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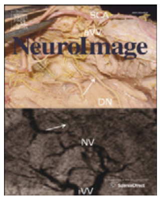

Alive and grasping: Stable and rapid semantic access to an object category but not object graspability

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ABSTRACT

How quickly do different kinds of conceptual knowledge become available following visual word perception? Resolving this question will inform neural and computational theories of visual word recognition and semantic memory use. We measured real-time brain activity using event-related brain potentials (ERPs) during a go/nogo task to determine the upper limit by which category-related knowledge (living/nonliving) and action-related knowledge (graspable/ungraspable) must have been accessed to influence a downstream decision process. We find that decision processes can be influenced by the living/nonliving distinction by 160 ms after stimulus onset whereas information about (one-hand) graspability is not available before 300 ms. We also provide evidence that rapid access to category-related knowledge occurs for all items, not just a subset of living, nonliving, graspable, or ungraspable ones, and for all participants regardless of their response speed. The latency of the N200 nogo effect by contrast is sensitive to decision speed. We propose a tentative hypothesis of the neural mechanisms underlying semantic access and a subsequent decision process.

Introduction

Millions of years of evolution have endowed a wide variety of organisms with peripheral and central nervous systems capable of acquiring, retaining, and retrieving knowledge about perceptible objects in their environment. However, only literate humans can rely on the indirect path to meaning (semantic access) from written language. Upon visually perceiving an inherently arbitrary symbol like “dolphin”, “dOLphIn”, or “𝒟𝒪ℒ𝒫ℋℐ𝒩”, for example, people can access the different kinds of knowledge they possess about dolphins, such as whether they are alive, their size, and their habitats—leading us to ask whether all knowledge is accessible at the same time upon word perception, or whether some kinds of knowledge become available prior to others? The current study examines the timing of semantic access during single word reading utilizing the high temporal resolution of the ERP technique.

Studies of the time course of visual object recognition (e.g., Clarke et al., 2011, 2012; Johnson and Olshausen, 2003; Liu et al., 2009; Schendan and Kutas, 2002; Thorpe et al., 1996; VanRullen and Thorpe, 2001) have advanced our understanding of the mechanisms of human and computer vision (Serre et al., 2007b; VanRullen and Thorpe, 2002). Several researchers also have examined the time course of visual word recognition, focusing primarily on the time course of orthographic, phonological, and lexical access (Barber and Kutas, 2007; Dehaene, 1995; Grainger and Holcomb, 2009; Hauk et al., 2006a, 2009; Pylkkanen and Marantz, 2003; Sereno and Rayner, 2003). Considerably less is known about the timing of access to conceptual knowledge for written words, and about how and when this process unfolds in the brain.

There are several good reasons to delineate the timing of semantic access. For one, a better understanding of the neural timing of semantic access will constrain computational models of semantic cognition and language comprehension (Laszlo and Plaut, 2012; McRae, 2004; Rogers et al., 2004). In particular, the latencies by which different kinds of information are available from written or spoken language will inform the question of whether the initial construction of word meaning involves automatic feed-forward mechanisms or top-down feedback mechanisms, as it has for theories of visual object recognition (Serre et al., 2007a; VanRullen and Thorpe, 2002). Specifying the time course of the availability of perceptual or motor-related knowledge versus that of more abstract forms of knowledge (e.g., encyclopedic information) also will inform current debates surrounding grounded or embodied cognition (Hauk and Tschentscher, 2013; Hauk et al., 2008). Specifically, timing information will be crucial to revealing the causal role of sensory, motor, and multimodal brain regions during language comprehension and in cognition more generally (Mahon and Caramazza, 2008; Pezzulo et al., 2011).

The current study focuses on the timing of access to two different kinds of knowledge that may be acquired by different kinds of experiences and represented in separate cortical systems. The relationship between sensory/motor cortex and action-related knowledge, and the relationship between supramodal/association cortex and taxonomic knowledge, have been studied in detail using fMRI, PET, and

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neuropsychological methods, but have received considerably less attention using techniques that provide real-time stimulus-evoked electrical brain activity. We asked our participants to decide whether a written word (e.g., "tiger", "hammer") refers to a living or nonliving entity; we assume that this type of decision does not necessarily involve previous sensory or motor experience with the entity. We also asked our participants to decide whether or not the same words refer to entities that are likely to be grasped with one hand; we assume that this decision is more likely to involve knowledge acquired via sensory and motor experience. More specifically, knowledge about actions afforded by objects is likely to be acquired by some combination of observation, practice/training, repetition, and implicit or explicit imitation, whereas acquiring knowledge about what an object is or is not, probably does not rely on these kinds of experiences.

Category-related object knowledge

The living/nonliving thing distinction was first investigated in the context of category-specific deficits, wherein knowledge about a specific object domain (e.g., living things, inanimate objects) is disproportionately degraded relative to other domains following brain damage due to herpes simplex encephalitis or stroke, for example (Warrington and Mccarthy, 1983; Warrington and Shallice, 1984). Subsequent brain imaging work has shown that higher-order visual cortex responds differentially to pictures or words denoting living versus nonliving things. Specifically, ventral regions of temporal occipital cortex exhibit a medial and lateral bias for nonliving and living things, respectively (Martin, 2007). Although visual experience likely shapes this category-related neural organization to some extent, it may not be necessary given that congenitally blind individuals exhibit a similar neural organization (Mahon et al., 2009); this finding suggests that regions in the temporal lobe may differentially represent living and nonliving thing concepts based on more than perceptually-grounded feature dimensions. In sum, several primary and associative cortical regions comprising but not confined to the temporal lobes are differentially active when participants decide whether a word denotes a living versus nonliving thing (Binder et al., 2009). This is consistent with the view that a widely distributed semantic memory system may be involved in access to category-related knowledge. As we review in a later section, preliminary evidence indicates particularly fast access to this kind of knowledge.

Action-related object knowledge

Action-related information (manipulability, graspability, etc.) constitutes an important subset of object knowledge in addition to sensory-related information such as color, taste, or sound. Humans routinely interact with medium-sized objects such as bananas, knives, and telephones, and do so largely with their hands. Proper interaction with these objects (e.g., grasping the handle rather than blade of a knife) depends in part on learned information such as the actions an object affords and the material from which it is made. Some scientists have argued that long-term memory evolved primarily to guide and plan actions (Gibson, 1979; Glenberg, 1997). Gibson (1979, p. 134), for instance, hypothesized that "what we perceive when we look at objects are their affordances," and that "[w]e can differentiate the dimensions of difference if required to do so in an experiment, but what the object affords us is what we normally pay attention to." If action affordance does play this central role in our conceptual representations of objects, it seems reasonable to predict that action-related knowledge can be accessed as quickly as category-related information but to our knowledge this prediction is untested.

Whereas a large literature exists on the physiological mechanisms of grasping behavior, fewer studies have examined the conceptual knowledge of actions afforded by objects. Creem and Proffitt (2001) showed that grasping common objects while attempting to recall previously learned semantic associates (e.g., pear–apple) impaired participants' ability to grasp the objects appropriately (e.g., by the handle), whereas performing a visuospatial imagery task (mentally rotating block letters) did not, despite equal task difficulty. They inferred that grasping behavior might recruit semantic resources. Myung et al. (2006) showed that action-related information may be automatically activated during language comprehension, in that words denoting manipulable objects ("typewriter") led to enhanced processing of words denoting perceptually disparate but manipulable objects ("piano"), and that eye movements were sensitive to whether distractor images depicted manipulable or visually-matched but unmanipulable objects. These findings suggest that action-related (at least manipulability) knowledge is activated during online single word reading, although they are silent as to when this information becomes available.

Using the go/nogo task and ERPs to monitor the time course of information access

The go/no-go task paired with electrophysiological recordings has been very useful for studying the timing of information access. When people execute (go) or withhold (nogo) a motor response to visual stimuli, ERPs at frontal sites exhibit a larger negativity for nogo trials versus go trials between 100 and 400 ms after stimulus onset (Gemba and Sasaki, 1989; Sasaki et al., 1993; Simson et al., 1977). The difference between the nogo and go ERPs is called the N200 or N2 effect. Thorpe et al. (1996) employed a go/nogo paradigm to examine rapid visual categorization of briefly presented scenes that either did or did not contain an animal; participants responded only when an animal was present (go response). The resulting N200 effect was evident by 150 ms, which was argued to represent an upper limit on the time by which the brain had processed sufficient visual information to determine that the scene did not contain an animal. This inference was questioned, however, as the scenes that contained animals and those that did not likely differed in low-level visual characteristics, which also have been found to influence electrophysiological activity before 150 ms (Johnson and Olshausen, 2003). In response to this concern, VanRullen and Thorpe (2001) ensured that the images from each category appeared equally often as targets and non-targets with the same images contributing to the average go and nogo ERPs. They found that the visual characteristics of the images affected ERPs by 80 ms, but also replicated the 150 ms N200 effect. This early nogo N200 effect was obtained in studies using images. The current study used words, which provide a less direct route to meaning and are less likely to engender low-level visual stimulus confounds. These differences between words and images could delay the time course of conceptual access for words relative to that for images.

