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Sensory and semantic activations evoked by action attributes of manipulable objects: Evidence from ERPs

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Abstract

“Two route” theories of object-related action processing posit different temporal activation profiles of grasp-to-move actions (rapidly evoked based on object structure) versus skilled use actions (more slowly activated based on semantic knowledge). We capitalized on the exquisite temporal resolution and multidimensionality of Event-Related Potentials (ERPs) to directly test this hypothesis. Participants viewed manipulable objects (e.g., calculator) preceded by objects sharing either “grasp”, “use”, or no action attributes (e.g., bar of soap, keyboard, earring, respectively), as well as by action-unrelated but taxonomically-related objects (e.g., abacus); participants judged whether the two objects were related. The results showed more positive responses to “grasp-to-move” primed objects than “skilled use” primed objects or unprimed objects starting in the P1 (0–150 ms) time window and continuing onto the subsequent N1 and P2 components (150–300 ms), suggesting that only “grasp-to-move”, but not “skilled use”, actions may facilitate visual attention to object attributes. Furthermore, reliably reduced N400s (300–500 ms), an index of semantic processing, were observed to taxonomically primed and “skilled use” primed objects relative to unprimed objects, suggesting that “skilled use” action attributes are a component of distributed, multimodal semantic representations of objects. Together, our findings provide evidence supporting two-route theories by demonstrating that “grasp-to-move” and “skilled use” actions impact different aspects of object processing and highlight the relationship of “skilled use” information to other aspects of semantic memory.

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Keywords

Event-Related Potentials; N400; Action; Skilled use actions; Grasp-to-move actions; Embodied cognition

Introduction

Grounded or embodied approaches to object representation suggest that sensory and motor information related to action experiences are constituents of manipulable object representations (e.g., Allport, 1985; Barsalou, 2008; Gallese and Lakoff, 2005). Object-related action information may be automatically retrieved upon object apprehension, such that judgments about object categories, orientations, or sizes are facilitated when signaled with a compatible response gesture (e.g., precision grip for key and power grip for hammer; Symes et al., 2008; Tucker and Ellis, 2001; see also Masson et al., 2011), and identification of pictures of graspable objects is influenced by compatibility between the objects and planned actions (Bub et al., 2013). Incidental retrieval of action information during object processing has been found even in the absence of action preparation, imagery, or execution (Green and Hummel, 2006; Harris et al., 2012; Helbig et al., 2006; Roberts and Humphreys, 2011; Wamain et al., 2014). For example, when searching for an object in an array, participants fixate more on related distractors sharing manipulation actions with the targets than on unrelated distractors (Lee et al., 2013; Myung et al., 2006).

Critically, action knowledge is not merely an incidental by-product of object processing, but plays a supportive role in object-related cognitive tasks. For example, engaging the hands (e.g., with a squeezing task) delays tool naming, but not animal naming (Witt et al., 2010; also see Pobric et al., 2010). Moreover, performing an incompatible manual task interferes with making semantic (abstract/concrete) judgments about objects, and the amount of interference is positively associated with the amount of participants' object-related manual experience (Yee et al., 2013).

On a number of accounts (Borghi and Riggio, 2015; Frey, 2007; Jax and Buxbaum, 2010; Valyear et al., 2011), there are two major classes of actions that play different roles in object processing. "Grasp-to-move" actions (also called "variable affordances", c.f. Borghi and Riggio, 2015) require computation of body and hand kinematics based on current visual information (e.g. size, orientation, and shape) about an object. In contrast, "skilled use" actions (or "stable affordances") are based on knowledge of how an object is used to serve a certain purpose, with the object knowledge abstracted over prior tool-use experience and not bound by the visuospatial specifics of a particular object exemplar. In support of this view, facilitated visual object perception has been obtained from "grasp-to-move" action primes (e.g., reduced change blindness effect in Symes et al., 2008) but not "skilled use" action primes.

