SHARED AND/OR SEPARATE REPRESENTATIONS OF ANIMATE/INANIMATE CATEGORIES – AN ERP STUDY

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This paper presents an ERP experiment examining the underlying nature of semantic representation of animate and inanimate objects. Time-locking ERP signatures to the onset of visual stimuli we found topological similarities in animate and inanimate object processing. Moreover, when mapping more general to more specific representation (auditory to visual stimuli) we found no difference between animates and inanimates in the N400 amplitude either. This study provides further evidence for the theory of unitary semantic organization, but no support for the feature-based prediction of segregated conceptual organization.

Surprisingly, it was also found that the P600 component, which has been thus far mostly related to syntactic processing to be a sensitive index of conceptual processing. The most apparent difference regarding P600 component was found between animate and inanimate matches, whereby animate matches elicited more positive ERP signatures in comparison to inanimate matches.

Key words: *mental representations, animacy, visual stimuli, ERP, N400*

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During our lifetime we acquire knowledge about many objects in the environment: we learn their names, their properties and we acquire general knowledge about them. The memory traces of these objects are stored in the brain. However, the question of how representations of these objects are stored and processed in the brain, although being in the focus of cognitive psychology for several decades now, remains without a complete answer and is still under intense investigation (Chang, 1996; Caramazza & Shelton, 1998; Sitnikova et al., 2006).

THEORETICAL APPROACHES OF CONCEPTUAL ORGANISATION

There are two major theoretical accounts regarding the conceptual structure of semantic knowledge, one of which proposes that semantic memories are organized in modality-specific semantic sub-systems (Caramazza & Mahon, 2003) while the other account (Tyler et al., 2000) suggests that all semantic information in the brain is organized within a unitary neural system. Furthermore, among the proponents of modality-specific semantic organization in the brain, there are two distinct theoretical approaches.

The first modality-specific approach suggests that conceptual knowledge in the brain is organized at the level of *whole objects*. The origin of this approach comes from neuropsychological studies of semantically impaired patients (Basso et al., 1988; Caramazza & Mahon, 2003; Damasio et al., 1996; De Renzi & Lucchelli, 1994; Farah & McClelland, 1991; Farah et al., 1991; Hart & Gordon, 1992; Humphreys & Forde, 2001; Laiacona et al., 1993, 1997; McCarthy & Warrington, 1988; Pietrini et al., 1988; Sitnikova et al, 2006) who show selective deficits in knowledge about particular object categories, like animals, plants or tools (Caramazza & Shelton, 1998). This restriction of selective impairments to specific semantic categories has often been taken as evidence for a discrete category specific organization of semantic representations in the brain. Therefore, according to the whole-object account, each semantic category has its own discrete, neuroanatomical structure in the brain.

The first proponents of the second modality specific theoretical approach of conceptual organization were Warrington & McCarthy (1987) and Warrington & Shallice (1984) who noticed that for some patients with semantic impairments there was no straightforward distinction between intact and impaired categories. They suggested that cognitive impairments could be better classified according to the type of attributes which are particularly important for identifying objects. For example, Warrington & Shallice (1984) identified patients who had difficulties with items whose visual features were important for object discrimination (such as animals or plants). On the other hand, there were also patients who were less able to discriminate objects for which functional features were more important (such as man-made objects or body

parts). This theoretical account is known as the *feature-based* account of semantic memory organization (Chao et al., 1999; Chao & Martin, 1999, 2000; Holcomb et al., 1999; Holcomb & McPherson, 1994; Martin & Chao, 2001; Martin et al., 1995, 1996; McPherson & Holcomb, 1999; Paivio, 1971, 1986, 1991; Sitnikova et al., 2003; Warrington & McCarthy, 1987; Warrington & Shallice, 1984; West & Holcomb, 2002). According to this account, neuroanatomical segregation is based on different types of object features (e.g. visual vs. functional). Furthermore, given that living things are more easily described and recognized by visual features whereas man-made objects by functional features (Warrington & Shallice, 1984), brain damage that affects visual semantic knowledge will lead to a greater deficit in the discrimination of living than of non-living things (Farah & McClelland, 1991). In contrast, non-living things are better described by functional features, and selective impairment of functional semantic knowledge will therefore lead to a greater deficit for non-living than for living things.

However, there have been reports of patients who had living-thing deficits without accompanying selective deficits for perceptual properties (Laiacona et al., 1997; Lambon Ralph et al., 1998; Moss et al., 1998) as well as cases of patients who had poor knowledge of visual information with no accompanying difficulty in discriminating between living and nonliving things (Lambon Ralph et al., 1998).

Moreover, Moss & Tyler (2000); Moss et al. (1998); Tyler & Moss (2001); Tyler et al. (2000, 2003b) noticed that patients with less severe brain damage had more difficulties identifying individual animals, whereas knowledge about inanimate objects remained. On the other hand, patients with more severe brain damage had more difficulties recognizing inanimate objects, whereas knowledge about animates was relatively intact. Furthermore, they found that living things had more shared and strongly semantically correlated features within each category and fewer distinctive features than inanimate objects. In contrast, inanimate objects had more distinctive features, but fewer semantically correlated features (Tyler et al., 2001). Taking into account the findings about inter-correlations among features underlying category structures, researches (Tyler et al. 2000a, 2003b; Devlin et al., 1998) have demonstrated that specific category deficits described above could emerge from a *distributed, unitary system* in which concepts are represented as patterns of activation distributed over multiple units corresponding to different semantic properties.

FMRI AND PET STUDIES OF SEMANTIC ORGANISATION

Studies about the organization of conceptual knowledge in healthy participants are nowadays usually carried out by applying functional magnetic resonance imaging (fMRI) and positron emission tomography (PET) (Martin, 2001; Martin & Chao, 2001; Martin, 2000). Most of these studies were designed to test the feature-based account

by comparing activity elicited by animate objects in comparison to inanimate objects. Typically, the fusiform gyrus, which is part of the ventral processing stream, is found to be activated in processing animate objects, and thus is believed to be involved in the visual representation of objects (Perani et al., 1995, 1999; Thompson-Schill et al., 1999, Grill-Spector, 2003, 2004). On the other hand, inanimate objects were found to evoke more activity in the left posterior middle temporal gyrus (Chao et al., 1999, 2002; Martin et al., 1996; Moore & Price, 1999; Mummery et al., 1998; Perani et al., 1999) as well as in the left posterior parietal cortical and left premotor regions (Chao & Martin, 2000; Chao et al., 2002; Grabowski et al., 1998; Grafton et al., 1997; Martin et al., 1996). In addition, for animate objects, both the posterior region of the superior temporal sulcus and amygdala were found to be more activated (Yang et al., 2005; Martin, 2007). Furthermore, the parahippocampal area was found to be selectively responsive to illustrations of places and buildings (Kanwisher, 2001) and to objects strongly associated to environmental context (e.g., traffic light, beech chair, Bar & Aminoff, 2003). Representations of food were found to be associated with the insula (involved in taste perception), the posterior orbital frontal cortex (also being linked to reward) and the amygdala (Killgore et al., 2003, Simmons et al., 2005). In contrast to these findings, Devlin et al. (2002); Pilgrim et al. (2002); Tyler et al. (2003a), failed to replicate differences in brain activation across animate vs. inanimate categories. Moreover, a wide range of category specific locations reported above turned out not to be entirely consistent across studies and often could not be linked with the data from semantic impairment.