The above experiments involved a single decision on each trial, but a handful of dual-task go/nogo ERP studies have employed a dual-task paradigm, in which participants make two different decisions per item: a go/nogo decision contingent upon one kind of information available from the stimulus, and a left/right hand decision on go trials contingent upon another kind of information available from the stimulus. Some dual-task studies, for example, used black and white line drawings, where the semantic decision was whether the image depicted an animal or an object (Rodriguez-Fornells et al., 2002; Schmitt et al., 2000), or whether the image depicted an object heavier or lighter than 500 g (Schmitt et al., 2001). In all cases the nogo ERP was characterized by a larger frontal negativity starting around 200 ms post-stimulus onset than the go ERP. This is somewhat later than nogo N200 effects in the visual object categorization studies, perhaps due to the use of line drawings instead of photographs, the use of longer stimulus duration latencies, differences in instructions, or some combination thereof.

Two go/nogo neurophysiological studies have employed words rather than pictures or images. Müller and Hagoort (2006) conducted a dual-task go/nogo ERP study to contrast a semantic decision (e.g., buildings vs. consumables; weapons vs. clothing) with a syntactic decision; they found a significant N200 effect beginning around 300 ms after stimulus onset—substantially later than those in the implicit picture naming or the visual categorization studies. Hauk et al. (2012) used a single-task paradigm with single words presented briefly (100 ms) in order to foster rapid decision-making along the lines of VanRullen and Thorpe (2001). They used a living/nonliving semantic decision rather than a more specific decision. In contrast to Müller and Hagoort (2006) they found that nogo and go ERPs at frontal sites significantly diverged by 168 ms for lexical decisions and by 166 ms for living/nonliving decisions. These onset latencies are very early—only slightly later than those reported in the rapid visual categorization studies (Thorpe et al., 1996; VanRullen and Thorpe, 2001), suggesting that people can begin to access conceptual information during visual word recognition almost as early as during visual object recognition.

Several questions remain unanswered, however. In particular, Hauk et al.'s evidence for rapid semantic access (i.e., <200 ms) in a decision-related paradigm is an important finding that calls for greater scrutiny. The main unanswered questions are whether information besides category-related information is accessed as quickly, and whether rapid semantic access can occur despite competition from another semantic task. The present study seeks to provide some answers. We compare the time course of semantic access in a single-task paradigm (Experiment 1) and dual-task paradigm (Experiment 2). Based on the reviewed studies we expect to find evidence for rapid semantic access (i.e., less than 200 ms) in the single-task paradigm but not the dual-task paradigm. For the first time we will directly compare semantic access to category-related knowledge (similar to many previous studies) and action-related knowledge, and we hypothesize that the semantic access will be faster for living/nonliving decisions than for graspable/ungraspable decisions. This prediction is based on the likelihood that certain graspability judgments may require mental simulation (e.g., running an implicit motor program) or some other additional process that will increase the time by which sufficient information is available to make the decision. On the other hand, if action affordance is central in peoples' conceptual representations of objects (Gibson, 1979), perhaps sufficient information becomes available to make the graspability decision as quickly as any decisions based on other kinds of conceptual information.

Experiment 1

Method

Participants

Twenty-six right-handed undergraduate students (10 males) between 18 and 30 years of age were recruited from the University of California, San Diego. The experiment was undertaken only with the understanding and written consent of each participant, who were awarded course credit and/or compensated at $7/h at the end of the experiment. Participants were native English speakers with no exposure to other languages before age 7, with normal or corrected-to-normal vision. Participants reported no major neurological or general health problems, and no psychoactive medication use.

Stimuli

Ninety nouns denoting nonliving things and 90 nouns denoting living things were selected from available object attribute norms (Amsel et al., 2012). Within each set, 45 nouns denoted highly graspable objects and 45 denoted highly ungraspable objects according to the Amsel et al.'s ratings, in which participants judged "how likely is someone to grasp this object with one hand?" on a scale from extremely unlikely (1) to extremely likely (8). Items in each of the four conditions were matched as closely as possible on the number of letters, syllables, and phonemes, familiarity according to Amsel et al., and two improved measures of lexical frequency: subtitle frequency and contextual diversity (Brysbaert and New, 2009).

Design

Each participant completed two blocks in which every noun was presented once per block. Four versions of the experiment were created such that half of the participants responded (i.e., go trials) to living things and graspable things, the other half responded to nonliving things and ungraspable things. The order of the blocks alternated across participants such that every fourth participant received the same version. The order of trial presentation was randomized within blocks and across subjects.

Procedure

Participants were tested individually while seated in a dimly lit, sound attenuating, electrically shielded chamber (Industrial Acoustics Company, Inc.), in front of a CRT monitor. Before each block the experimenter explained the particular decision criterion including examples. Verbal instructions for each kind of decision are shown in the Appendix A. The experimenter then presented eight example decisions (4 positive, 4 negative), and ensured that the participant understood the correct decision for each. Finally, the participant completed 32 practice trials identical to the experimental trials with the exception that the experimental and practice stimuli did not overlap.

The experimental trials in each block were performed in 5 segments of 36 trials separated by rest periods. Each block lasted approximately 20 min and the entire experiment typically lasted less than 2.5 h. Each trial began with a centrally-presented fixation cross (+) presented for a randomly selected interval between 1000 and 1250 ms. An experimental item replaced the fixation cross and remained on the screen for 2000 ms during which responses were registered, and after which the screen appeared blank for a randomly selected interval between 500 and 1500 ms. Words were presented in white Helvetica font against a black background and each letter subtended about 0.7 and 0.5° of visual angle in height and width at a viewing distance of 112 cm. Participants were instructed to rest their arms on their laps and rest their right thumb on a response button mounted on a rubber handle. Participants were asked to refrain from blinking and other movement from the onset of the fixation cross to the offset of the word.

Apparatus and recording

Response latencies were measured from word onset; responses occurring after 2000 ms were not registered. The electroencephalogram (EEG) was continuously recorded from 26 geodesically-arranged tin electrodes embedded in an ElectroCap (impedances were kept below 5 kΩ), and referenced to the left mastoid. Eye movements and blinks were monitored with electrodes placed on the left and right lower orbital ridges, and left and right external canthi. The EEG was digitized at a sampling rate of 250 Hz and bandpass filtered between 0.01 and 100 Hz with James Long amplifiers (www.JamesLong.net).

Potentials were re-referenced offline to the mean of left and right mastoids. Averages were obtained for 1200 ms epochs including a 200 ms pre-stimulus baseline period. Trials of correct responses were visually inspected for each subject. Trials containing vertical or horizontal eye movements, amplifier blocking, or any other artifacts within the critical time window were discarded. The mean percentage of rejected trials (19%) did not reliably differ between the decision categories or between go and no-go trials.

Results

During debriefing the experimenter asked if any decision for any item was particularly difficult or confusing, and certain trials were mentioned by more than a single subject. For example two participants reported difficulty deciding whether "beehive" was a living thing or not, and another two participants reported difficulty deciding whether "saucer" denoted a graspable or ungraspable object (one participant was not familiar with its meaning). The overall mean response times for these two items were 1003 ms and 981 ms in comparison with the grand mean of 770 ms across all items. In fact, upon inspection of the mean go trial response times for each item, we found that several items in each condition were uncharacteristically slow (and typically less accurate). Because our goal was to examine relatively early and automatic access to semantic knowledge, and not strategic processing, we elected to remove all behavioral and EEG data from the 10 slowest items in each of the four conditions from further analyses. Among the remaining items were seven compound words ("doorknob", "handgun", "earmuffs", "bathtub", "bookcase", "dishwasher", "sailboat"). These item removals lowered the grand mean of all go trials to 741 ms. Importantly, the differences between the mean RT and accuracy measures across experimental conditions did not significantly change, nor did the matched characteristics of items in each condition (Table 1).

Behavioral responses

Accuracy. Hit rates were above 90% in both conditions (Category = 95.8%; Graspability = 94.2%), as were correct rejections (Category = 94.9%; Graspability = 91.6%). Neither measure differed statistically between conditions.

