 ms) and P1 (90 – 120 ms) responses, respectively, in the 60 – 120 ms post–stimulus interval. Unlike for the same–different category contrast, no relevant differences could be appreciated for this contrast within the latency windows taken into account.

Figure 9. *Semantic categorical processing*: grand–average ERP waveforms evoked by animal and man–made object pairs over parietal, central, lateral frontal, inferior frontal and fronto-polar homologous electrodes. ERPs and RT time scales were the same as in Figure 7. Worth noting here is data double dissociation indicating that N2

and N400 components were overall of greater amplitude for man–made objects than for animals, whereas, conversely, the LPC was greater to animals than to man–made objects.

Figure 10. *Categorical processing*: Temporal series of scalp current density (SCD) difference maps obtained by subtracting brain activity related to animal shape pairs from activity related to objects–category shape pairs every 5 ms during the N400 (350 - 470 ms) response.

(1a)


Supra-categorical processing
[Same]
Vs.
[Different]
Categorical processing
[Animals
Vs.
Objects]
Vs.
[Mixed]
Or

(1b)

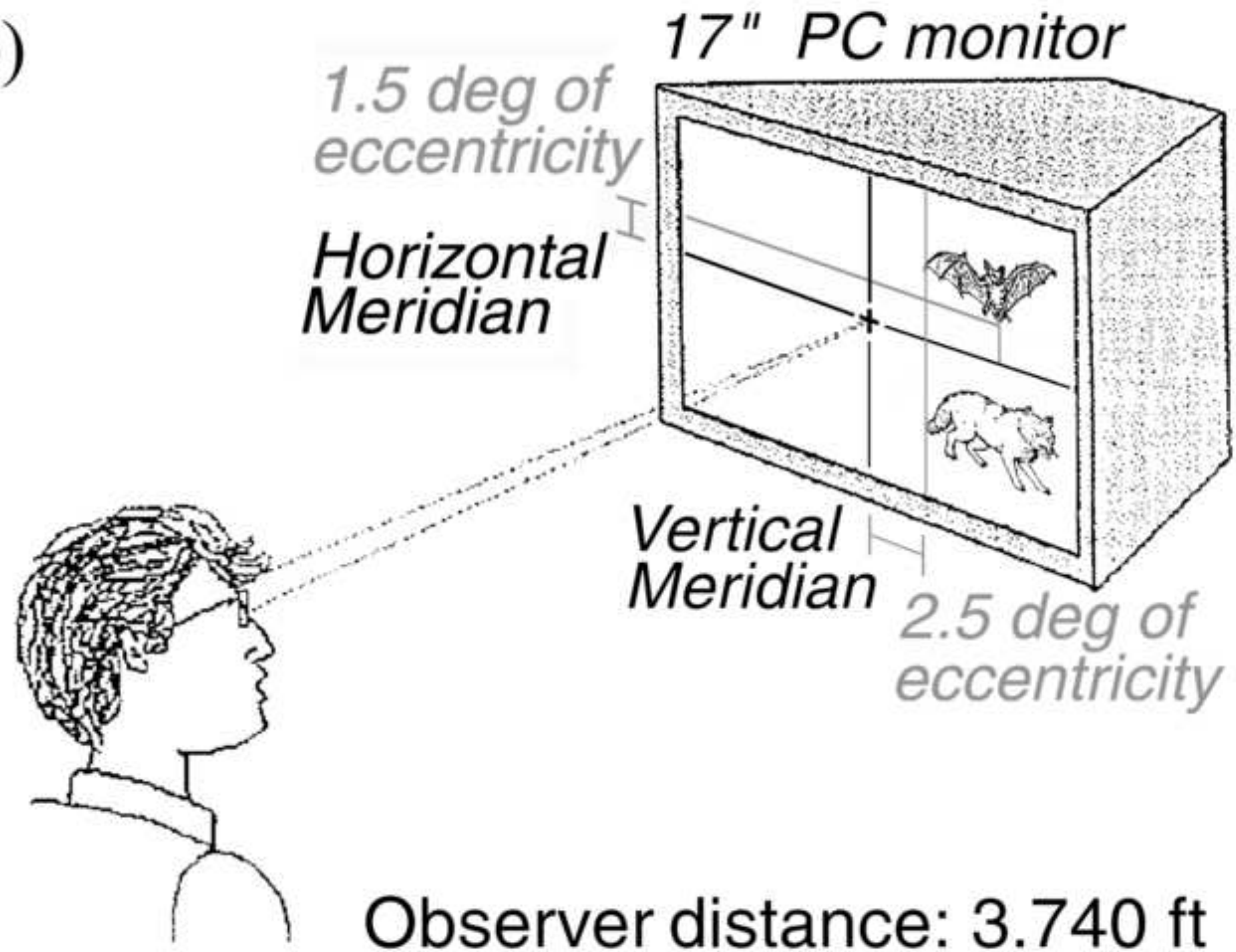
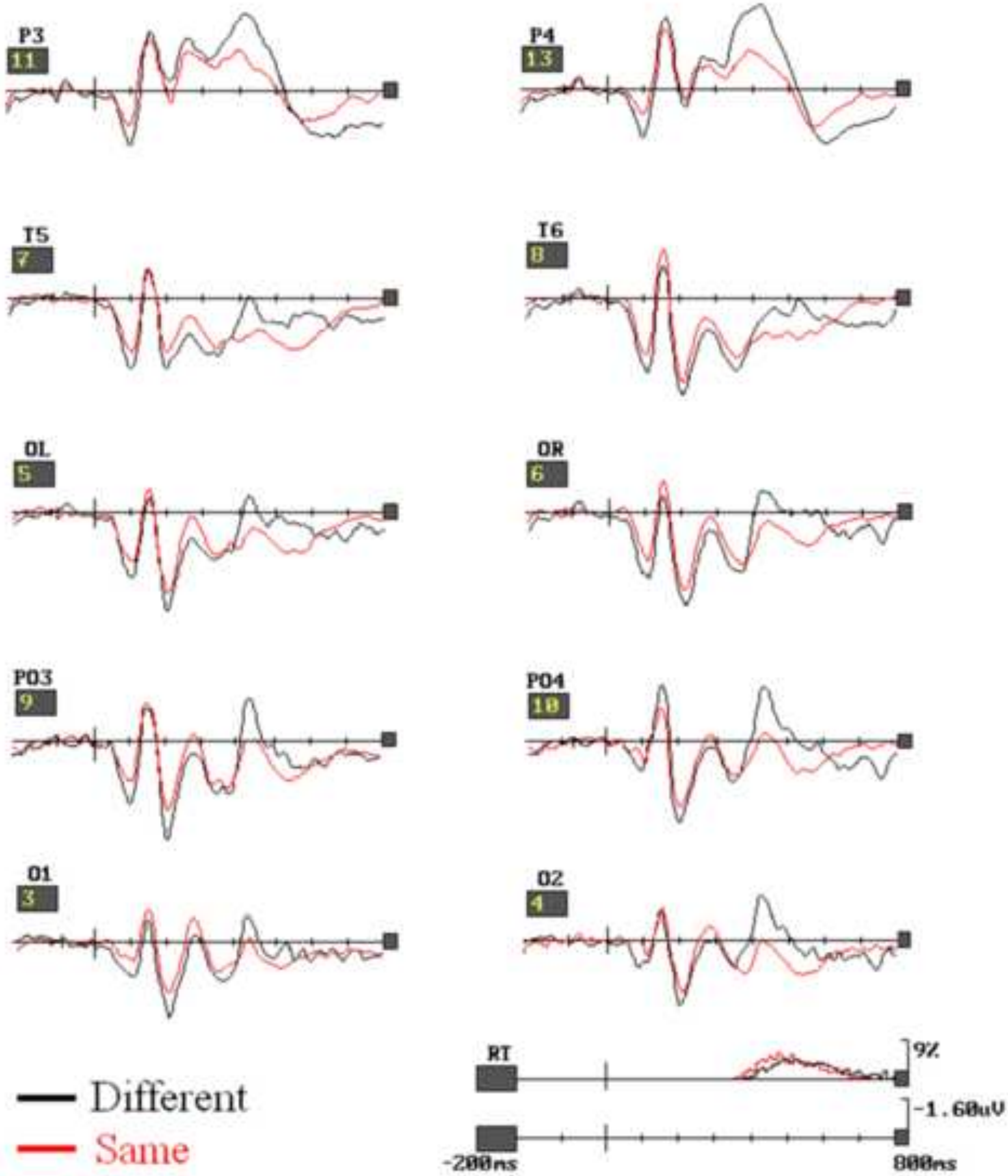
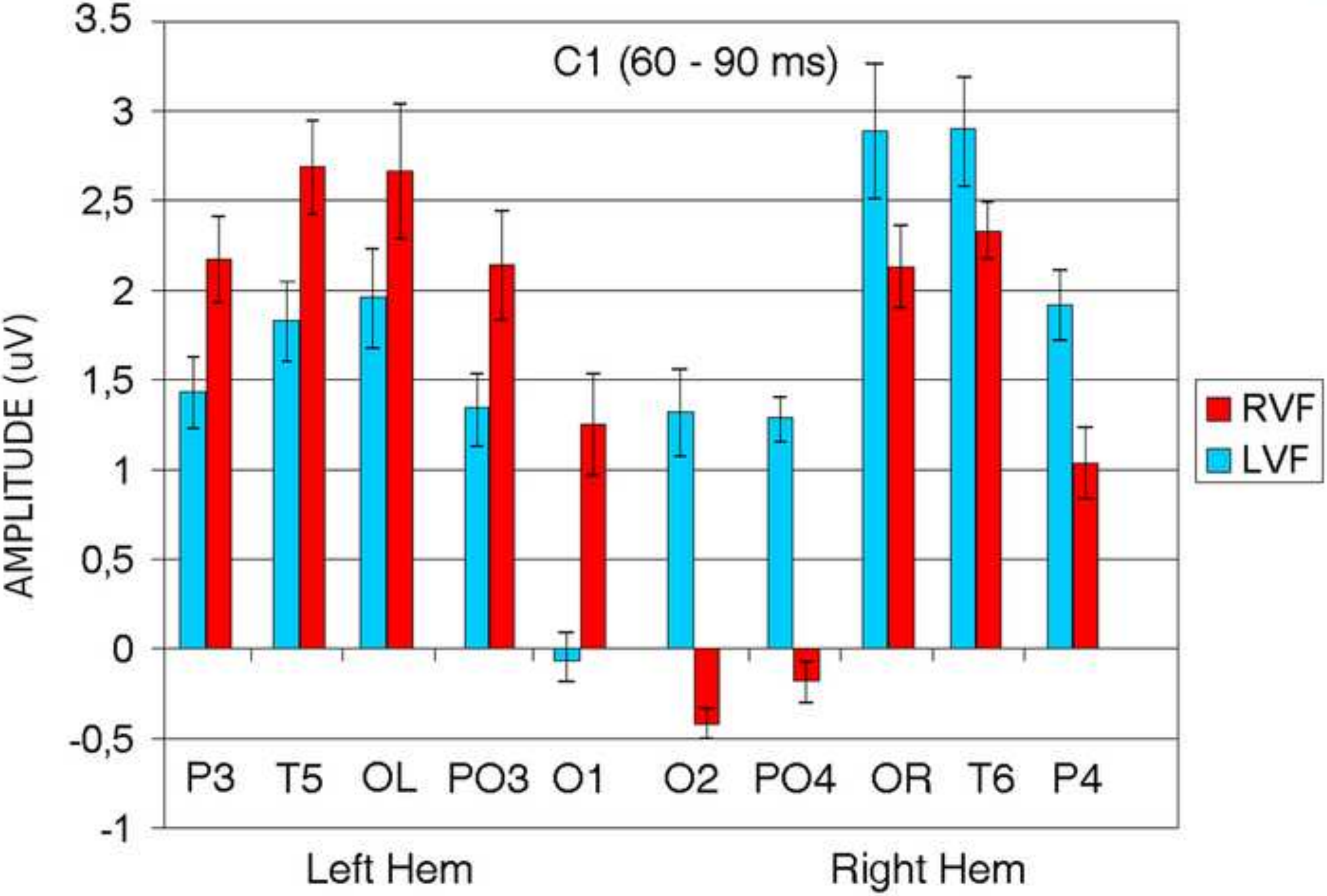