Taken together, some of these studies do support the feature-based account of semantic organization and discrete organization of semantic representation in the brain, whereas other studies failed to detect such a discrete, neuroanatomical structure. By applying Event Related Potential (ERP) technique this paper aimed at examining the underlying nature of semantic representations further. Event-related potentials are averaged scalp-recorded responses extracted from on-going brain activity and time-locked to selected stimuli. Unlike the previously described studies focusing on the spatial activation elicited by different semantic categories in the brain using fMRI which has a high level of spatial resolution, the ERP is a good indicator of *when* something happens in the brain given that it has a temporal resolution of milliseconds. ERP 'components' i.e., changes in field potentials observed at the scalp, their timing and amplitude, can reveal much about underlying neural and cognitive processes engaged in the task.

ERP STUDIES OF SEMANTIC ORGANISATION

The N400 component, a negative component peaking at around 400ms after stimulus onset has been shown to vary greatly with the processing of semantic

information (Kutas & Hillyard, 1980, 1984; Holcomb, 1988; Friedrich & Friederici, 2004). The currently prevailing view is that the N400 is sensitive to 'contextual integration' (Kutas & Federmeier, 2000). That is to say, when the eliciting stimulus and context-based information are consistent, the N400 is reduced in amplitude, but when the semantic features of the eliciting stimulus do not fit the contextual information, the N400 amplitude is increased. Furthermore, the N400 elicited by visual stimuli is typically distributed over anterior electrode sites (Barrett & Rugg, 1990; Hamm et al., 2002; Holcomb & McPherson, 1994; McPherson & Holcomb, 1999; West & Holcomb, 2002; Sitnikova et al., 2006). The N400 distribution over anterior regions elicited by visual stimuli seems somewhat counterintuitive, given that the visual cortex is in the occipital part of the human brain (Kolb & Whishaw, 2003). This discrepancy points towards shortcoming of ERPs in localizing brain activity. In fact, it may as well be that the brain waves elicited by visual stimuli, despite the differences observed more frontally, were generated in the occipital region. But, as mentioned already, the ERP methodology is not sensitive to spatial resolution, but is rather a good indicator of temporal processing. Differences in scalp topographies between ERP components have been interpreted as at least demonstrating non-identical underlying neural sources (Holcomb et al., 1999; Kutas, 1993), even if the location of these sources cannot be established. Moreover, the N400 component has been argued to be sensitive to distinct feature-specific semantic neural networks. For instance, anterior negativities evoked by visual stimuli are believed to reflect the activation of semantic representations of visual features (Holcomb et al., 1999).

In line with these findings, according to the feature-based account of semantic memory organization, one would expect processing differences between animate and inanimate objects to be reflected through the distribution of N400 as well. Some recent behavioral studies using picture–name matching and object-decision have found faster and better processing of animates in comparison to inanimates (Gerlach, 2001, Gerlach, et al., 2004, Gerlach, et al., 2006, Lag, 2005 and Lag et al., 2006). These researchers suggested that such differences may be explained by higher within-category similarity for animates in comparison to inanimates. Furthermore, according to Laws and Neve (1999) the possible cause for processing animates differently may be because animates are more structurally similar and thus, their visual recognition may be based on more global shape, whereas inanimate objects have higher 'intra-item representational variability'. In fact, Proverbio et al. (2007) have recently reported a greater N400 component being elicited by artefacts than animals in the centro-parietal brain region. This finding was interpreted as a result of higher variability between items within the inanimate category relative to the animate category which tend to have higher intra-group similarity. It seems plausible that the differences regarding intra-group similarity could be reflected through the different magnitude of the N400. However, the difference in N400 magnitude is not sufficient evidence for the claim that animates and inanimates are processed by two distinct neural sources. In order to make such a claim one would need to demonstrate that the scalp topography for animates is different from scalp topography for the inanimates. Such a finding would

support feature-based account of semantic memory organization, whereas identical topographical distributions would suggest a unitary conceptual system. More specifically, animate objects should elicit greater anterior activation due to increased activity of visual features, whereas a different pattern of activation would be expected in inanimates (Martin & Chao, 2001; Warrington & McCarthy, 1987; Sitnikova et. al., 2006).

In categorization tasks, a further exploration of semantic representation through studying the N400 component is possible by introducing within- and between- category violations (Federmeier & Kutas, 1999; Kutas & Federmeier, 2001; Federmeier, 2002; Federmeier, 2007; Torkildsen et al., 2006) where objects are labeled incorrectly (e.g. a picture of a cow labeled as 'bear'). Within-category violations share many features in common with the expected exemplar and, thus, typically elicit a smaller N400 in the context of sentence processing in comparison to between-category violations which tend to have greater N400 amplitude (Kutas & Federmeier, 2000). Based on these findings, one would expect an inanimate label presented in the context of an animate object (e.g. lion-'hat') to produce a greater N400 than an animate label in the presence of another animate label (e.g. lion-'deer'). In other words, given that category coordinates tend to share more features than objects from different categories, between-category mismatches would expect to show an enhanced N400 in comparison to within-category mismatches.

The current study will directly contrast brain activation elicited by animate and inanimate objects, but also between within- and between-category mismatches, time-locking the ERP responses to the onset of visual stimuli.

METHOD

Participants

Fifteen healthy, normal, right-handed, native speakers of English were recruited for the first ERP study. They all had normal hearing and normal or corrected to normal vision. All of the participants were undergraduate students from the University of Oxford and were given course credit for their participation. One of the participants was excluded from the analysis due to extensive blinking and another one due to experimenter error.

Visual stimuli

A set of three-hundred-twenty animate and inanimate photographs were mainly chosen from the CD-ROM Graphic Interchange Format Data (Hemera, 2000) and some

of them were chosen from commercial internet pages. All of the visual stimuli were subsequently edited using Adobe Photoshop CS software to remove any background and to introduce a ten percent gray-background to reduce the brightness on the screen. The whole sample consisted of 240 visual objects (40 animate-matches, 40 inanimate-matches, 40 animate-mismatches-within category, 40 inanimate-mismatches-within category, 40 animate-mismatches-between categories, 40 inanimate-mismatches-between categories) and eighty fillers (40 animate and 40 inanimate objects). For the animate/inanimate object labels which appeared in the match, mismatch within and mismatch between conditions, three versions of the corresponding static computer images were chosen to avoid priming effects and adaptation to the images. For each of the chosen fillers (animate and inanimate labels) a corresponding static computer image was chosen. All of the pictures were of the same size and were presented to the participants in the left profile view. All of the selected stimuli were aimed to be highly typical exemplars of their categories and typicality ratings were collected from a separate group of participants (Kovic, 2008).