Response times (hits). All correct responses with latencies between 200 and 2000 ms were retained. Living/nonliving decisions ($M = 716$, $SD = 219$) were significantly faster than graspability decisions ($M = 765$, $SD = 222$), $t(25) = 2.8$, $p = 0.01$, as shown in Fig. 1.

ERPs

For each correct trial, data were averaged across trials to create ERPs for each participant and poststimulus potentials were measured relative to mean amplitude during the prestimulus baseline interval from −200 to 0 ms. N1 and P1 are present at all but posterior sites, followed by a P2 peaking shortly after 200 ms at all but posterior sites, and a negative-going deflection peaking around 420 ms at central and frontal sites (N2). Beginning around 500 ms, a sustained frontal positivity is present for the remainder of the epoch. At prefrontal sites, the N2 and P3 components are visibly larger for no-go versus go trials in both response conditions.

Repeated-measures ANOVAs were conducted on the mean amplitudes of different ERPs obtained by subtracting go ERPs from no-go ERPs at five prefrontal electrodes (left/right medial, left/right lateral, and midline) in two time windows (150 to 200 ms, and 300 to 600 ms). Electrode sites were selected based on the known frontal maximum for the no-go minus go difference (Müller and Hagoort, 2006; Schmitt et al., 2000; Thorpe et al., 1996). Time windows were selected by inspecting the grand average go and no-go waveforms collapsed across experimental conditions, and by consulting previous go/no-go studies of visual word and object recognition (Hauk et al., 2012; Müller and Hagoort, 2006; VanRullen and Thorpe, 2001). For all ANOVAs with greater than two degrees of freedom in the numerator, *p*-values are reported after Huynh–Feldt epsilon correction for repeated measures; uncorrected degrees of freedom and *F* ratios are reported for interpretability.

Table 1
Means and standard deviations of item characteristics.

Variable	Nonliving thing		Living thing	
	Graspable	Ungraspable	Graspable	Ungraspable
Graspability	7.2 (.4)	1.7 (.3)	7.3 (.4)	1.6 (.4)
Familiarity	7.3 (.2)	7.2 (.3)	7.5 (.2)	7.0 (.2)
Frequency	2.4 (.5)	2.5 (.4)	2.3 (.4)	2.4 (.4)
Contextual diversity	2.3 (.5)	2.3 (.4)	2.1 (.4)	2.1 (.4)
Length	5.8 (1.4)	6.0 (1.8)	5.7 (1.6)	5.8 (1.5)
Phonemes	4.9 (1.4)	4.9 (1.6)	4.9 (1.6)	4.7 (1.6)
Syllables	1.7 (.7)	1.9 (.8)	1.9 (.8)	2.0 (.8)

The difference between no-go and go trials was larger for category versus graspability judgments in the P2 window, although the main effect of condition was not statistically significant ($p = .22$). Planned paired-sample t-tests at the midline prefrontal site within the P2 window revealed that the no-go waveform was already significantly more positive than the go waveform for category decisions, $t(25) = 2.1$, $p < .05$, difference = .44 μV, but that the no-go and go ERPs did not differ for graspability decisions, $t < 1$, difference = −.18 μV (see Fig. 1). The greater negativity for no-go versus go trials was visibly larger for graspability versus category judgments in the N2 window, but the main effect of condition did not reach the conventional significance level, $F(1, 25) = 2.7$, $p = .11$. Planned paired-sample t-tests at the midline prefrontal site, however, revealed that within the N2 window the no-go waveform was significantly more negative than the go waveform for graspability decisions, $t(25) = 2.3$, $p < .05$, difference = 1.06 μV, whereas the no-go and go ERPs did not differ for category decisions, $t < 1$, difference = .19 μV (Fig. 1).

Experiment 2

Experiment 2 was identical to Experiment 1 with three exceptions. First, following Schmitt et al. (2000), response competition was introduced whereby one kind of decision (e.g., graspability) was mapped onto the go/nogo criterion and the other kind of decision (e.g., category) was mapped onto a handedness criterion (i.e., left versus right button press). Second, we increased statistical power in comparison to Experiment 1 by presenting four rather than two blocks per participant. Third, the 10 items per condition that were excluded before analyses in Experiment 1 were not presented in Experiment 2.

Method

Participants

Twenty-six undergraduate students (9 males). Inclusion criteria, recruiting practice, and subject characteristics identical to Experiment 1.

Stimuli

The 35 items/condition from Experiment 1 (see Table 1).

Design

Four conditions were formed by crossing go/nogo criterion (category, graspability), and response hand (left button press, right button press). Each participant completed four blocks in total and every item was presented once per block. In two blocks, the go/nogo criterion was determined by graspability and the left/right button criterion was determined by category. The other two blocks contained the reverse pairing. Left/right hand and go/no-go responses were counterbalanced for each item across two versions of the experiment such that half of the participants received one version and the other half received the other version. Items appeared in a different random order in every block within and across subjects, and block order was randomized across subjects.

Procedure, apparatus, and recording

The experimental procedure, apparatus, and recording parameters were identical to Experiment 1 except that participants were familiarized with the dual-task paradigm rather than the single-task paradigm. The experimenter ensured that participants understood that each trial should be performed as quickly as possible. Participants completed four blocks lasting approximately 15 min each, and the entire experiment typically lasted less than 3 h. The percentage of rejected trials due to EEG artifacts did not reliably differ between category (16.2%) and graspability (14.0%) decisions, but did statistically differ between go (12.6%) and no-go trials (17.5%).

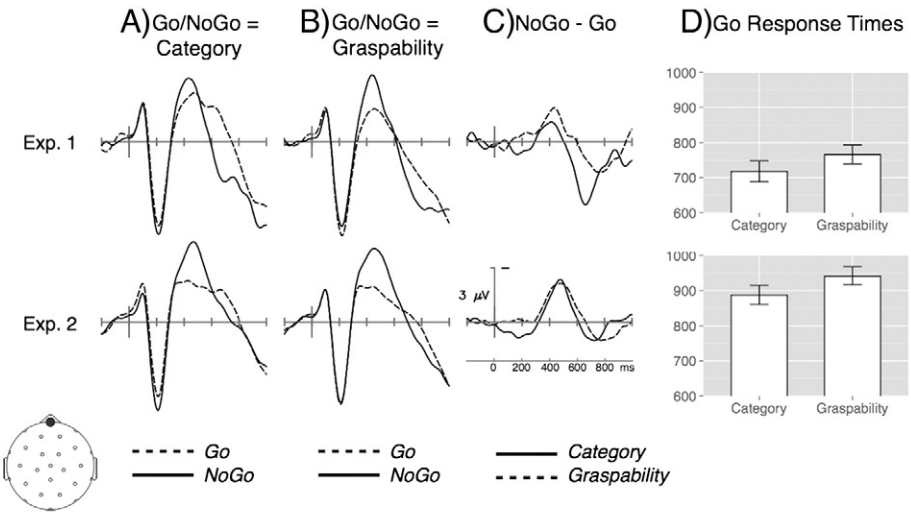

Fig. 1. Experiment 1 and 2 ERPs for the category (living/nonliving) decision (Panel A), graspability (graspable/ungraspable) decision (Panel B), corresponding NoGo–Go difference waves (Panel C) and go response times (Panel D). Between 150 and 200 ms in both experiments, no-go ERPs were significantly more positive than go ERPs for category but not graspability judgments. Between 200 and 600 ms in Experiment 1, no-go ERPs were significantly more negative than go ERPs for graspability but not category judgments, and no significant difference between go and no-go trials was found in Experiment 2. As shown in the far right column, response times for go trials were significantly faster when the go/no-go decision criterion was contingent upon object category versus graspability in both experiments, and overall mean response times were substantially slower in Experiment 2.

Results

Behavioral responses

All correct responses were submitted to the behavioral analyses.

Accuracy. Hit rates for category decisions (95.3%) were higher than for graspability decisions (88.5%), and correct rejections were higher for category (97.4%) than for graspability (96.1%) decisions. A within-subjects ANOVA with response hand and decision type as factors revealed that the hit rate difference was statistically significant, $F(1,25) = 5.8$, $p < .05$, the correct rejection difference was not $p < .2$, and hand did not interact with decision type.

Response times (hits). All correct responses with latencies above 200 ms were retained.

Across subjects, category judgments ($M = 890$, $SD = 142$) were significantly faster than graspability judgments ($M = 943$, $SD = 129$), $t(25) = -2.3$, $p = 0.01$, as shown in Fig. 1.