17" PC monitor
1.5 deg of eccentricity
Horizontal Meridian
Vertical Meridian
2.5 deg of eccentricity
Observer distance: 3.740 ft

Fig 2


P3
11
P4
13
T5
7
T6
8
OL
5
OR
6
PO3
9
PO4
10
O1
3
O2
4
RT
9%
-1.60uV
-200ms
800ms
Different
Same

Figure(s)


C1 (60 - 90 ms)
AMPLITUDE (uV)
3.5
3
2,5
2
1,5
1
0,5
0
-0,5
-1
P3
T5
OL
PO3
O1
O2
PO4
OR
T6
P4
Left Hem
Right Hem
RVF
LVF

Earliest Neural Processing Related to Supra-Categorical Decision

(Different cat. - Same cat.)

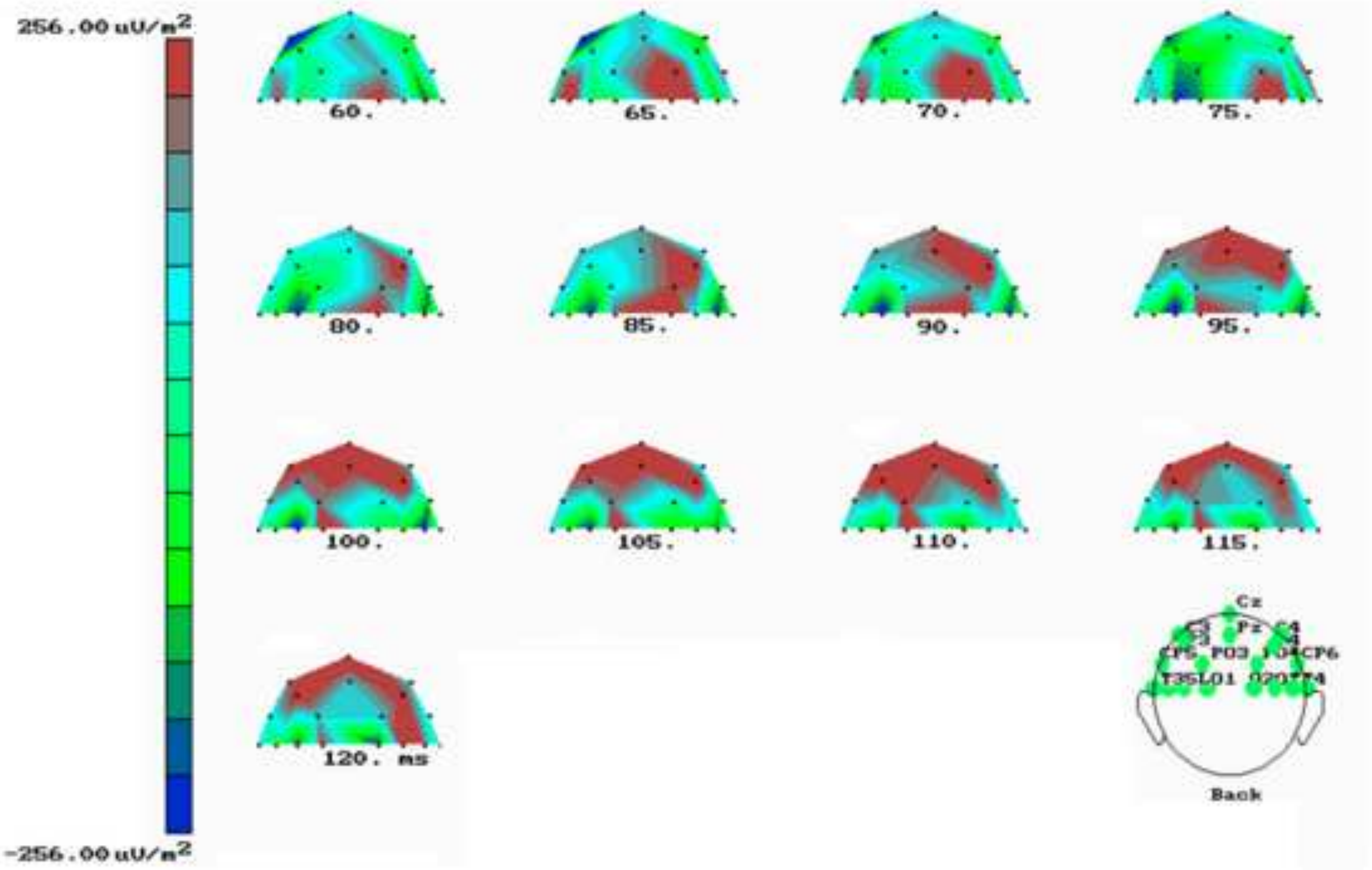
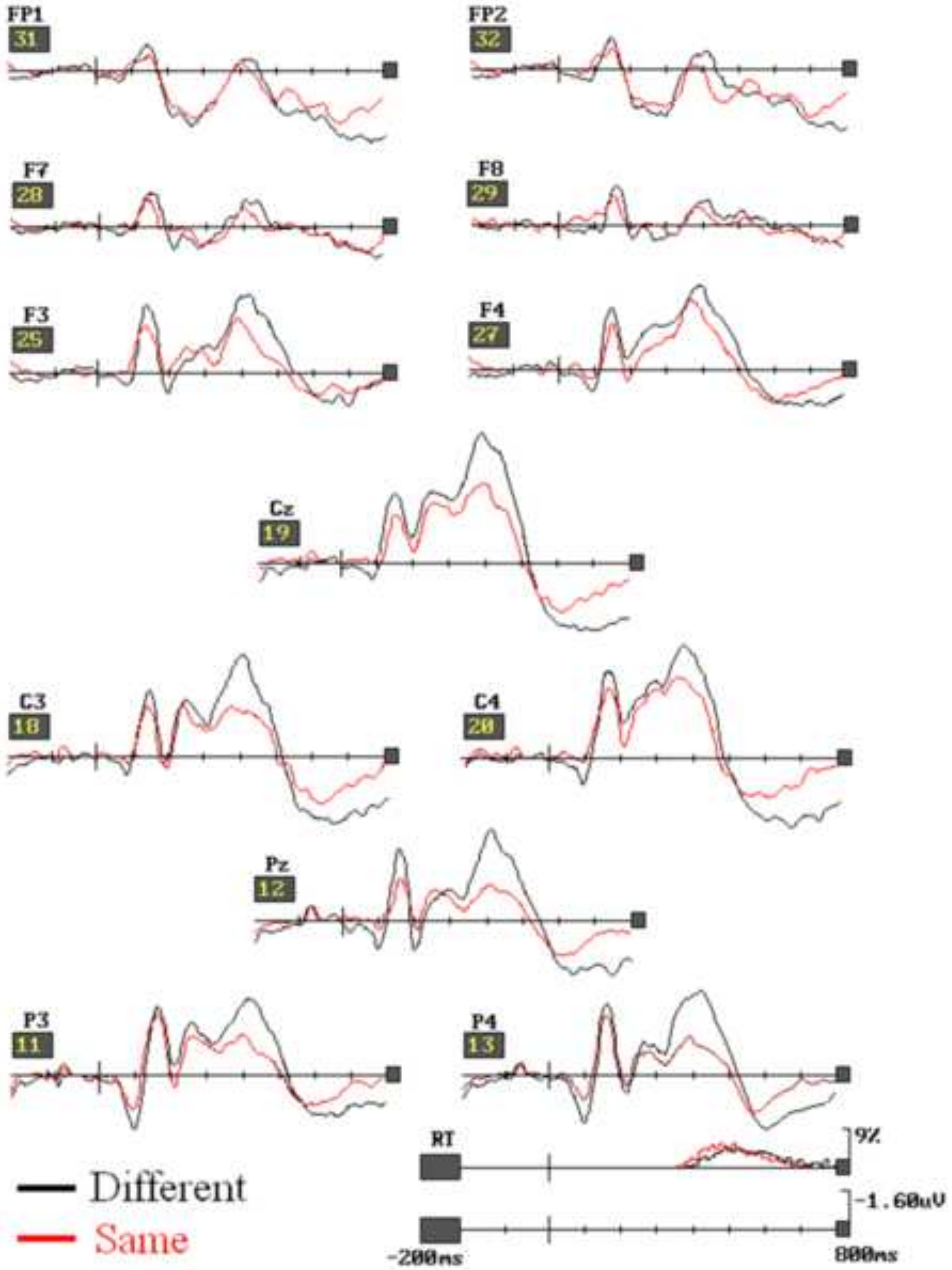