Auditory stimuli

One-hundred and sixty animate and inanimate labels were digitally recorded in stereo during a single session at 44.11 kHz sampling rate into signed 16-bit files. All of the recorded stimuli were subsequently edited in the GoldWave 5.10 software to remove head and tail clicks and background noise and to match for peak-to-peak amplitude. Eighty of those selected labels were used for creating animate and inanimate matching pairs (e.g. lion-lion, book-book), mismatching pairs within categories (e.g. lion-deer, phone-key) and mismatching pairs between categories (e.g. lion-hat). Forty auditory stimuli were selected from the animate category and the other half was selected from the inanimate category. Another eighty labels (half of which were animate and half of which were inanimate) were used as match filler trials in order to have an equal number of match and mismatch trials.

Experimental design

The experiment consisted of 8 experimental conditions with 40 trials per condition. The first experimental condition was the *animate match* condition where participants were presented with the auditory and visual stimuli from the animate category that matched one another (e.g. participants heard label 'dog' and saw the picture of the dog). Likewise, in the *inanimate match* condition they were presented with the matching animate pairs (e.g. with the label 'hat' and a picture of a hat). The *mismatch within* (animate and inanimate) categories conditions involved presentation of the label and the visual stimuli from the same category, but the label and

object mismatched (e.g. animate pair: giraffe-sheep or inanimate pair: bus-comb). The *mismatch between* (animate and inanimate) categories conditions involved presentation of a label from an animate category for an inanimate object (e.g. zebra-pipe) and vice versa. Forty animate and inanimate *filler match* trials were introduced in order to equalize the number of match and mismatch responses and these trials were not analyzed afterwards.

The labels and objects in the mismatch trials were paired in a way to avoid phonological onset competition (cat-cow) or rhyme (dog-frog) as well as semantic association, such as cat-dog combinations (Leech et. al, 2001).

The time sequence of each trial was as follows: the fixation cross was displayed at the start of the trial for approximately 2300ms; the label was played at 900 ms (±200ms) from the onset of the trial; 2300 ms (±200ms) from the trial onset the visual stimulus was displayed for 1000 ms (±200ms) after which a question mark appeared at the centre of the screen. Upon seeing the question mark participants were instructed to press either the 'match' or 'mismatch' button on the keyboard in order to indicate if the label matched or mismatched the visual object. The presentation of the next trial automatically followed the participants' responses (see Figure1). The presentation of the picture-label pairs was randomized for each subject.

A jitter of ± 200 ms was introduced prior to the presentation of the auditory stimuli, visual stimuli and question mark appearance in order to avoid preparatory movement potentials during the task (Luck, 2005). Preparatory movement potentials are well known to appear as contingent negative variations (CNV), a low frequency negative wave preceding an expected stimulus (Luck, 2005).

The presentation of the question mark was introduces in order to slow down participants reaction times to these highly familiar objects, so that ERPs could be recorded without movement artefacts resulting from the participants pressing the key.

Figure 1: The time sequence of the auditory/visual stimuli presentation
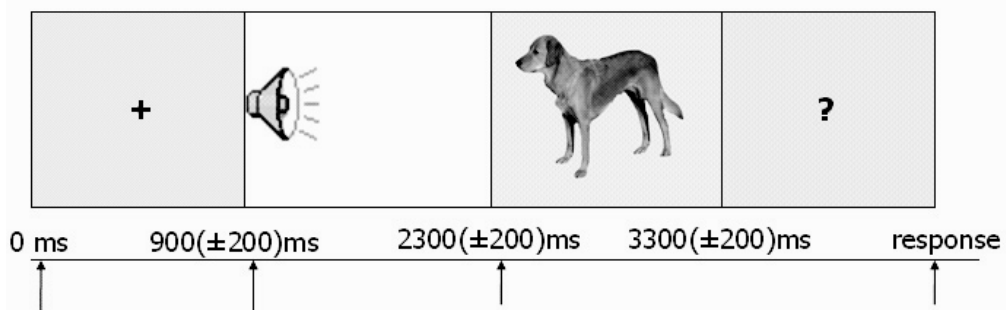
Procedure

Participants were seated approximately a meter away from the monitor displaying centrally presented visual stimuli (~2.4° of visual angle) with a pair of loudspeakers

above the screen for presenting auditory stimuli. The monitor was positioned in such a way that the centre of the screen was approximately at the participants' eye-level.

At the beginning of the experimental session participants were given brief instructions explaining the procedure and task. Subjects were then fitted in the easy-cap and each electrode was filled with electroconductive gel. Electrode impedance was reduced until it was less than 5KΩ at each site. After the set-up procedure participants were given a keyboard to position on their lap and were asked to position their index fingers on the two marked buttons for making responses (match/mismatch). Each of the participants was also given a brief demonstration prior to onset of the task to see how the brain waves change with head and body movements, eye-blinks etc.

The instruction for the actual task was to focus on the presented visual and auditory stimuli and to press the 'match' button for the match trials or 'mismatch' button for the mismatch trials upon seeing the question mark on the screen, and to make their decision as accurate as possible. Furthermore, participants were asked to try to sit still during the study and to try to avoid blinking during presentation of visual stimuli.

Once the participants had settled down, the experiment started. The experimental room remained semi-darkened and silent throughout the experiment. The experimenter remained out of the participants' sight during the task and managed the experimental computers.

At the beginning of the experiment participants were asked to sign a consent form and at the end of the experiment they were given a full explanation of the experimental procedure as well as a demo of their brain responses conducted during the study. The whole procedure lasted approximately 50 minutes.

ERP methodology

The EEG was continuously recorded from the following sites: FP1, FP2, F7, F3, FZ, F4, F8, FC5, FCZ, FC6, T7, C3, CZ, C4, T8, CP5, CP1, CP2, CP6, P7, P3, PZ, P4, P8, O1 and O2, using AgCl sintered ring electrodes. The electrode montage is shown in Figure2. Electrical activity was monitored using a NeuroScan Nuamps amplifier linked to a PC computer running Windows XP and digitized at 1000Hz, corresponding to a sampling bin of 1ms, high pass filtered at 0.1 Hz and low-passed filtered at 70 Hz. Testing did not precede until electrode impedances were reduced to less than 5KΩ at each site. Additionally, the electro-occulogram was recorded from electrodes placed over and under the left eye to detect trials on which blinks and vertical eye movements occurred, and from left and right frontal electrodes to detect trials on which horizontal eye movements occurred. Trials with artefacts related to ocular movement were rejected offline and individual rejection thresholds were set for each participant based on visual inspection of the EEG epochs time-locked to the onset of the visual stimuli. The baseline activity was recorded from 300ms prior to the onset of visual stimuli. All

electrodes were referenced to the left mastoid and re-referenced to average mastoids during the analysis. Only epochs corresponding to correct responses were included in the analysis. Prior to the analysis, all of the EEG files were cleaned, that is, noisy portions of the data were marked and removed from further analysis. The portions of data which were excluded from the analysis were caused by participants' head or body movements, or occasionally coughing and sneezing. The percentage of the excluded trials from each of the experimental conditions and for each of the subjects was never above 5%.