ERPs

A 2 (decision type) × 5 (prefrontal electrode site) repeated-measures ANOVA revealed a main effect of decision type in the 150 to 200 ms window, $F(1, 25) = 5.7$, $p < .03$, such that the no-go–go difference was significantly larger for category decisions than for graspability decisions. Paired-sample t-tests at the midline prefrontal site revealed that whereas nogo ERPs were significantly more positive than go ERPs for category decisions, $t(25) = 3.1$, $p < .01$, difference = 1.0 μV, the equivalent ERPs did not differ for graspability decisions, $t < 1$, difference = .2 μV (Fig. 1). The N2 difference waves appear very similar across response conditions (Fig. 1), and no significant effects were found in this window.

The time courses of the nogo–go ERP difference waves are examined in two additional ways. We inspect global signal strength by computing root-mean square (RMS) curves given by $RMS = \sqrt{\frac{1}{k}\sum_{i=1}^{k} a_i^2}$, where k is the number of electrode sites and a is mean amplitude. Fig. 2 presents RMS curves for each decision criterion computed across two sets of electrodes corresponding to anterior and posterior/central scalp sites. An early peak for object category decisions is clearly visible in the anterior RMS curves within the 150 to 200 ms window (delineated by two vertical dashed lines), whereas no such peak occurs for graspability decisions. After 300 ms, the relatively larger N2 effect begins to develop in both conditions. Posterior RMS curves reveal essentially no change from baseline in either response condition until a relatively late effect begins to develop in both conditions after about 400 ms.

Fig. 3 depicts the fine-grained time course of effects in the go–nogo difference waves for each condition as determined by mass-univariate analysis. Two raster plots show the results of repeated-measures t-tests at all time points between 140 and 600 ms at all 26 scalp sites for category judgments (top row) and graspability judgments (bottom row). Given the large number of comparisons, false discovery rate (FDR) was controlled with an adaptive linear step-up procedure (Benjamini et al., 2006) implemented in the mass univariate ERP toolbox (http://openwetware.org/wiki/Mass_Univariate_ERP_Toolbox). Although this procedure is not guaranteed to control FDR, simulation studies with ERP data suggest that it strikes a practical balance between adequate control of the FDR rate and retention of statistical power (Groppe et al., 2011). In order to increase statistical power, we excluded time points prior to 140 ms after determining that this region contained no significant comparisons. T-tests that are significant at an FDR level of 0.05 are marked in white (positive difference wave) or black (negative difference wave) and non-significant tests are shown in gray. Beginning after 152 ms in the object category difference wave, the amplitude difference reaches corrected statistical significance for 8 consecutive t-tests (until 184 ms) at the midline prefrontal site, and for several temporally contiguous tests at other pre/frontal sites within the same window. At the 156 to 160 ms interval, significant t-tests are present at ten different electrode sites. In contrast, this early frontal effect is absent in the graspability difference waves, where a run of 8 consecutive significant t-tests does not begin until about 340 ms.

Fig. 4A shows waveforms for both decision criteria at two lateral and one midline prefrontal electrode at a finer time scale. Fig. 4B shows the distribution of averaged potentials across the scalp between 150 and 200 ms according to spherical spline interpolation. The prefrontal maximum of the object category ERP difference is clearly visible along with the absence of any such effect in the graspability scalp map.

Next we examined whether specific subsets of items were driving the differences in the latency or amplitude of relevant ERP effects. Figs. 5 and 6 show the ERPs, difference waves, and response times associated with each decision type broken down into living and nonliving items (Fig. 5) and graspable and ungraspable items (Fig. 6). Together these waveforms constitute the grand average waveforms in the bottom

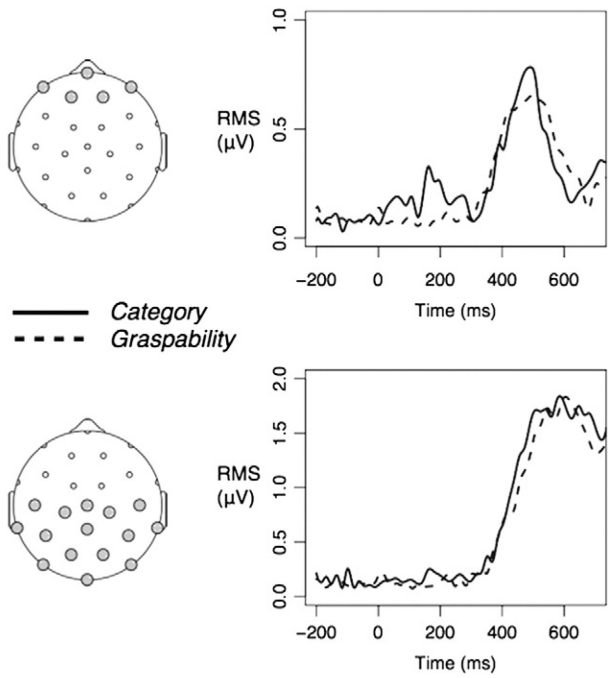

Fig. 2. Time course of global signal strength of the NoGo–Go ERP difference in Experiment 2. Root-mean square (RMS) curves for each decision criterion are computed across two sets of electrodes corresponding to anterior and posterior/central scalp sites. An early peak for object category decisions is visible in the anterior RMS curves (top row) between 150 and 200 ms, whereas no such peak occurs for graspability decisions. After 300 ms, the relatively larger N2 effect begins to develop in both conditions. Posterior RMS curves (bottom row) reveal essentially no change from baseline in either response condition until a relatively late effect begins to develop in both conditions after about 350 ms.

row of Fig. 1. For example, the left-most column of Fig. 5 shows ERPs computed after retaining only the trials containing a living thing item, the second column shows ERPs computed after retaining only the trials containing a nonliving thing item, the third column contains the corresponding difference waves, and the final column shows corresponding go response times.

When the go/nogo decision is contingent on object category, the magnitude of the P2 difference appears larger (and peaks later) when only nonliving thing items are retained (Fig. 5). Within the 150 to 200 ms time window, however, which encompasses the initial portion of this positive-going deflection, a 2 (decision: category, graspability) × 2 (item type: living, nonliving) repeated-measures ANOVA at the midline prefrontal site revealed a main effect of decision, $F(1,25) = 7.7$, $p = .01$, but no effect of item type and no interaction ($Fs < 1$). During the N2 window, the magnitude of the difference for both decision contingencies is larger for trials including living but not nonliving thing items, $F(1, 25) = 5.1$, $p = .03$, and item type does not interact with decision, nor does decision type differ independently from item type ($Fs < 1.5$). In sum, the rapid access to object category knowledge was observed for both living thing objects such as fruits, trees, and animals, and nonliving thing objects such vehicles, utensils, or buildings. Second, the larger N2 effect for living thing items regardless of the go/nogo decision criterion suggests the presence of a task-independent difference between processing words denoting living versus nonliving things. Also note that the increased N2 effect is associated with decreased response times in both decision contingencies.

When the go/nogo decision is contingent on graspability, the P2 difference is clearly visible when either graspable or ungraspable items are retained in the average waveform (Fig. 5). A 2 (decision: category, graspability) × 2 (item type: graspable, ungraspable) repeated-measures ANOVA at the midline prefrontal site revealed a main effect of decision, $F(1,25) = 4.1$, $p = .05$, but no effect of item type and no interaction ($Fs < 1$). During the N2 window the magnitude of the differences for graspable versus ungraspable items appears almost identical for category decisions and although numerically different for the graspability decision, ANOVA did not reveal any significant effects in this time window ($Fs < 1$).In sum, consistent with the previous item-based analysis, the rapid access to object category knowledge was not confined to generally smaller graspable objects such as fruits, small animals, tools, and utensils, and was not confined to generally larger objects such as trees, large mammals, vehicles, and buildings. In contrast to the previous analysis, the N2 effect was not modulated by item graspability, and there was no evidence for a systematic relationship between N2 amplitude and response time.