Fig 5


FP1
31
FP2
32
F7
28
F8
29
F3
25
F4
27
Cz
19
C3
18
C4
20
Pz
12
P3
11
P4
13
RT
9%
-1.60uV
-200ms
800ms
Different
Same

N400 Late-latency Neural Processing Related to Supra-Categorical Decision

(Different cat. - Same cat.)

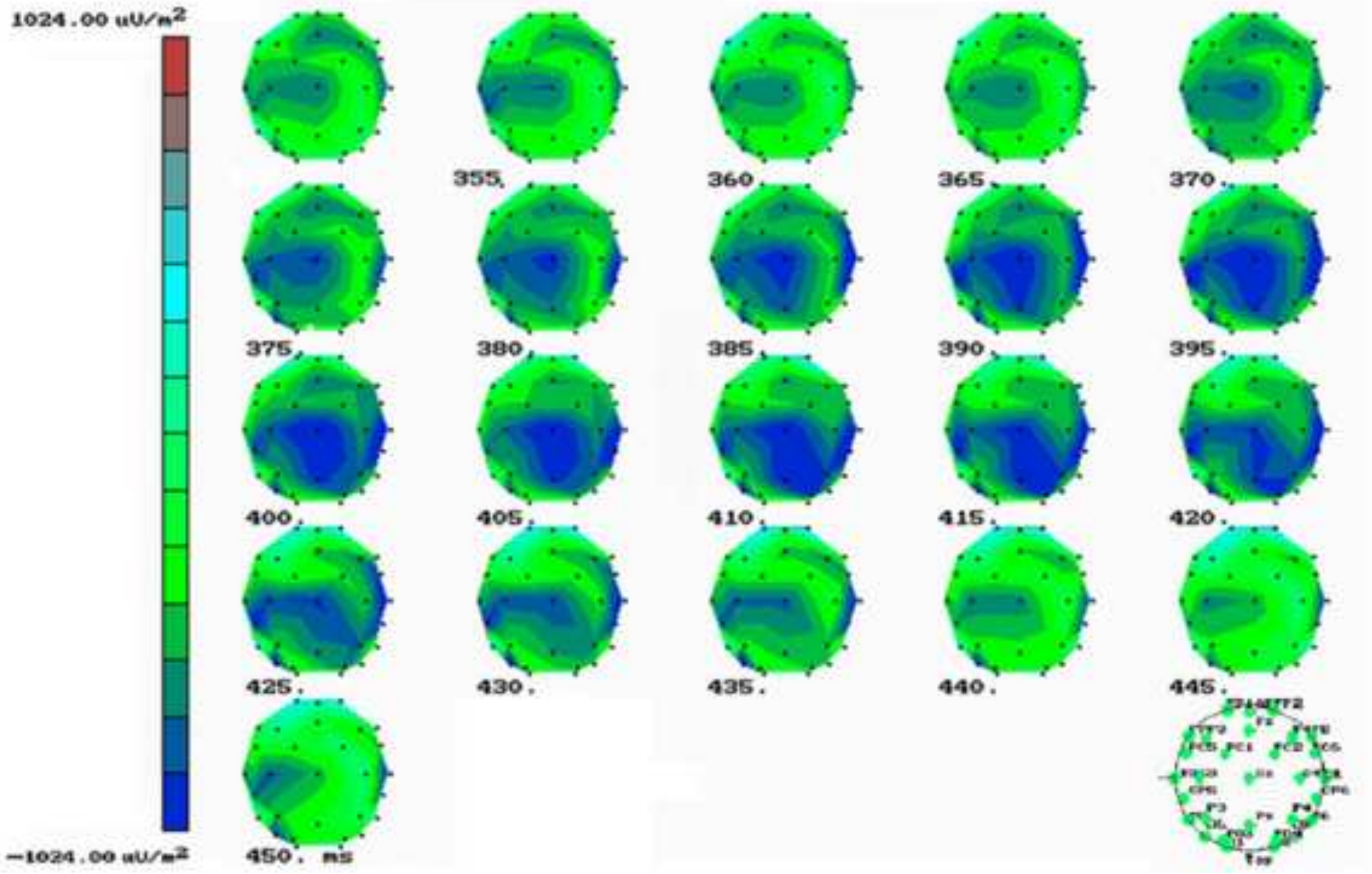
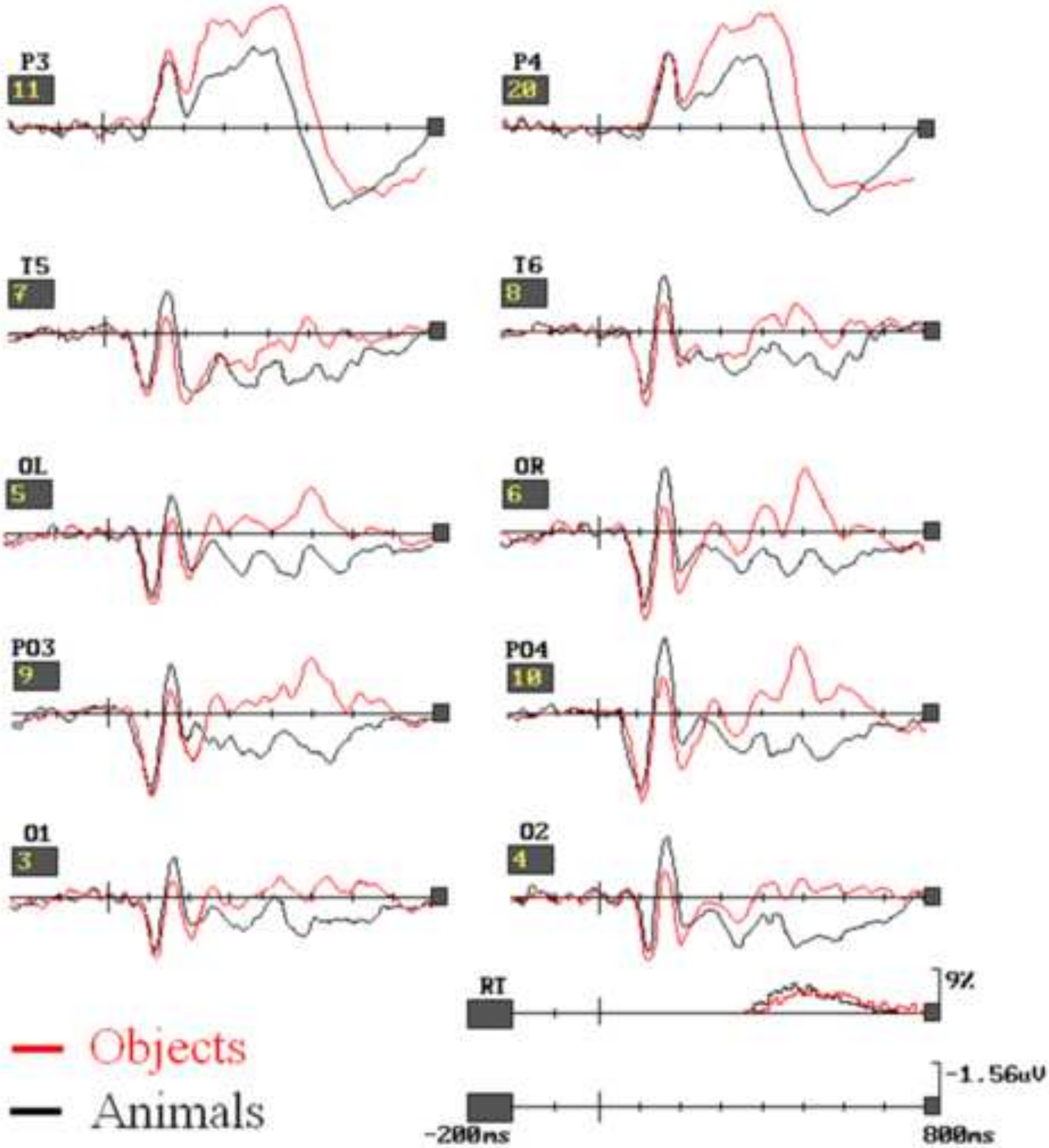
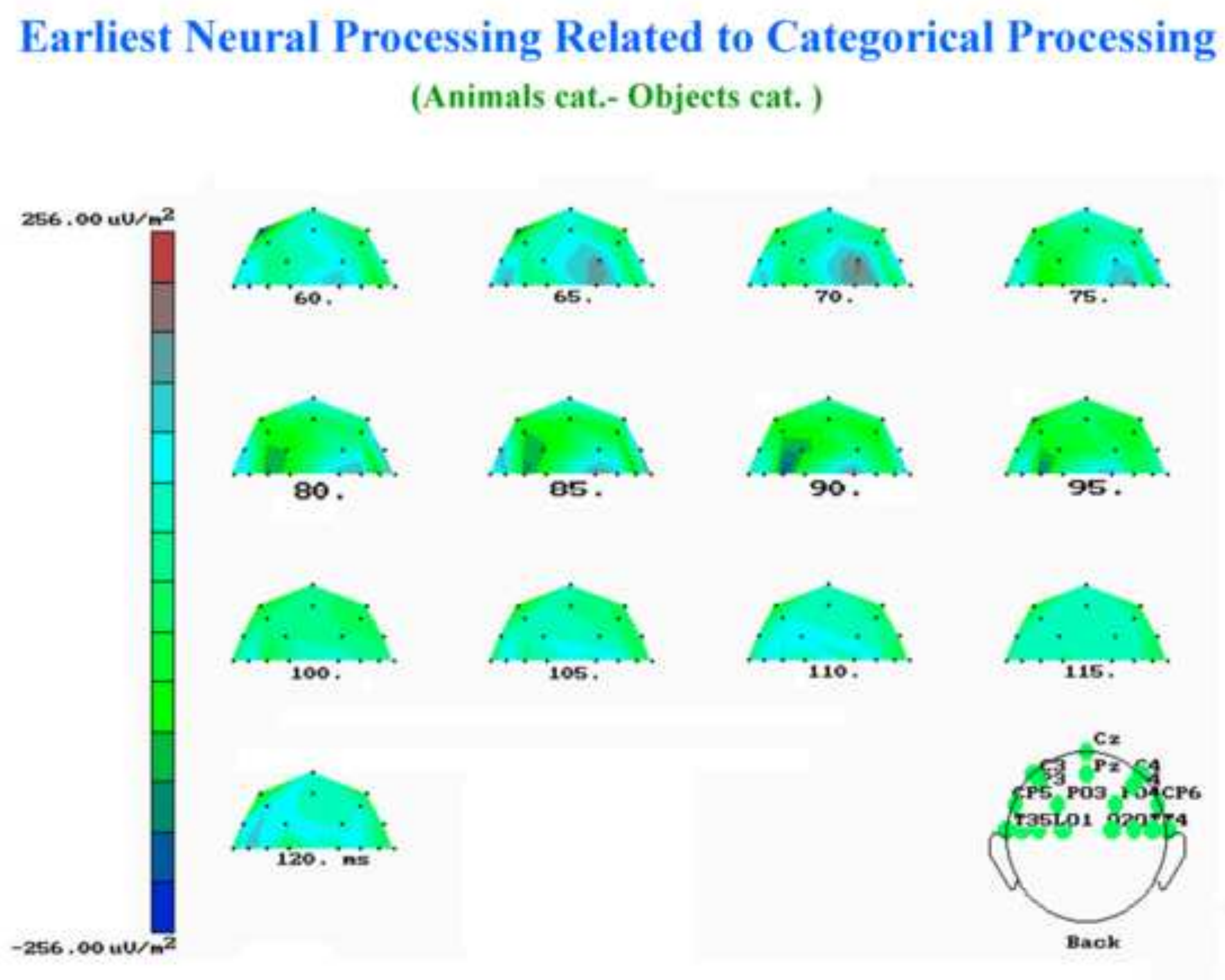