Figure 2: The electrode montage used in the ERP studies
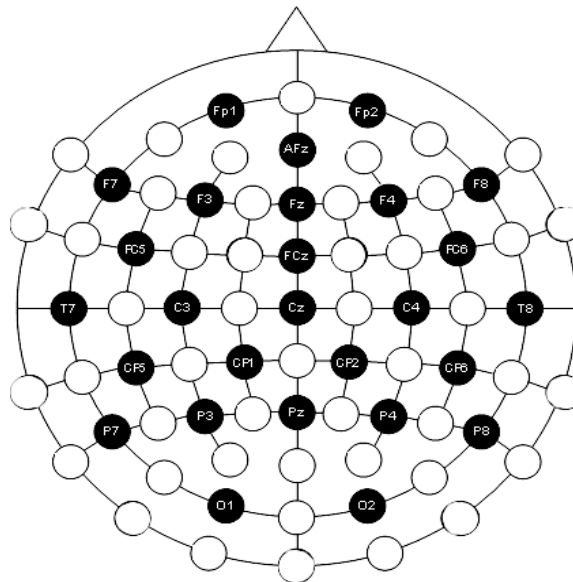
The ERP data analysis was conducted by extrapolating mean amplitude measurements from the continuous EEG signal into 20ms bins for each participant across all of the experimental conditions. Only significant differences between conditions where neighboring 20ms bins were also significant at the p<.05 level (Eddy et al. 2006) are reported here. EEG signatures were time-locked to the onset of visual stimuli.

The data analysis revealed two time windows within which neighboring 20ms bins were found to be significantly different across experimental conditions. The first time interval was shorter and less distributed across the sites. It started at around 320 ms and lasted until 400 ms from the onset of the visual stimuli. During this time interval ERP signatures diverged particularly at the T7, C3 and CZ sites. The mean amplitude measurements at these sites revealed a very similar pattern of results. Hence, the mean amplitudes were averaged across the three sites and presented together.

Figure 3: 320-400ms time window: T3, C3 and CZ sites

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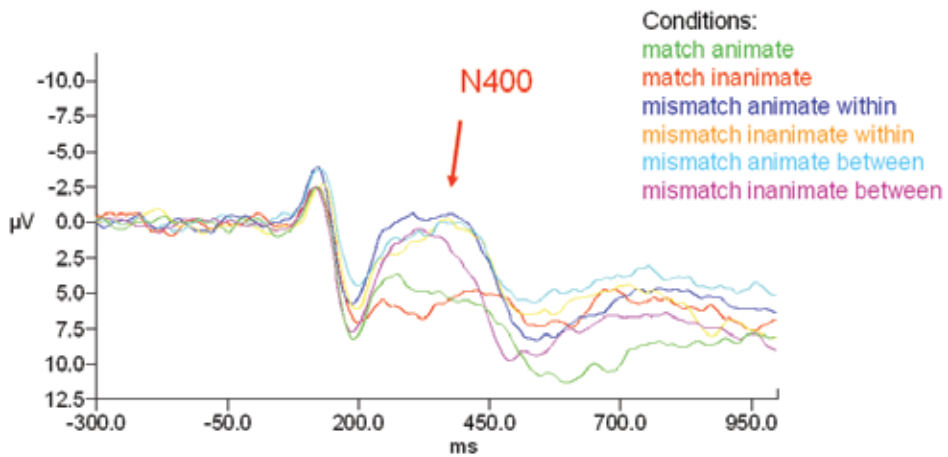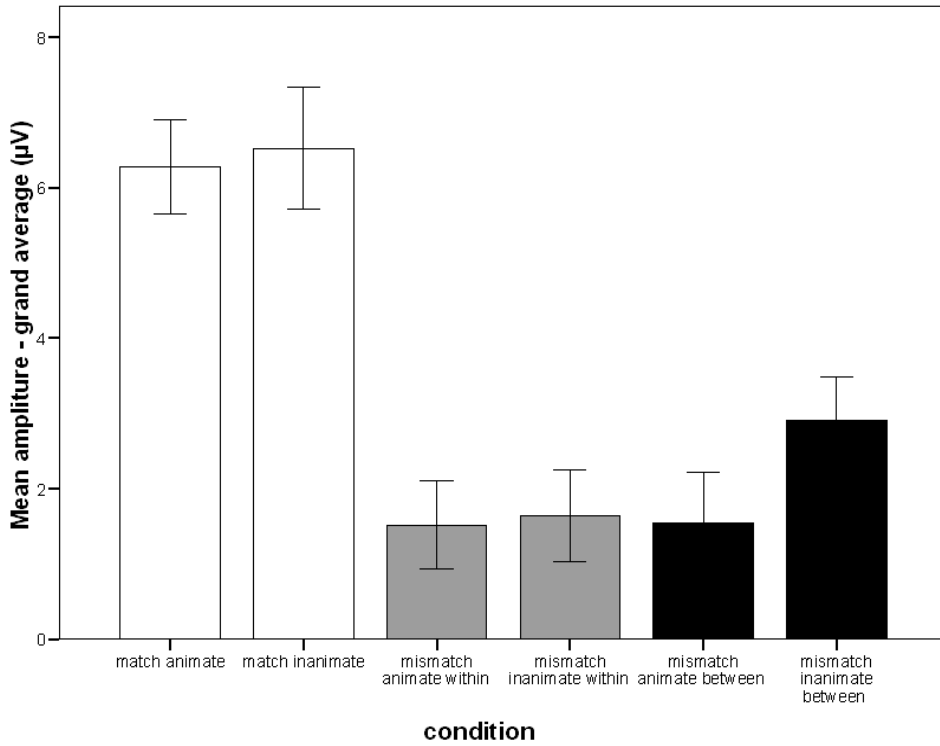
[2] Traditionally, negative μV are shown upwards to avoid false impression of negative being smaller voltage.