Structure-based "grasp-to-move" actions and function-based "skilled use" actions also have different neurocognitive substrates and thus may be involved in object processing via different neural pathways. It has been shown that impairment in these two action types doubly dissociates in patients (impairment in grasping but not using objects in patients with

optic ataxia: Andersen et al., 2014; Buxbaum and Coslett, 1998; Jakobson et al., 1991; deficits for using but not grasping objects in patients with ideomotor apraxia (IMA): Buxbaum et al., 2003; Haaland et al., 1999; Sirigu et al., 1995). These lesion studies and other converging neuroimaging data (Buxbaum et al., 2006; Culham and Valyear, 2006; Johnson-Frey, 2004) have given rise to the Two Action System Plus (2ASp) theoretical model, postulating that “grasp-to-move” actions are subserved by the dorso-dorsal visual processing stream (including bilateral intraparietal sulci and dorsolateral fronto-parietal regions) specialized for online sensory-motor control; by contrast, “skilled use” actions are linked to the ventral-dorsal stream in the left hemisphere, including the left posterior temporal/inferior parietal regions that are postulated to store relationships between objects and skilled actions in semantic memory (Fridman et al., 2006; Johnson-Frey, 2004; Pisella et al., 2006; see Buxbaum, 2017 for a review). Under this view, the semantic representation of a familiar manipulable object (such as a tool) is a distributed, multi-modal entity composed of auditory, visual, somatosensory, and skilled use action “features”.

Evidence to date suggests that the two major classes of action have different time-courses of activation. Structure-based “grasp-to-move” action attributes appear to be available rapidly but transiently upon sight of the object, and may facilitate sensory processing. In contrast, function-based “skilled use” actions require longer time to access but also remain activated longer, consistent with the view that “skilled use” actions are a component of semantic memory. Measuring eye gaze fixations on nontarget objects that shared only “grasp-to-move” or “skilled use” action attributes with the targets, Lee et al. (2012) found task-incident activation of action information for both types of action attributes, albeit with different characteristics. In particular, structure-based “grasp-to-move” activation occurred more rapidly and transiently than function-based “skilled use” action activation. In addition, Jax and Buxbaum (2010) found that the experience of using “conflict” objects—objects used and grasped with different actions (e.g., a computer keyboard is poked to use but clenched to pick up and move) interfered (indexed by longer initiation time) with grasping the same object later (but not the other way around). This suggests that using an object induces a relatively long lasting influence of “skilled use” action attributes upon subsequent actions, whereas grasping an object does not induce this long-lasting activation (see replication by Osirak et al., 2013; also see Campanella and Shallice, 2011).

Despite the different time courses shown for the two action classes in behavioral and eyetracking studies (Jax and Buxbaum, 2010; Lee et al., 2013), no direct evidence has been obtained linking “grasp-to-move” actions to sensory aspects of object representations and “skilled use” actions to semantic aspects. Consequently, the observed effects could be due to quantitative differences such as magnitude or latency of a single route or mechanism. In view of this possibility, the present study utilized Event-Related Potentials (ERPs) to provide evidence regarding hypothesized differences in the characteristics of the two action types during manipulable object processing. Picking up cortical electrical potentials, ERPs provide a direct, instantaneous, and continuous measure of neural activity. ERPs are highly multi-dimensional, as their polarity, amplitude, latency, and scalp topography can be jointly considered to help delineate activity patterns that, with other measures, are difficult to dissociate. These characteristics make ERP an excellent technique for capturing the moment-to-moment dynamics of brain responses during object processing and investigating

whether ‘grasp-to-move’ and ‘skilled use’ actions are differentially linked to qualitatively distinct neurophysiological signatures of perceptual versus semantic processing.

We recorded participants’ ERP responses while they viewed two sequentially presented object pictures that were either similar or different in their associated actions, and shared no other semantic attributes. The specific types of action attributes shared between prime and target pictures were manipulated, yielding the following conditions: (1) “Skilled use Action Related”: primes and targets shared similar skilled use but not grasp-to-move actions (e.g., prime: electronic car-key fob; target: flashlight; both are used with a poke action, but the former is grasped with a pinch while the latter with a clench action) (see Fig. 1 for illustrations), (2) “Grasp-to-move Action Related”: primes and targets shared similar grasp-to-move but not skilled use actions (e.g., prime: paint-roller; target: flashlight; both are grasped with a clench action, but the former is used with a clench action while the latter with a thumb-push action), (3) “Action-Unrelated”: primes and targets shared neither grasp-to-move nor skilled use actions (e.g., prime: bottle cap; target: flashlight; the bottle cap is grasped with a pinch action but used with a twist action). To serve as a basis for comparison, we also included conditions that have been shown to elicit semantic priming for object pictures, using primes and targets that were from the same semantic category and hence shared non-sensorimotor features: “Taxonomically Related” pairs, wherein objects shared category membership but not action attributes (e.g., whistle and hand bell: both are devices that make musical sounds) as compared to “Taxonomically Unrelated” pairs from different categories having no overlapping semantic features (e.g., prime: thin paint brush; target: hand bell).