Finally, we examined the go/nogo differences as a function of response time. The first piece of evidence that the early object category effect at the midline prefrontal site is not related to response time is

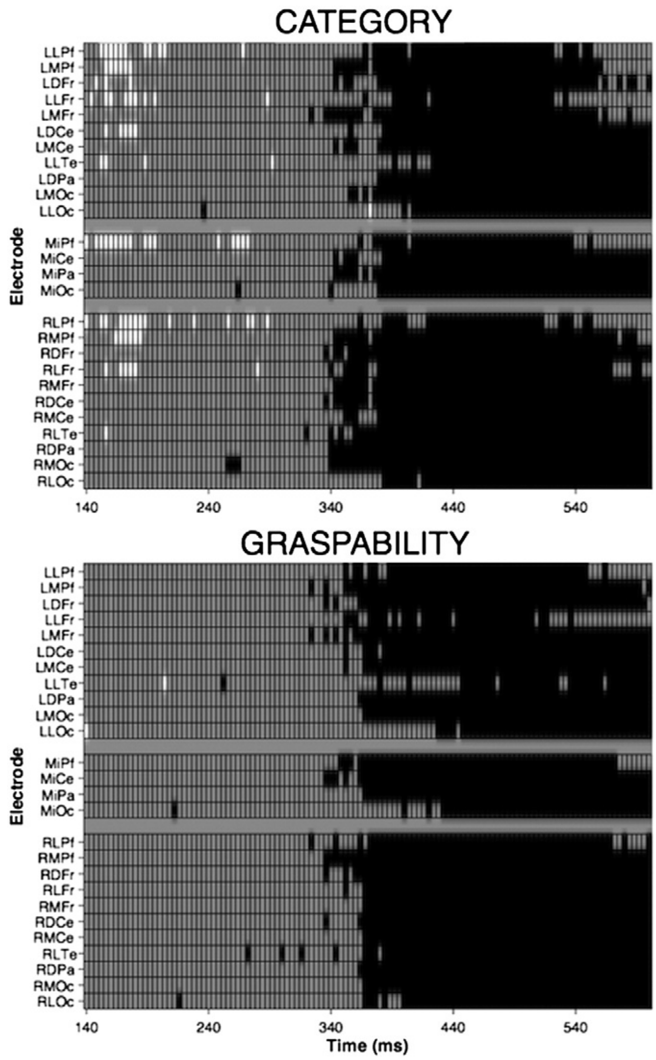

Fig. 3. Mass univariate statistical analysis of the time course of ERP differences for each decision criterion in Experiment 2. Raster plots convey the results of repeated-measures t-tests at every 4 ms interval between 140 and 600 ms at all 26 scalp sites for category (living/nonliving) judgments (top row) and graspability (graspable/ungraspable) judgments (bottom row). Laterality (left, middle, right) is represented by the top, middle, and bottom sections of each plot. Within each section the electrode sites are listed in an anterior-to-posterior progression. False discovery rate (FDR) was controlled with an adaptive linear step-up procedure, and t-tests that are significant at an FDR level of 0.05 are marked in white (positive difference wave) or black (negative difference wave) and non-significant tests are shown in gray. Beginning after 152 ms in the object category difference wave, the difference reaches statistical significance for 8 consecutive t-tests at the midline prefrontal site. In contrast, an early frontal effect is absent in the graspability difference waves, where a run of 8 consecutive significant t-tests reflecting the N2 effect does not begin until about 340 ms at more posterior scalp sites.

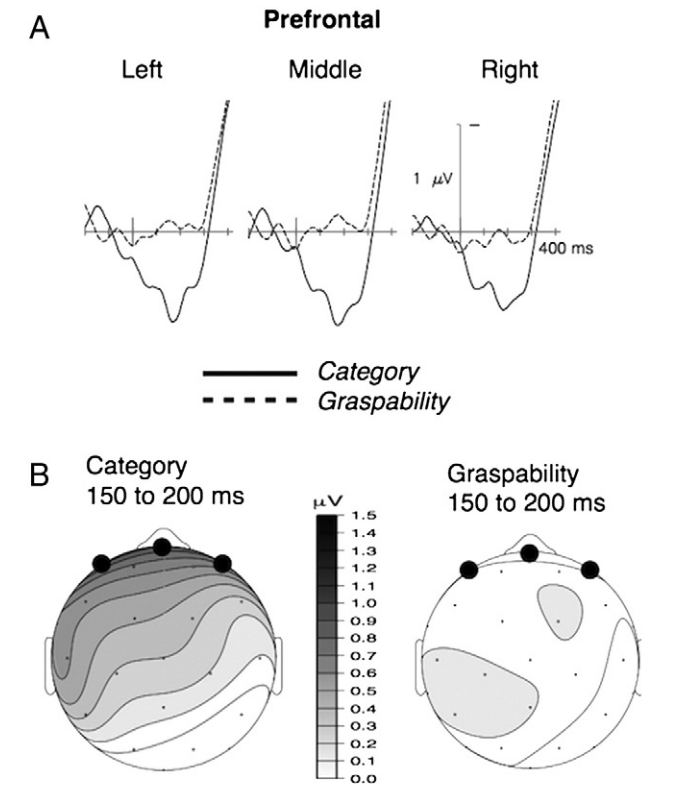

Fig. 4. A). Experiment 2 NoGo–Go ERPs at three prefrontal electrodes. The early effect in the category (living/nonliving) decisions is most pronounced between 150 and 200 ms, during which no difference is present for the graspability (graspable/ungraspable) decisions. B) Distributions of mean grand average potentials between 150 and 200 ms according to spherical spline interpolation. Small black circles surround the three prefrontal sites shown in A). The prefrontal maximum of the category ERP difference is clearly visible, and no such effect is visible in the graspability scalp map.

that we found the effect in both experiments, despite the 170 ms difference in overall response times for go = category trials across experiments. To further test for an influence of response times on a by-subject basis we divided participants into fast and slow responders by computing a median split of go response times (hits) averaged across both decision criteria. Fig. 7 shows the ERPs and difference waves divided by responder type. The mean response times for fast and slow responders for each decision type are shown in the right-most column, which differ dramatically across groups in comparison with any within-subject RT differences (i.e., fast responders are approximately 250 ms faster than slow responders). Despite this marked difference in task performance, the early nogo–go effect for object category judgments is clearly visible for both fast and slow responders. A mixed-factor ANOVA was computed on mean difference amplitudes at both established time windows, with go/nogo decision criterion and electrode site (five prefrontal) as within-subjects factors and responder (slow, fast) as a between-subjects factor. Decision criterion was significant in the 150 to 200 ms time window, $F(1, 24) = 5.5$, $p = .03$, but responder type was not significant and did not interact with decision (Fs < 1). Although the N2 time window (200 to 600 ms) did not reveal any effects of decision or responder type (Fs < 1), the N2 difference wave for both types of decisions is visibly larger and possibly earlier for fast versus slow responders, and a later positive deflection resembling the frontal P3a component clearly peaks earlier in fast versus slow responders. The proficiency of participants in terms of response time does not appear to influence the rapid access to object category information, but does appear to influence later processes.

Discussion

We presented an identical set of words in a single-task and dual-task go/nogo decision paradigm, and showed that information that can be used to differentiate living from nonliving things was available by 160 ms, whereas the information that can be used to differentiate graspable from ungraspable objects was not available before around 300 ms. Moreover, we find that rapid access to object category knowledge can occur during a more difficult dual-task paradigm, and when stimuli remain on the screen during the entire decision interval rather than for a brief interval. Data from the dual-task paradigm (Experiment 2) show that this effect is quite stable in that it occurs (*i*) whether ERPs are created exclusively from trials in which the word refers to generally larger ungraspable objects versus smaller graspable objects, (*ii*) whether the ERPs are created exclusively from trials in which the word refers to living or nonliving things, and (*iii*) in subsets of participants who performed the behavioral component of the task (i.e., go trials) relatively quickly or slowly. In situating our results with studies concerning the

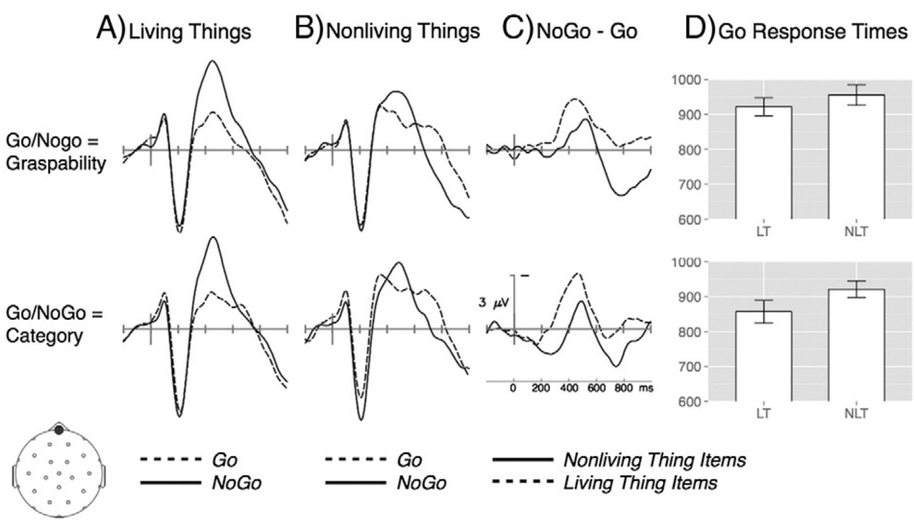

Fig. 5. Experiment 2 ERPs for living thing items (Panel A), nonliving thing items (Panel B), corresponding NoGo–Go difference waves (Panel C) and response times (Panel D). Rapid access to category knowledge was found for nonliving thing objects such as vehicles, utensils, or buildings as well as living thing objects such as fruits, trees, and animals. Although the NoGo–Go difference peaks later and is more pronounced for nonliving thing items, within the 150 to 200 ms time window item type (living thing vs. nonliving thing items) did not interact with the decision criterion. During the N2 window, the magnitude of the difference for both decision contingencies is larger for trials including living but not nonliving thing items and item type does not interact with decision, nor does decision type differ independently from item type.