Figure 4: 580-740ms time window: average of FC5, FCZ, FC6, T7, C3, CZ, T8, C4, PZ, P4 sites
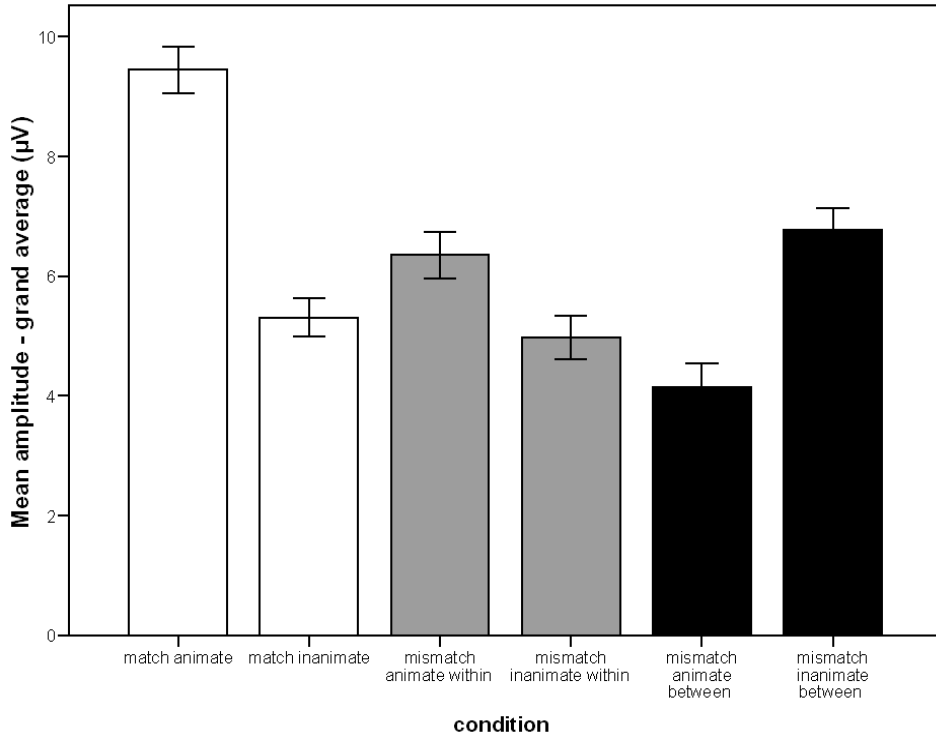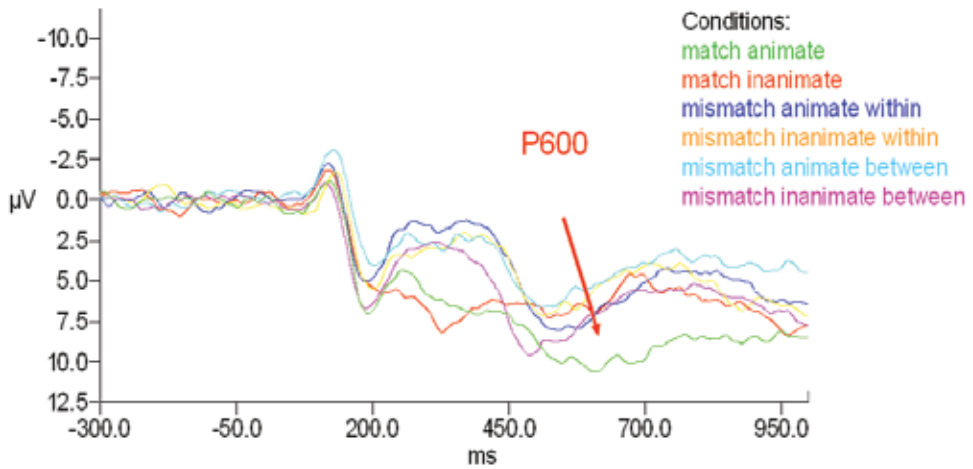

Figure 4a: P600 effect at the C4 site

A univariate ANOVA across all three sites with factors Match (label-object match, mismatch within categories and mismatch between categories) and Animacy (animate vs. inanimate) revealed a significant main effect of Match ($F_{(2,384)}$= 32.595, p<.001), but not of Animacy ($F_{(1,384)}$=1.173, p=0.279). There was no significant interaction ($F_{(2,384)}$=0.553, p=0.576). Post-hoc analysis revealed significant differences between match trials and mismatch-within-category trials as well as match and mismatch-between-categories trials for both animates and inanimates (Animates: M(match)=6.28μV, s.e.m.=0.627, M(mismatch within)= 1.151μV, s.e.m.=0.588, M(mismatch between)=1.549μV, s.e.m.=0.665; match vs. mismatch within: t(1,128)=5.538, p<.001; match vs. mismatch between: t(1,128)= 5.173, p<.001; Inanimates: M(match)=6.528μV, s.e.m.=0.805, M(mismatch within) =1.632, s.e.m.=0.609, M(mismatch between)=2.908μV, s.e.m.= 0.569; match vs. mismatch within: t(1,128)=4.847, p<.001 match vs. mismatch between: t(1,128)= 3.670, p<.001), see Figure3/3a. Mismatch-within-category and mismatch-between-categories trials did not differ systematically for animates vs. inanimates (at p<.05 level)[3].

The second time interval during which the distinct ERP signatures across experimental conditions emerged was more distributed across the scalp and lasted longer. It started at around 580ms from the onset of the visual stimuli and continued until 740 ms. The different ERP signatures across the experimental conditions during this time interval were found at the following sites: FC5, FCZ, FC6, T7, C3, CZ, T8, C4, PZ and P4.

A univariate ANOVA with factors Match (label-object match, mismatch within categories and mismatch between categories) and Animacy (animates vs. inanimates) revealed a significant main effect of Match ($F_{(2,618)}$=16.187, p<.001), a significant main effect of Animacy ($F_{(1,618)}$=10.219, p<.001) and a significant interaction effect ($F_{(2,618)}$=42.056, p<.001).

Post-hoc analysis for animate objects revealed significant differences between match trials and mismatch-within-category trials, between match trials and mismatch-between-categories trials as well as between mismatch-within- and mismatch-between-categories trials (M(match)=9.444μV, s.e.m.=0.386, M(mis-match within)=6.352μV, s.e.m.=0.387, M(mismatch between)=4.153μV, s.e.m.= 0.394; match vs. mismatch within: t(1,206)=5.648, p<.001; match vs. mismatch between: t(1,206)=9.587, p<.001; mismatch within and mismatch between: t(1,206) =3.976, p<.001), see Figure4.

A detailed analysis for inanimate objects revealed significant differences between match trials and mismatch-between-categories trials as well as between mismatch-within- and mismatch-between-categories trials, but not between match trials and mismatch-within-category trials (M(match)=5.309μV, s.e.m.=0.317, M(mismatch within)=4.973μV, s.e.m.=0.357, M(mismatch between)=6.769μV, s.e.m.=0.372; match vs. mismatch within: t(1,206)=0.705, p=0.482; match vs. mismatch between: t(1,206)=2.985, p<.003; mismatch-within and mismatch-between: t(1,206)=3.482, p<.001).

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[3] Bonferroni corrections were applied when necessary due to multiple comparisons.

The difference between animate and inanimate match trials was also found to be significant (t(1,206)=3.487, p<.001), as well as differences between animate and inanimate mismatch-within-category trials (t(1,206)=8.270, p<.001) and animate and inanimate mismatch-between-categories trials (t(1,206)=2.617, p<.01).

DISCUSSION

Theoretical approaches to understanding the conceptual structure of semantic knowledge have been mainly developed through studying the system in which normal processing has broken down, for example following traumatic brain injuries (Warrington & Shallice, 1984; Caramazza & Mahon, 2003; Moss & Tyler, 2000). Recently, however, methods such as positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) have been applied to advance our understanding of the conceptual organization of semantic knowledge in healthy participants (Martin, 2001; Martin & Chao, 2001; Martin, 2000). In general, selective impairments to specific semantic categories as well as pinpointing category specific brain locations have often been taken as evidence for a discrete neuroanatomical organization of semantic representations in the brain. Nevertheless, a wide range of category specific locations reported in this research were not consistent across studies and often could not be linked with semantic impairment data. Therefore, an alternative account was proposed suggesting a distributed, unitary system in which concepts are represented as patterns of activation distributed over multiple units corresponding to different semantic properties (Tyler et al. 2000, 2003b; Devlin, Gonnerman, Andersen & Seidenberg, 1998).