ERP components that might show priming effects include the earlier visual evoked potentials (visual P1, N1, P2, and N300) associated with processing of lower-and higher-level visual properties and the N400 component that has been linked to semantic access (Luck and Kappenman, 2013). Peaking before ~250 ms post-stimulus-onset, the visual P1, N1, and P2 components constitute part of the normal response to all visual stimuli. The amplitude of the P1 is usually maximal over lateral occipital scalp, whereas the N1 and P2 can be seen both frontally and posteriorly (albeit with different peak latencies). Although, overall, the P1, N1, and P2 reflect obligatory, exogenous sensory responses, some of their subcomponents are attention-sensitive (Hillyard et al., 1998; Luck et al., 2000). In particular, lateral occipital P1, anterior and posterior N1, and anterior P2 effects have been thought to reflect top-down gain-control of the initial feed-forward sensory activity, visual discrimination, and detection of expected visual features respectively (Luck, 2013; Luck and Kappenman, 2013). Modulation of these visual ERP components (e.g., P1) has been found when an object is preceded by another object affording similar actions (e.g. frying pan; dust pan) (Kiefer et al., 2011). This prior study, however, did not differentiate between the two action classes. With specific manipulation of “grasp-to-move” actions that heavily require sensory computations, we expect to see robust influences on these sensory components.

Visual processing is also reflected in a later component, the N300, which is a negative-going deflection peaking between 200 and 300 ms post stimuli onset that has been shown to be sensitive to higher-level visual properties in picture stimuli (e.g., McPherson and Holcomb, 1999). The N300 tends to have an anteriorly-biased distribution, and has been shown to be

larger in amplitude for unidentified than for identified objects and for unusual (untrained) views of objects than for canonical (trained) views (which are also easier to identify) (Schendan and Kutas, 2002, 2003). The N300 has been hypothesized to reflect aspects of visual structural processing that are important for visual categorization (Hamm et al., 2002; Schendan and Kutas, 2002, 2007), and, more generally, to index a ‘convergence zone’ between visual structural and semantic knowledge (Schendan and Kutas, 2003).

Following the visual processing components is the semantic component of interest—the N400. The N400 is a negative-going voltage deflection peaking at around 400 ms post stimulus onset, with a wide-spread scalp topography (whose specific form varies to some degree with modality and stimulus type). It has been considered a reflection of the activation states of a distributed, multimodal semantic network (see Kutas and Federmeier, 2011 for a comprehensive discussion), as N400 amplitudes are quite sensitive to factors relevant to semantic processing. Reduced (less negative/more positive) N400 amplitudes are associated with ease of semantic processing.²

The current design allows for the following predictions. For the baseline condition—the taxonomic pairs that share semantic but not visual sensory features—we expected to see modulations on the N400, but not on the earlier sensory components, compared to the matched unrelated primes (cf, McPherson and Holcomb, 1999). For action pairs, on the other hand, we expected differential modulation of both the sensory and the N400 components. One possibility is that we would observe a double dissociation: sensory modulation from “grasp-to-move” primes, but not from “skilled use” primes, and N400 modulation from “skilled use” primes but not “grasp-to-move” primes. Based on hypothesized interactivity and known neuroanatomic crosstalk between the two action systems (Mahon et al., 2007; Rushworth et al., 2006; Webster et al., 1994; Zhong and Rockland, 2003), however, priming of “grasp-to-move” information may also lead to a downstream semantic processing benefit reflected by an N400 reduction. Finally, we expected that the N400 effects elicited by taxonomic and action primes could differ in topographic distribution. Scalp distributions of N400s can vary as a function of stimulus type or modality resulting from non-identical neural sources engaged within the distributed semantic system. Thus, the scalp distribution of N400 effects induced by sensorimotor-relevant action information may differ from that evoked by taxonomic relations (typically widespread but maximal central-posteriorly, as seen in McPherson and Holcomb, 1999), which are often based on non-sensorimotor features.