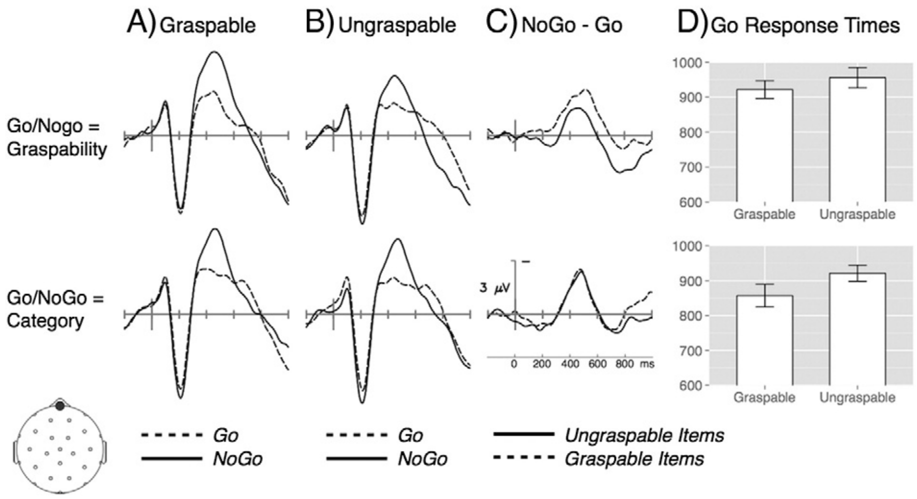

Fig. 6. Experiment 2 ERPs for graspable items (Panel A), ungraspable items (Panel B), corresponding NoGo–Go difference waves (Panel C) and response times (Panel D). Rapid access to object category knowledge was not confined to generally smaller graspable objects such as fruits, small animals, tools, and utensils, and was not confined to generally larger objects such as trees, large mammals, vehicles, and buildings. Within the 150 to 200 ms time window, item type did not interact with decision category. During the N2 window the magnitude of the differences for graspable versus ungraspable items appears somewhat different for graspability decision and almost identical for category decisions, but neither comparison reached statistical significance.

time course of information access, we find it helpful to place our findings alongside other relevant findings on a timeline (Fig. 8).

ERP components and the time course of accessing stimulus information

Thorpe et al. (1996) argued that the difference between nogo and go trials is generated by neural activity specific to nogo trials. The onset of the nogo–go difference in their experiment occurs at about 150 ms and reflects a larger positive-going waveform associated with go trials relative to nogo trials—a difference most prominent over frontal sites. The difference continues in the form of a negativity that is larger for nogo trials relative to go trials, dissipating after about 350 ms. This negativity essentially replicates the timing, polarity, and amplitude differences reported in initial studies of the N2 effect in humans (Gemba and Sasaki, 1989; Simson et al., 1977). Go/nogo ERP studies of language processing have used the latency of the nogo N2 effect to infer when different kinds of information are available and these studies report a range of latencies, all post 200 ms (Müller and Hagoort, 2006; Rodriguez-Fornells et al., 2002; Schmitt et al., 2000, 2001). In the current experiments, both semantic decision criteria generate nogo N2 effects that are statistically indistinguishable from each other in latency, and which fall within the latency range of other studies of language processing.

Inspection of these nogo N2 effects could lead one to conclude that different kinds of semantic information available from a single word are accessed at about the same time, albeit substantially later than in rapid visual categorization studies. However, our data and those from another recent study (Hauk et al., 2012) suggest otherwise. We find that the living/nonliving decision but not the graspable/ungraspable decision produces a nogo–go difference by 160 ms at prefrontal electrode sites, corresponding to the initial positive-going slope of a positivity that resembles the P2 component. The frontal P2 is typically larger for stimuli that contain a target feature (color, orientation, size), and has been argued to reflect the detection and analysis of task-relevant features (Luck and Hillyard, 1994). The frontal P2 is also reportedly larger in amplitude when a target word is preceded by a highly constraining

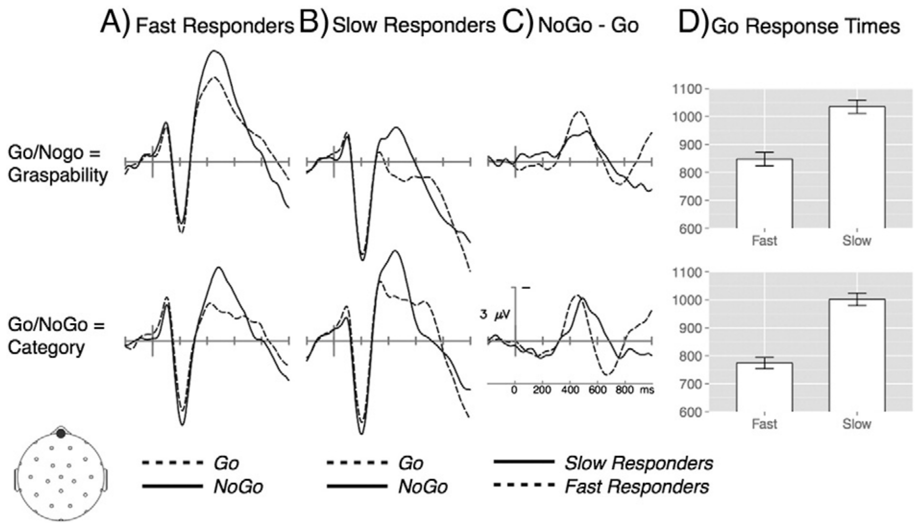

Fig. 7. Experiment 2 ERPs and difference waves for fast responders ($N = 13$) and slow responders ($N = 13$). The mean go response times for fast and slow responders (median split) for each decision type are shown in D); fast responders have a 250 ms advantage over slow responders. Despite this marked difference in behavior, the NoGo–Go difference for category (living/nonliving) decisions is clearly visible in both groups between 150 and 200 ms.

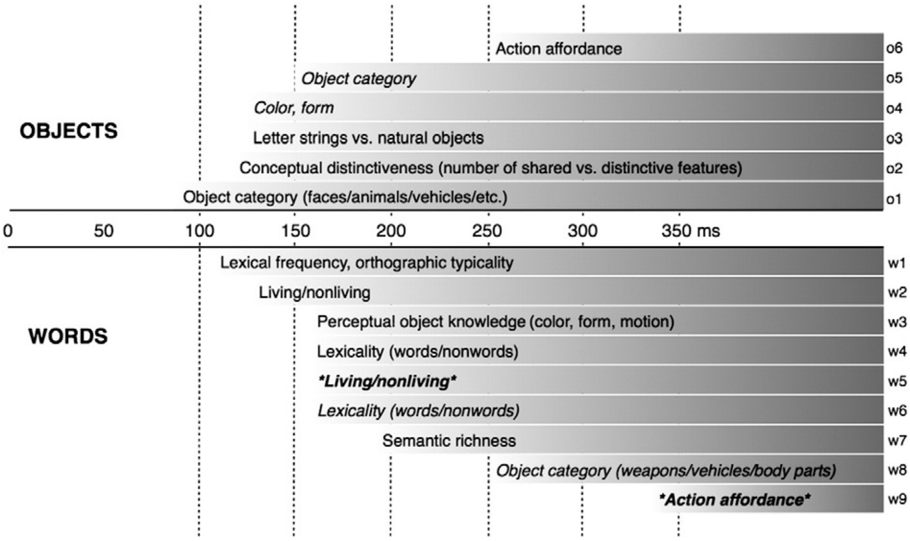

Fig. 8. Results of electrophysiology and MEG studies relevant to the time course of information access in word and object recognition. Entries above the timeline correspond to experiments that employed object stimuli (line drawings, photos, digitally-rendered images) and entries below the timeline correspond to experiments that employed visual word stimuli. The left-hand border of each entry depicts a rough estimate of the onset latencies of experimental effects—namely that the listed type of information is differentiated in real-time dependent measures of brain activity. Each entry is based on at least one reference (rightmost legend corresponds to references below), and represents a temporal region rather than an attempt to establish a specific onset. Italicized entries signify effects obtained during tasks requiring an overt behavioral marker of stimulus recognition such as those used in the current experiments. Non-italicized entries represent effects that were obtained in tasks that did not require an overt marker of stimulus recognition, and could be driven in part by bottom-up activation of low-level visual properties. The effects found in the current study are bolded. **References**. *Words*. (w1) Assadollahi and Pulvermüller (2003); Dambacher et al. (2006); Hauk et al. (2006a, 2006b); Sereno et al. (1998). (w2) Chan et al. (2011). (w3) Amsel (2011); Moscoso del Prado et al. (2006). (w4) Hauk et al. (2006a); Sauseng et al. (2004). (w5) **Current study**; Hauk et al. (2012). (w6) Hauk et al. (2012). (w7) Amsel (2011); Kounios et al. (2009); Rabovsky et al. (2012). (w8) Müller and Hagoort (2006). (w9) **Current study**. *Objects*. (o1) Liu et al. (2009); VanRullen and Thorpe (2001). (o2) Clarke et al. (2012). (o3) Allison et al. (1999); Nobre et al. (1994); Schendan et al. (1998). (o4) Vogel and Luck (2000). (o5) VanRullen and Thorpe (2001). (o6) Proverbio et al. (2011).