This paper aimed to enhance our understanding of the underlying nature of semantic representations in the light of existing theories of conceptual organization, by employing ERP methodology.

The ERP studies with animate and inanimate object processing focused on the N400 component which is well known as a sensitive index of semantic processing (Kutas & Hillyard, 1980, 1984; Holcomb, 1988; Friedrich & Friederici, 2004). Its amplitude varies depending on the semantic integration of stimuli with a given context (Kutas & Federmeier, 2000). Furthermore, topographical differences regarding the distribution of semantic activation would indicate non-identical or distinct neural generators, whereas distributional similarities would imply a similar processing mechanism.

The topography of the N400 elicited by visual stimuli in the present study was mainly distributed across the anterior-central scalp region, similar to the findings of earlier studies demonstrating an anterior distribution of the N400 in visual stimuli (believed to reflect the activation of semantic representations of visual features, Holcomb et al., 1999).

Furthermore, given that the N400 anterior-central distribution was found for both animates and inanimates, this experiment did not provide evidence for the feature-based account of semantic processing which would predict greater anterior activation for animate objects (due to increased semantic representation of visual features) and a different pattern of activation for inanimates (due to increased semantic representation of functional features).

Regarding the amplitude of the N400, there were no systematic differences between animate and inanimate matches or animate and inanimate mismatches within and between categories, suggesting that both animate and inanimate visual stimuli in the current study were processed in a similar way.

In accordance with previous studies (Kutas and Hillyard, 1980; Friedrich & Friederici, 2004; 2005) we predicted that label-picture matches would give rise to different ERP signatures than label-picture mismatches. The results confirmed this prediction, demonstrating different ERP signatures elicited by both within- and between-category mismatches in both animate and inanimate objects in comparison to label-picture matches, peaking at around 320 to 400 ms. These results are in an agreement with previously reported studies suggesting that the N400 component is a sensitive index of 'contextual integration' (Kutas and Federmeier, 2001).

Furthermore, under the assumption that objects from the same category tend to share more features than objects from different categories, one would expect a more enhanced N400 to be elicited by between-category (animate-inanimate) mismatches than by within-category mismatches (animate-animate). In fact, a greater N400 amplitude for between-categories mismatches in comparison to within-category mismatches has been reported in the context of sentence processing (Kutas & Federmeier, 2001). However, the results of the present study revealed no systematic differences between within- and between-categories mismatches for either animate or inanimate objects. Now, if the visual items presented here were perceived as mental tokens (that is more specific mental representations) rather than mental types (more general mental representations), one could manipulate intra-group variability effects, by swapping around the presentation order between auditory stimuli (mental types) and visual stimuli (mental tokens). Consequently, more effort was expected when mapping auditory to visual (more general to more specific representation), than in an experimental design which would involve mapping visual to auditory stimuli. Thus, the twist in stimulus sequence would provide a way of controlling for the abstractness or generality of a mental representation, whereby auditory presented labels would be considered as more abstract and general (mental types), and visual stimuli as more concrete and specific (mental tokens).

Finally, it is worth pointing out that, surprisingly, at the later stages of visual object processing in the time window corresponding to the P600 component, differences in processing animate and inanimate visual stimuli were observed across a wide range of electrode sites (mainly in the anterior-central-parietal region). A rather complex pattern of results was observed: animate matches differed significantly from both within- and between-category mismatches, whereas there was no such difference between

inanimate label-object matches and within- and between-category mismatches. Also, label-object mismatches within the animate category in this time window elicited more positive ERP signatures in comparison to label-object mismatch between categories. In contrast, label-object mismatches within the inanimate category elicited significantly less positive ERPs in the same time-range in comparison to label-object mismatch between categories.

The most apparent difference regarding P600 component was found between animate and inanimate matches, whereby animate matches elicited more positive ERP signatures in comparison to inanimate matches. A similar result was recently reported in two other studies investigating word-picture matching and natural/ artifactual object categorization by Mazerolle et al., (2007) and Paz-Caballero et al., (2006). These studies also suggest that the P600 component might be a sensitive index of object category processing. Thus, even though the P600 component has been thus far mostly related with syntactic processing rather than semantic processing, based on these results we cannot exclude the possibility of P600 being responsive to conceptual processing as well. This new component is interesting as the extent of its effect across studies thus far remains unresolved and requires further exploration.

REFERENCES

Bar, M., & Aminoff, E. (2003). Cortical analysis of visual context, *Neuron,* 38**,** 347–358.

Barrett, S. E., & Rugg, M. D. (1990). Event-related potentials and the semantic matching of pictures. *Brain and Cognition, 14*, 201–212.

Basso, A., Capitani, E., & Laiacona, M. (1988). Progressive language impairment without dementia: a case with isolated category specific semantic defect. *Journal of Neurology, Neurosurgery and Psychiatry, 51*, 1201–1207.

Caramazza, A., & Mahon, B. Z. (2003). The organization of conceptual knowledge: The evidence from category-specific semantic deficits. *Trends in Cognitive Sciences, 7*, 354–361.

Caramazza, A., Shelton, J. R., (1998). Domain-specific knowledge systems in the brain the animate–inanimate distinction. *Journal of Cognitive Neuroscience, 10*, 1–34.

Chang, T. (1996). Semantic memory: facts and models. *Psychological Bulletin*, *99*, 199–220.

Chao, L. L., Haxby, J. V., & Martin, A. (1999). Attribute-based neural substrates in temporal cortex for perceiving and knowing about objects. *Nature Neuroscience, 2*, 913–919.

Chao, L. L., & Martin, A. (1999). Cortical regions associated with perceiving, naming, and knowing about colors. *Journal of Cognitive Neuroscience, 11*, 25–35.

Chao, L. L., & Martin, A. (2000). Representation of manipulable man-made objects in the dorsal stream. *Neuroimage, 12*, 478–484.

Chao, L. L., Weisberg, J., & Martin, A. (2002). Experience-dependent modulation of

category-related cortical activity. *Cerebral Cortex, 12*, 545–551.

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

De Renzi, E., & Lucchelli, F. (1994). Are semantic systems separately represented in the brain? The case of living category impairment. *Cortex, 30*, 3–25.

Devlin, J. T., Gonnerman, L. M., Anderson, E. S., & Seidenberg, M. S. (1988). Category-specific semantic deficits in focal and widespread brain damage: a computational account. *Journal of Cognitive Neuroscience, 10*, 77-94.

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

Eddy, M., Schmid, A., & Holcomb, P. J. (2006). Masked repetition priming and event-related brain potentials: a new approach for tracking the time-course of object perception. *Psychophysiology*, *43*(6), 564-568.

Farah, M. J., & McClelland, J. L. (1991). A computational model of semantic memory impairment: modality specificity and emergent category specificity. *Journal of Experimental Psychology: General, 120*, 339–357.

Farah, M. J., McMullen, P. A., & Meyer, M. M. (1991). Can recognition of living things be selectively impaired? *Neuropsychologia, 29*, 185–193.

Federmeier, K. D. (2002). The impact of semantic memory organization and sentence context information on spoken language processing by younger and older adults: an ERP study. *Psychophysiology, 39*, 133–146.