Fig 7

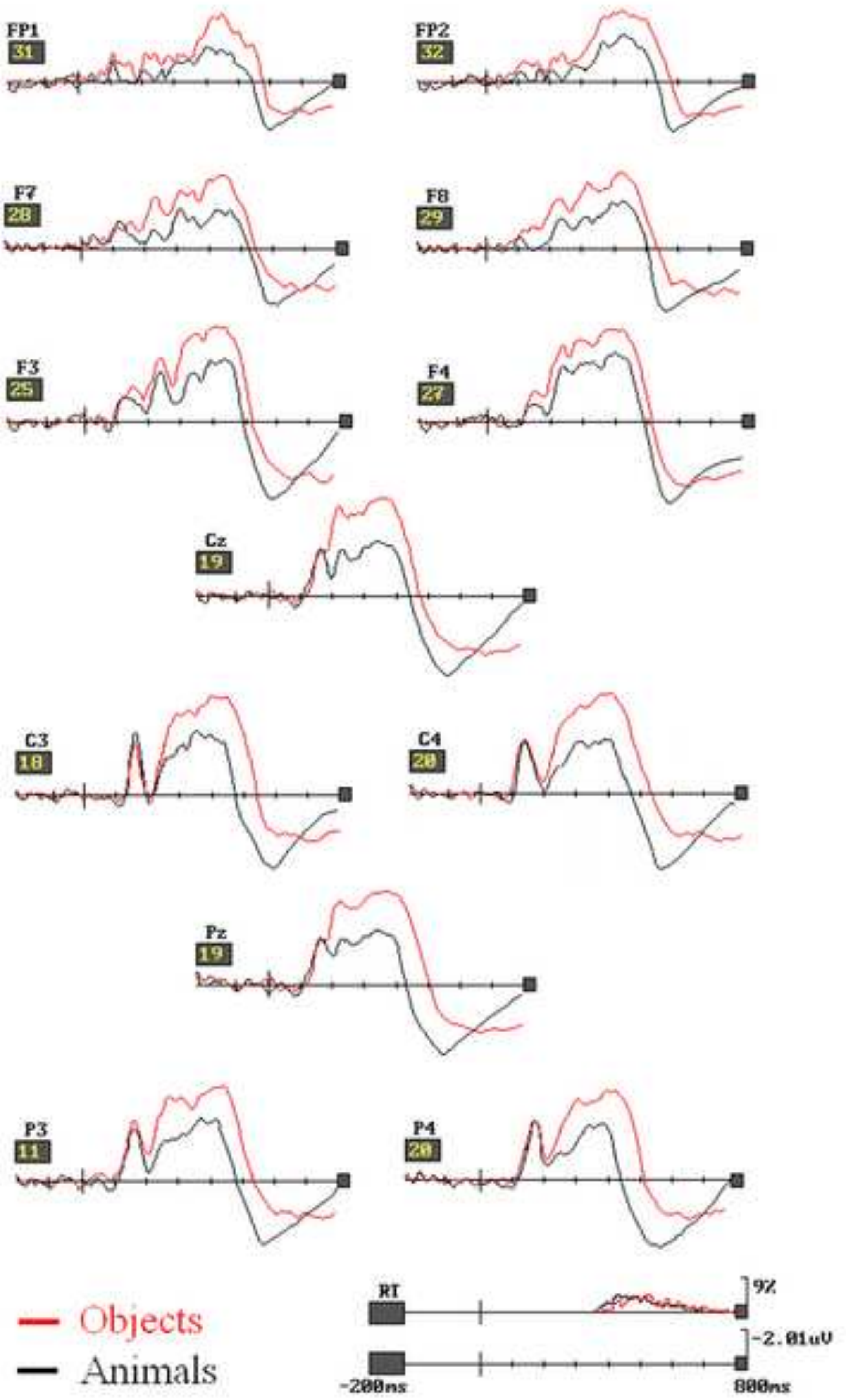

P3
11
P4
20
T5
7
T6
8
OL
5
OR
6
PO3
9
PO4
10
O1
3
O2
4
RT
9%
-1.56uV
-200ms
800ms
Objects
Animals



Earliest Neural Processing Related to Categorical Processing

(Animals cat.- Objects cat.)

Fig 9


FP1
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F3
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F4
27
Cz
19
C3
18
C4
20
Pz
19
P3
11
P4
20
Objects
Animals
RT
9%
-2.01uV
-200ms
800ms

N400 Late-latency Neural Processing Related to Categorical Decision

(Objects cat. - Animals cat.)