sentence context versus a less constraining context (Federmeier et al., 2005; Wlotko and Federmeier, 2007), which may reflect top-down facilitation of visual feature extraction. It is unclear how these views of the functional significance of the visual P2 can inform our finding that the frontal P2 is larger for nogo versus go trials when the go/nogo decision is contingent upon the living versus nonliving distinction. Participants must keep the go/nogo criterion in mind during a given block of trials, which could provide top-down facilitation of access to a specific kind of meaning. However, the visual properties of the stimuli remain constant across both decision criteria and across go and nogo trials, thereby ruling out top-down facilitation of a strictly perceptible stimulus feature.

Hauk et al. (2012) obtained an equally early nogo–go difference when the go/nogo decision was contingent upon object category (living/nonliving) or upon lexicality (words/pseudowords). Consistent with Hauk et al., the initial nogo–go difference beginning after about 160 ms occurs on a positive-going component followed by a larger nogo–go difference at the negative-going N200 component that peaks after 300 ms. The earlier frontal P2 component thus may constitute the earliest evidence that sufficient information has been accessed to influence the decision outcome. Moreover, although understanding the functional significance of the P2 and N2 components in the go/nogo task can inform frontal lobe mechanisms including inhibition and response conflict, for example, our goal of delineating the time course of semantic access is largely orthogonal to these issues. The onsets of nogo–go differences and the response time distributions for living/nonliving and lexical decisions were very similar in the Hauk et al.'s (2012) study, suggesting commensurate time courses of decision processes for both kinds of decisions. In the current study, the difference between onsets of nogo–go effects across decision tasks was at least 160 ms, whereas the analogous difference in response times was only about 50 ms. One possibility for this difference is that the decision process takes less time for graspability decisions. Another possibility is that the accumulation of evidence for or against any particular decision begins much earlier in the living/nonliving trials, but takes more time to reach a decision threshold. The combination of an early onset and an extended period of evidence accumulation could account for the temporal difference between neural and behavioral measures. We discuss the notion of evidence accumulation in more detail later.

Rapid access to category-related knowledge is stable

Based on the go/nogo ERP literature we hypothesized rapid semantic access (i.e. less than 200 ms) in the single-task paradigm but not in the relatively more difficult dual-task paradigm. On the contrary, however, we found an early nogo–go difference at the midline prefrontal site for living/nonliving decisions in both single and dual-task paradigms. Unlike in other reported dual-task go/nogo studies, our participants were required to access two different kinds of semantic information on each trial, rather than some semantic information and some other kind of information related to word form (e.g., the first letter or the syntactic gender of the word). One possibility thus is that the category-related information was accessed first, with the action-related information accessed only later, thereby leading to the delay in response times. A related possibility is that coarse-grained conceptual information is obligatorily computed during word processing whereas action-related information is computed only in a situation-specific manner.

Our results also suggest that rapid access to information that differentiates living from nonliving things does not occur selectively only for certain kinds of concepts. This finding could have been driven primarily by words denoting living things. In Experiment 2, participants were faster to respond to living things when the go/nogo decision as well as when the handedness decision was contingent upon the living/nonliving distinction (Fig. 5). Other studies have reported a similar advantage. Borghi et al. (2007), for example, found that people were faster at categorizing words denoting natural objects versus artifact concepts, even when the decision was based on manipulability ("Can you pick up this object and put it in a backpack?"). Despite this type of behavioral advantage, our early category-related ERP effect was present for the living and nonliving thing words. We do note, however, that the retention of nonliving thing items seemed to influence the ERP at a slightly later latency—the P2 component was larger and peaked later. Likewise, the early category-related effect could have been dependent on words referring to graspable objects. In Experiment 2, participants were faster to respond to graspable items when the go/nogo decision as well as when the handedness decision was contingent upon graspability (Fig. 6). Despite this behavioral advantage, however, the early category-related ERP effect was present for both graspable and ungraspable items.

The early category-related effect also could have been confined to people who could perform the task quickly (compared to those who are slower). However, response speed had no discernible effect on either the morphology of the early category-related ERP effect (Fig. 7) or the conclusions drawn from the statistical analyses. At the same time, the fast responder group does appear to generate a slightly earlier N2 effect when the decision is contingent upon the object category.

Implications for visual word recognition and semantic memory

Taken together with a handful of recent reports, our data speak to the questions of the extent to which lexical and semantic access occur in parallel, and of how early semantic information is available in relation to orthographic (visual) information. One commonly held view of word processing is that stimulus-related brain activity reflects orthographic processing until about 250 ms or so, after which access to lexical or semantic information can occur. For example, Pylkkanen and Marantz (2003) claim that pre-lexical processing occurs between 250 and 350 ms, followed by the activation of a "mental lexicon" as reflected in a brain response that is sensitive to factors such as lexical frequency. Grainger and Holcomb (2009) have proposed that visual form processing occurs before 250 ms, lexical access occurs by 325 ms, and the initial portion of the N400 component reflects contact between lexical and conceptual processes (however they are open to the possibility that whole word shape information can be used to make fast guesses at word identity). Our results are not consistent with these timelines of word recognition. Rather, our finding that category-related semantic access can occur by 160 ms is more consistent with a growing number of reports of temporally overlapping semantic and lexical effects before 250 ms (Amsel, 2011; Chan et al., 2011; Hauk et al., 2012; Pulvermüller et al., 2009; Sereno et al., 1998).

The timing of semantic access depends on the kind of accessed information

Our results, moreover, indicate that the timing of semantic access is variable. This accords with the more general assumption that information becomes available in a graded and temporally extended manner following stimulus perception. Several N400 studies have argued for an obligatory feedforward process of semantic access that is not dependent on a gated information state (recognition), and is flexibly drawn out in time (Kutas and Federmeier, 2011; Laszlo and Federmeier, 2009, 2011). Dennett (1991, p. 134) paints a similar picture of conscious awareness, where "at different times and different places, various 'decisions' or 'judgments' are made; more literally, parts of the brain are caused to go into states that discriminate different features." On this view, we can further ask why does accessing knowledge about the graspability of an object require substantially more time than knowledge about whether that object is a living or nonliving thing?

Warrington (1975) described a patient with semantic dementia who performed superordinate judgments accurately (e.g., animal/non-animal) but was markedly impaired at differentiating objects on the basis of their properties (e.g., function, material, or color), which suggests that the temporal difference between accessing object category and object graspability knowledge may reflect a distinction in semantic memory structure and/or organization. Warrington and Shallice (1979, p. 61) proposed that "the precise meaning of a word may well be accessed only as the end result of a process which involves the attaining of increasingly specific semantic representations." This work on specific semantic impairments led to several sensory/motor property models of semantic memory organization (Martin, 2007), according to which object concepts are represented as distributed networks of sensory, motor, and possibly verbal/encyclopedic properties. The temporal delay between access to object category and object graspability in our study thus might reflect the engagement of distinct neural circuits involved in the representation of visual/categorical knowledge and action-based knowledge, respectively. It is important to note that whereas the current graspability judgments required participants to use their real-world knowledge about the grasping actions objects afford, a previous study using a passive reading task found differential neurophysiological activity underlying arm-related vs. leg-related vs. face-related words by about 200 to 230 ms (Hauk and Pulvermüller, 2004). Perhaps deciding whether a word denotes a graspable or ungraspable object (versus passively reading action-related words) involves the partial re-enactment of specific motor programs in primary or secondary motor cortex.