Federmeier, K. D. (2007). Thinking ahead: the role and roots of prediction in language comprehension. *Psychophysiology, 44,* 491–505.

Federmeier, K. D., & Kutas, M. (1999). A rose by any other name: long-term memory structure and sentence processing. *Journal of Memory and Language, 41*, 469–95.

Friederici, A. D., Pfeifer, E., & Hahne, A. (1993). Event-related brain potentials during natural speech processing: effects of semantic, morphological and syntactic violations. *Cognitive Brain Research, 1*, 183–192.

Friedrich, M., & Friederici, A. D. (2004). N400-like semantic incongruity effect in 19-month olds: processing known words in picture contexts. *Journal of Cognitive Neuroscience, 16*, 1465-1477.

Friedrich, M., & Friederici, A. D. (2005). Phonotactic knowledge and lexical-semantic processing in one-year-olds: brain responses to words and nonsense words in picture contexts. *Journal of Cognitive Neuroscience*, *17*, 1785–1802.

Gerlach, C. (2001). Structural similarity causes different category-effects depending on task characteristics. *Neuropsychologia, 39***,** 895–900.

Gerlach, C., Law, I., & Paulson, O. B. (2004). Structural similarity and category-specificity: a refined account. *Neuropsychologia, 42***,** 1543–1553.

Gerlach, C., Law I., & Paulson, O. B. (2006). Shape configuration and category-specificity. *Neuropsychologia, 44***,** 1247–1260.

Grabowski, T. J., Damasio, H., & Damasio, A. R. (1998). Premotor and prefrontal correlates of category-related lexical retrieval. *Neuroimage, 7*, 232–243.

Grafton, S. T., Fadiga, L., Arbib, M. A., & Rizzolatti, G. (1997). Premotor cortex activation during observation and naming of familiar tools. *Neuroimage, 6*, 231–236.

Grill-Spector, K. (2003). The neural basis of object perception. *Current Opinion in Neurobiology, 13*, 1-8.

Grill-Spector, K., Knouf, N., & Kanwisher, N. (2004). The FFA subserves face perception not generic within category identification. *Nature Neuroscience, 7*(5), 555-562.

Hagoort, P., & Brown, C. M. (2000). ERP effects of listening to speech: semantic ERP effects. *Neuropsychologia, 38*, 1518–1530.

Hamm, J. P., Johnson, B. W., & Kirk, I. J. (2002). Comparison of the N300 and N400 ERPs to picture stimuli in congruent and incongruent contexts. *Clinical Neurophysiology, 113*, 1339–1350.

Hart, J., & Gordon, B. (1992). Neural subsystems for object knowledge. *Nature, 359*, 60–64.

Holcomb, P. J. (1988). Automatic and attentional processing: an event-related brain potential analysis of semantic priming. *Brain and Language, 35*, 66–85.

Holcomb, P. J., Kounios, J., Anderson, J. E., & West, W. C. (1999). Dual-coding, context-availability, and concreteness effects in sentence comprehension: an electro-physiological investigation. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 25*, 721–742.

Holcomb, P. J., & McPherson, W. B. (1994). Event-related brain potentials reflect semantic priming in an object decision task. *Brain and Cognition, 24*, 259–276.

Humphreys, G. W., & Forde, E. M. (2001). Hierarchies, similarity, and interactivity in object recognition: ''Category-specific'' neuropsychological deficits. *Behavioral Brain Science, 24*, 453–509.

Kanwisher, N. (2001). Faces and places: of central (and peripheral) interest. *Nature Neuroscience, 4*, 455–456.

Killgore, W. D., Young, A. D., Femia, L. A., Bogorodzki, P., Rogowska J., & Todd D. A. (2003). Cortical and limbic activation during viewing of high- versus low-calorie foods. *Neuroimage, 19*, 1381–1394.

Kolb, B., & Whishaw, I. Q. (2003). *Fundamentals of human neuropsychology* (5th ed.). New York: Worth.

Kovic, V. (2008). *Words and pictures: The effect of labelling on visual object processing*. Unpublished doctoral thesis, University of Oxford, UK.

Kutas, M. (1993). In the company of other words: electrophysiological evidence for single-word and sentence context effects. *Language & Cognitive Processes, 8*, 533–572.

Kutas, M., & Federmeier, K. D. (2001). Electrophysiology reveals semantic memory use in language comprehension. *Trends in Cognitive Sciences*, *4*, 463–70.

Kutas, M., & Hillyard, S. A. (1980). Reading senseless sentences: brain potentials reflect semantic incongruity. *Science, 207*, 203–205.

Kutas, M., & Hillyard, S. A. (1984). Brain potentials during reading reflect word expectancy and semantic association. *Nature, 307*, 161–163.

Kutas, M., & Van Petten, C. K. (1994). Psycholinguistics electrified: event related brain potential investigations. In M. A. Gernsbacher (Ed.), *Handbook of Psycholinguistics* (pp. 83–143). San Diego: Academic Press Inc.

Laiacona, M., Barbarotto, R., & Capitani, E. (1993). Perceptual and associative knowledge in category specific impairment of semantic memory: a study of two cases. *Cortex, 29*, 727–740.

Laiacona, M., Capitani, E., & Barbarotto, R. (1997). Semantic category dissociations: a longitudinal study of two cases. *Cortex, 33*, 441–461.

Lambon Ralph, M. A., Howard, D., Nightingale, G., & Ellis, A. (1998) Are living and non-living category-specific deficits causally linked to impaired perceptual or associative knowledge? Evidence from a category-specific double dissociation. *Neurocase, 4*, 311–338.

Laws, K. R., & Neve, C. (1999). A 'normal' category-specific advantage for naming living things. *Neuropsychologia, 37*, 1263–1269.

Lag, T. (2005). Category-specific effects in object identification: what is 'normal'? *Cortex, 41*, 833–841.

Lag, T., Hveem, K., Ruud, K. P. E., & Laeng, B. (2006). The visual basis of category effects in object identification: evidence from the visual hemifield paradigm. *Brain and Cognition, 60*, 1–10.

Leech, G., Rayson, P., & Wilson, A. (2001). *Word Frequencies in Written and Spoken English: based on the British National Corpus*. London: Longman.

Luck, S. J. (2005). *An introduction to the event-related potential technique.* Cambridge (MA): MIT Press.

Martin, A. (2001). Functional neuroimaging of semantic memory. In R. Cabaza & A. Kingstone (Eds.), *Handbook of Functional Neuroimaging of Cognition* (pp. 153–186). Cambridge (MA): MIT Press.

Martin, A. (2007). The Representation of Object Concepts in the Brain. *Annual Review of Psychology*, *58*, 25-45.

Martin, A., & Chao, L. L. (2001). Semantic memory and the bra structure processes. *Current Opinions in Neurobiology, 11*, 194–201.

Martin, A., Haxby, J. V., Lalonde, F. M., Wiggs, C. L., & Ungerleider, L. G. (1995). Discrete cortical regions associated with knowledge of color and knowledge of action. *Science, 270*, 102–105.