Methods

Materials

Eighty grey-scale object pictures were chosen as targets, including 48 conflict manipulable objects (e.g. a calculator, grasped with a clench and used with a poking action) for action pairs and 32 manipulable objects for taxonomic pairs. These targets were paired with a

²Despite sometimes similar scalp distributions and overlapping time courses between the N300 and N400, careful examination of the scalp topographies, functional differences, and different estimated cortical source locations for N300 and N400 congruity effects suggest that they are two distinct effects that can occur independently (Hamm et al., 2002; McPherson and Holcomb, 1999).

different set of 80 greyscale prime pictures of objects based on the following relations: (1) “Skilled use Action Related”, (2) “Grasp-to-move Action Related”, (3) “Action-Unrelated”, (4) “Taxonomically Related”, and (5) “Taxonomically Unrelated”. Pairs in action conditions shared no other semantic attributes and both related and unrelated pairs in the Taxonomic conditions were grasped-to-move and used differently (Fig. 1). These objects were carefully matched for their action, meaning, and visual attributes based on a series of behavioral rating studies, including pantomime to sight of objects, familiarity, visual similarity and taxonomic relatedness ratings. Details of these rating studies are provided in the supplementary materials.

Based on the results of behavioral ratings, 48 pairs were selected for each of the three action conditions, and 32 pairs were selected for each of the two taxonomic conditions, totaling 208 pairs. All were highly familiar objects and all obtained high agreement in how they should be grasped-to-move and skillfully used (Table 1). Critically, degrees of Skilled use action match for Skilled use related pairs and Grasp-to-move action match for Grasp-to-move related pairs were equivalently high (means = 0.9, $p = 1$) and both were higher than the degrees of action match for the other action in the same pairs and both actions for other pairs ($ps < 0.05$). In addition, taxonomic similarity was higher for taxonomically related pairs than taxonomically unrelated pairs and all three other action pairs ($ps < 0.05$). All pairings in the related conditions were more visually similar than their unrelated counterpart ($ps < 0.05$), but visual similarity for pairings in the three related conditions was statistically equivalent ($ps > 0.1$).

Targets were rotated through 6 lists such that within each list each target appeared once, and, across lists, each action target was paired with all three action conditions (grasp-to-move/skilled use/action unrelated) and each taxonomic target appeared in both related and unrelated conditions. Each participant was tested on two lists. Thus for each participant, each prime and target was shown twice, but was paired with a different object each time with at least a 10-min interval in between. In total, each participant experienced 32 trials in each condition.

Participants

Twenty-four University of Illinois undergraduate students (12 males; mean age 19.5 years, range 18–21 years) participated in the study for course credit or payment. All participants were right-handed as assessed by the Edinburgh inventory (Oldfield, 1971). All were monolingual speakers of English and had no history of neurological/psychiatric disorders or brain damage.

Procedure

Participants were seated 100 cm in front of a 21⁰⁰ computer monitor in a dim, quiet testing room. They were given written instructions and a 10-trial practice before the experiment to familiarize them with the experimental environment and the task. The procedure is shown in Fig. 2. At the start of each trial, a series of plus signs appeared in the center of the screen for 1 s. After an SOA ranging randomly between 500 and 1000 ms (jittered to lessen the influence of slow, anticipatory potentials on the average ERPs), the prime and target pictures

were displayed in succession in the center of the screen for 500 ms with an interval of 400 ms. A question mark shown in red then appeared on the screen for 200 ms, 500 ms after the offset of the target. Participants were instructed that when the question mark appeared, they should press one of two buttons, held in each hand, to indicate whether or not they felt the two pictures were related in any way; hand used to respond “yes” was counter-balanced. To make it clear that participants could vary their criteria for relatedness from trial to trial, examples for possible ‘yes’ judgments were given from each of the ‘taxonomic’, ‘skilled use’, and ‘grasp-to-move’ related types (‘chocolate’ and ‘cake’; ‘an ATM’ and ‘a vending machine’; ‘a needle’ and ‘a bead’ respectively), and emphasis was given that there was no absolute right or wrong answer. The question mark disappeared upon the participant’s button-press response. The next trial then began two and a half seconds after the offset of the response. Participants were told that some pictures would be presented twice during the experiment, but paired with different pictures each time and that there were no systematic relations between the two appearances of the same picture. The whole experiment was divided into four blocks, each lasting for about 5 min.