On an alternate view of semantic memory knowledge about object affordance, visual properties, and other sensory and encyclopedic characteristics of objects constitute different components of a common knowledge base (Caramazza et al., 1990; Tyler and Moss, 2001), possibly centered in the anterior temporal lobe (Patterson et al., 2007). Supporting evidence for this view includes semantic dementia patients who are similarly impaired on tasks that do not require action-related knowledge and those that do (e.g., demonstrating the correct use of common objects, Hodges et al., 2000). Under this view the temporal difference between accessing category and action-related knowledge in our study might reflect structural differences within a unitary semantic hub. Rogers and Plaut (2002) describe a connectionist implementation of this account in which a hidden layer of semantic units (corresponding to the amodal hub) develops semantic representations through indirect contact with the environment, and acts to mediate activity among visual, verbal, and action representations. Processing dynamics of activation moving between the semantic and visual, verbal, or action layers, and the correlational structure of the information contained in each modality, could conceivably mirror the differential time courses of semantic access in the current study.

Does the time course of semantic access mirror the time course of object recognition?

Words can be considered as just another kind of visually perceptible object. The mechanisms and computations underlying visual word perception then may not differ qualitatively from those involved in the perception of other finely detailed visually perceptible objects (Norris and Kinoshita, 2012; Pelli et al., 2006). The cortical region termed the "visual word form area" (Cohen et al., 2000), may be a more general visual processor (Price and Devlin, 2003; Vogel et al., 2012). The obvious difference between words and other visual objects is the arbitrary mapping between word forms and their meanings: the perceptible visual characteristics of greyhounds, huskies, and golden retrievers overlap considerably, in ways that the visual and phonological properties of their names do not. Upon perception of images depicting different dogs, some portion of activity in early visual regions could be correlated with the object category DOG, and could aid the system in recognition (e.g., Johnson and Olshausen, 2003). No such correlation can exist for word perception. Considering this key difference, it is remarkable that the evidence for early semantic access during visual word recognition begins to accrue at almost the exact same latency (150 to 160 ms) as for recognition of photographed objects (Johnson and Olshausen, 2003; Thorpe et al., 1996; VanRullen and Thorpe, 2001), and that this latency does not decrease even with extensive stimulus exposure and training (Fabre-Thorpe et al., 2001). Furthermore, the onset latency of the nogo–go difference appears to be ~160 ms even when the decision is contingent upon simple perceptual information (Gemba and Sasaki, 1989). Comparison of the various kinds of effects that begin around

160 ms in the upper and lower panels of Fig. 8 highlights the range of information and conditions that produce a difference at around this same latency. Perhaps 160 ms post stimulus onset is a multi-informational “starting block” of information access for visual stimuli.

In contrast to category-related knowledge, access to knowledge about action affordance appears to take substantially more time regardless of stimulus properties. Proverbio et al. (2011) selected pictures of objects that afford manual manipulation (e.g., typewriter, paintbrush) and pictures of objects that do not (e.g., pillow, computer monitor), matching the pictures on size, average luminance, and perceptual familiarity. Participants viewed the pictures one at a time while monitoring for live plants. ERPs associated with manipulability diverged around 240 ms—almost 100 ms later than typical category-related effects. We cannot know from this result whether the information available at this latency was sufficient to influence a decision contingent upon action affordance. To our knowledge our study is the first to examine the time course of access to grasping-related knowledge in a task that requires the use of this knowledge in a decision paradigm. Despite our choice of words versus pictures, explicit recognition-dependent task, and dual-task paradigm (in Experiment 2), we find that action-based object knowledge is available to a decision system by around 350 ms.

From semantic access to decision-making in the brain

Upon viewing a word, feed-forward activity carrying visual information is propagated from visual cortex anteriorly along the temporal lobes where the signal is increasingly abstracted away from the original visual form, and begins to carry view-invariant word level information (Dehaene et al., 2005). By about 130 to 160 ms, intracranial single-unit, multi-unit, and synaptic activity in middle layers of inferotemporal, perirhinal, and entorhinal cortices can be used to decode whether the referent of a word is a living or nonliving thing (Chan et al., 2011). Between 150 and 170 ms, Hauk et al. (2012) and the current study observe a go/nogo ERP difference prominent over anterior scalp sites that reflects activation of at least as much semantic information as Chan et al.'s study. Although we did not perform source localization, we assume in line with the literature that the likely neural generators of the frontal nogo ERPs are in prefrontal cortex (Lavric et al., 2004; Sasaki et al., 1989, 1993). Based on this assumption we can ask what is the nature of the information used by neurons in prefrontal cortex to influence a downstream decision mechanism before 160 ms?

One class of perceptual decision mechanisms maintains that neurons in posterior cortex provide evidence for or against a target feature to neural assemblies in the frontal lobes, which in turn signal the motor system to respond whenever the evidence reaches a response threshold (Heekeren et al., 2004; Smith and Ratcliff, 2004). These neural assemblies in frontal cortex may transiently represent the most likely candidates of the sensory input and use this information to facilitate the feedforward activity in posterior cortex (Bar et al., 2006; Summerfield et al., 2006). Bar and colleagues have shown that low spatial frequency information about a visual object is fast-tracked to orbitofrontal cortex 50 ms before activity in posterior perceptual regions begins to differentiate object categories. They argue that the rapid access to category-related knowledge reported in Thorpe and colleagues' go/nogo ERP studies might reflect top-down facilitation, whereby activated information in frontal cortex “sensitizes the representations of the most likely candidate objects in the temporal cortex as a predictive ‘initial guess’ (p. 451).” However, this purported mechanism is unlikely to account for our findings because low spatial frequency information would facilitate processing at the whole word level (Allen et al., 1995), and thereby benefit processing of both decision criteria equally; it thus could not account for the rapid access to category-related but not action-related knowledge.

We hypothesize that within about 150 ms following stimulus onset, the first pass of stimulus-specific activity propagating anteriorly along the inferior temporal lobe begins to provide coarse-grained information about a word's referent to a decision system in frontal cortex. We suggest that two additional processes can facilitate a successful decision in the current paradigm, namely attention and expectation (Summerfield and Egner, 2009). A mechanism in frontal cortex could maintain a semantic attentional set (Kiefer and Martens, 2010; Martens et al., 2011) attuned to the current decision category (e.g., living things), and neural assemblies in prefrontal cortex could provide top-down support to the bottom-up activation of conceptual knowledge in posterior cortex. The information maintained in the attentional set used to sensitize representations in posterior cortex may be a feature or set of features that can discriminate between decision categories. If the decision category is living things for example, a discriminating feature could be goal-directed motion (e.g., plants move towards the sun, animals move towards a food source, Opfer and Siegler, 2004). Accumulation of evidence defined by information about one or more such features could proceed until a threshold is crossed and a winner-take-all signal (i.e., go or nogo) would be propagated to the motor system. Future work could test the possibility that evidence accumulation for a graspability judgment requires simulation in sensory/motor cortex, in which case the number and duration of neural processing steps may be substantially higher than is the case for the accumulation of evidence for a category-related distinction.

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Conflict of Interest Statement

The authors declare no conflicts of interest.

Appendix A. Instructions for Experiments 1–2

Graspability. Each word in this part of the experiment denotes an object that is either likely or unlikely to be grasped (in its entirety) by a human being; the particular configuration of the hand and fingers when grasping the object is less important than whether the object is graspable or not. Note, here graspability refers to the whole object and whether or not it (and not just part of it) is graspable in one hand. Let's consider a few examples: (1) a knife is graspable, even though one would only grasp it by the handle. (2) Likewise, an egg is graspable, either in the palm of one's hand, or with one's fingers. (3) A mouse is also graspable even if you personally haven't done so, or wouldn't even consider doing so. (4) In contrast, a motorcycle as a whole is not graspable, even though you would grasp certain parts like its handlebars or gas cap. (5) Likewise, a walrus is not graspable, even though one can imagine grasping different parts of its body. Importantly, you may encounter certain words that, upon careful reflection, would not fit neatly into either category. Nonetheless, we would like you to respond as quickly as you can on each trial, rather than take more time to reflect upon the decision.

Object category. Each word in this part of the experiment denotes an object that is either a living thing or is not. Living things include animals, birds, plants, trees, and vegetables. Nonliving things include vehicles, buildings, tools, weapons, and musical instruments. Certain entities such as lipstick or a guitar can contain some amount of biological material. This however is not sufficient for inclusion as “living thing” in this experiment. On the other hand, there are certain kinds of vegetables that you may have eaten from a can or in a cooked meal, but have never actually seen “alive”. Nevertheless, we ask that you still classify these as living things. Importantly, you may encounter certain words that, upon careful reflection, would not fit neatly into either category. Nonetheless, we would like you to respond as quickly as you can on each trial, rather than take more time to reflect upon the decision.

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