Martin, A., Ungerleider, L. G., & Haxby, J. V. (2000). Category-specificity and the brain: the sensory-motor model of semantic representations of objects*. In M. S. Gazzaniga (Ed.), *The Cognitive Neurosciences* (pp. 1023–1036). Cambridge (MA): MIT Press.

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

Mazerolle, E. L., D'Arcy, R. C., Marchand, Y., & Bolster, R. B. (2007). ERP assessment of functional status in the temporal lobe: Examining spatiotemporal correlates of object recognition. *International Journal of Psychophysiology*, *66*, 1, 81-92.

McCarthy, R. A., & Warrington, E. K. (1988). Evidence for modality-specific meaning

systems in the brain. *Nature, 334*, 428–430.

McPherson, W. B., & Holcomb, P. J. (1999). An electrophysiological investigation of semantic priming with pictures of real objects. *Psychophysiology, 36*, 53–65.

Moss, H.E. & Tyler, L.K. (2000). A progressive category-specific semantic deficit for non-living things. *Neuropsychologia, 38*, 60–82.

Moss, H. E., Tyler, L. K., Durrant-Peatfield, M., & Bunn, E. M. (1998). Two eyes of a see-through: Impaired and intact semantic knowledge in a case of selective deficit for living things. *Neurocase, 4*, 291–310.

Paivio, A. (1971). *Imagery and Verbal Processes*. New York: Holt, Rinehart & Winston.

Paivio, A. (1986). *Mental Representations: A Dual Coding Approach.* New York: Oxford University Press.

Paivio, A. (1991). Dual coding theory: retrospect and current status. *Canadian Journal of Psychology, 45*, 255–287.

Paz-Caballero, D., Cuetos, F., & Dobarro, A. (2006). Electrophysiological evidence for a natural/artifactual dissociation. *Brain Research, 1067*, 189–200.

Perani, D., Cappa, S. F., Bettinardi, V., Bressi, S., Gorno-Tempini, M., Matarrese, M., & Fazio, F. (1995). Different neural systems for the recognition of animals and man-made tools. *Neuroreport, 6*, 1637–1641.

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

Pietrini, V., Nertempi, P., Vaglia, A., Revello, M. G., Pinna, V., & Ferro-Milone, F. (1988). Recovery from herpes simplex encephalitis: selective impairment of specific semantic categories with neuroradiological correlation. *Journal of Neurology, Neurosurgery and Psychiatry, 51*, 1284–1293.

Pilgrim, L. K., Fadili, J., Fletcher, P. & Tyler, L. K. (2002). Overcoming confounds of stimulus blocking: an event-related fMRI design of semantic processing. *Neuro-image*, *16*, 713–723.

Proverbio, A. M., Del Zotto, M., & Zani, A. (2007). The emergence of semantic categorization in early visual processing: ERP indexes of animal vs. artifact recognition. *BMC Neuroscience*, *8*, 1, 24.

Simmons, W. K., Martin, A., & Barsalou, L.W. (2005). Pictures of appetizing foods activate gustatory cortices for taste and reward. *Cerebral Cortex, 15***,** 1602–1608.

Sitnikova, T., Kuperberg, G., & Holcomb, P. J. (2003). Semantic integration in videos of real-world events: an electrophysiological investigation. *Psychophysiology, 40*, 160–164.

Sitnikova, T., West, W. C., Kuperberg, G. R., & Holcomb, P. J. (2006). The neural organization of semantic memory: electrophysiological activity suggests feature-based anatomical segregation. *Biological Psychology*, *71*, 326-340.

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

Torkildsen, J. V. K., Sannerud, T., Syversen, G., Thormodsen, R., Simonsen, H. G., & Moen, I. (2006). Semantic organization of basic level words in 20-month-olds: An ERP study. *Journal of Neurolinguistics, 19*, 431–454.

Tyler, L. K., Bright, P., Dick, E., Tavares, P., Pilgrim, L., Fletcher, P., Greer, M., & Moss, H. (2003a). Do semantic categories activate distinct cortical regions? Evidence for a distributed neural semantic system. *Cognitive Neuropsychology, 20*, 541–559.

Tyler, L. K., Stamatakis, E. A., Dick, E., Bright, P., Fletcher, P., & Moss, H. (2003b). Objects and their actions: evidence for a neurally distributed semantic system. *Neuroimage, 18*, 542–557.

Tyler, L. K., & Moss, H. E. (2001). Towards a distributed account of conceptual knowledge. *Trends in Cognitive Sciences, 5*, 244–252.

Tyler, L. K. Moss, H. E. Durrant-Peatfield, M. R. & Levy, J. P. (2000). Conceptual structure and the structure of concepts: a distributed account of category-specific deficits. *Brain and Language, 75*, 195–231.

Van Berkum, J. J., Hagoort, P., & Brown, C. M. (1999). Semantic integration in sentences and discourse: evidence from the N400. *Journal of Cognitive Neuroscience, 11*, 657–671.

Warrington, E. K., & McCarthy, R. A. (1987). Categories of knowledge. Further fractionations and an attempted integration. *Brain, 110*, 1273–1296.

Warrington, E. K., & Shallice, T. (1984). Category specific semantic impairments. *Brain, 107*, 829–854.

West, W. C., & Holcomb, P. J. (2002). Event-related potentials during discourselevel semantic integration of complex pictures. *Cognitive Brain Research, 13*, 363–375.

Yang J. J, Francis, N., Bellgowan, P. S. F., & Martin, A. (2005). Object concepts in human amygdala: enhanced activity for identifying animals independent of input modality and stimulus format. Presented at *12th Annual Meeting Cognitive Neuroscience Society*, New York.

REZIME

JEDINSTVENE I/ILI RAZLIČITE MENTALNE REPREZENTACIJE ŽIVIH I NEŽIVIH OBJEKATA – ERP STUDIJA.

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U ovom članku je predstavljena ERP studija koja se bavi istraživanjem prirode mentalnih predstava živih i neživih objekata. Vezujući ERP signale za početak prezentacije vizuelnih stimulusa, došli smo veoma sličnih topografija pri procesiranju živih i neživih objekata. Štaviše, u slučaju mapiranja od opštijih ka specifičnijim mentalnim reprezentacijama (prezentacija slušnih podražaja, pa vizuelnih objekata) nijesmo našli razlike između živih i neživih objekata u amplitudi N400 komponente. Rezultati ove studije idu u prilog teoriji o jedinstvenoj semantičkoj organizaciji, a nikako u prilog teoriji o razdvojenosti mentalnih reprezentacija.

Neočekivano, takođe smo došli do nalaza da je P600 komponenta, koja je do sada uglavnom dovođena u vezu sa sintatičkim procesiranjem, takođe indikator konceptualnog procesiranja. Najočigledniju razliku, kada se tice P600 komponente, našli smo prilikom procesiranja tačno imenovanih živih i neživih vizulenih objekata, kom prilikom je procesiranje živih objekata proizvodilo intezivnije ERP signale u odnosu na procesiranje neživih objekata.

Ključne riječi: *mentalne reprezentacije, živi/neživi objekti, vizuelni stimulisi, ERP, N400*