EEG recording and data analysis

The electroencephalogram (EEG) was recorded from twenty-six evenly-spaced silver/silver-chloride electrodes attached to an elastic cap. All scalp electrodes were referenced on-line to the left mastoid and re-referenced off-line to the average of the right and the left mastoids. In addition, one electrode (referenced to the left mastoid) was placed on the left infraorbital ridge to monitor for vertical eye movements and blinks, and another two electrodes (referenced to one another) were placed on the outer canthus of each eye to monitor for horizontal eye movements. Electrode impedances were kept below 3 k Ω . The continuous EEG was amplified through a bandpass filter of 0.02–100 Hz and recorded to hard disk at a sampling rate of 250 Hz.

Epochs of EEG data were taken from 100 ms before stimulus onset to one and a half seconds after. Those containing artifacts from amplifier blocking, signal drift, eye movements, or muscle activity were rejected off-line before averaging, using thresholds selected for each participant through visual inspection of the data. Trials contaminated by eye blinks were corrected for 6 participants who had enough blinks to obtain a stable filter (Dale, 1994); for all other participants, trials with blink artifacts were excluded from analysis. Trial loss averaged 2.77%. Artifact-free ERPs were averaged by stimulus type after subtraction of the 100 ms pre-stimulus baseline. Prior to statistical analyses, ERPs were digitally filtered with a bandpass of 0.2–20 Hz. Analyses were conducted in three time windows. To capture the P1 effects that have been described in the prior literature (Kiefer et al., 2011), we took measurements between 0 and 150 ms; this time window also encompasses N1 effects that, over posterior sites, follow the P1 but, over frontal sites, are often temporally copresent with the P1. The N400, which peaks around 400 ms in young adults, was measured between 300 and 500 ms; taxonomic pairs would be expected to show clear effects in this time window, with a posterior distribution (e.g., Kutas and Federmeier, 2011). Finally, for completeness, we also measured the 150–300 ms window, which broadly encompasses later sensory processing and attention effects that precede semantic access (as indexed by the N400). Because several effects were expected to have distributional

characteristics that differed over anterior and more posterior scalp locations, we included this distributional factor in our analyses as well.

Results

Behavioral relatedness judgment test

Ninety-two percent of the Taxonomically related object pairs were judged as related. The majority of the other types of object pairs, however, were rated as unrelated (judged as unrelated: Skilled use related: 60%; Grasp-to-move related: 77%; Action unrelated: 89%; Taxonomically unrelated: 68%).

ERPs

Fig. 3 overlays the grand average ERPs to target objects from related and unrelated conditions for all three relation types.

Mean amplitude analysis—For action pairs, mean amplitudes measured in time windows associated with early sensory processing (0–150 ms), late sensory processing (150–300 ms), and semantic processing (N400 responses; 300–500 ms) were submitted for analyses of variance (ANOVAs) for each relation type (Skilled use, Grasp-to-move, and Taxonomic) separately, with within-subjects factors of Relatedness (related vs. unrelated), Anteriority (anterior vs. central-posterior), and Electrode (anterior electrode sites, including MiPf, LLPf, RLPf, LMPf, RMPf, LDFr, RDFr, LMFr, RMFr, LLFr, and RLFr, and central/posterior electrode sites, including MiCe, LMCE, RMCE, LDCE, RDCE, MiPa, LDPa, RDPa, MiOc, LMOc, and RMOc). For all analyses, main effects of electrode and interactions with electrode sites are not reported unless they are of theoretical significance. To correct for violations of sphericity associated with repeated measures, the Huynh–Feldt adjustment to the degrees of freedom was applied for each analysis of variance (ANOVA). Consequently, for all *F* tests with more than 1 degree of freedom in the numerator, the corrected *p* value is reported.

Early sensory processing (0–150 ms)—As expected, for both *taxonomic* pairs and *skilled use* action pairs, there was no reliable effect of Relatedness or Relatedness by Anteriority interaction ($ps = 0.5$). However, for *grasp-to-move* action pairs, there was a main effect of Relatedness [$F(1,23) = 10.44$; $p < 0.005$] that was not modulated by Anteriority ($p = 0.5$). Because this effect for the *grasp-to-move* action pairs is early, we wanted to confirm that it indeed emerged post-target-onset (instead of constituting a continuation of some kind of difference in response to the prime). We therefore conducted an ANOVA on the baseline period for the *grasp-to-move* action pairs (with baseline correction now done from 200 ms to 100 ms before onset), and the results showed no condition differences nor modulation by Anteriority ($ps > 0.2$). Thus, the effect indeed becomes reliable only after presentation of the target.

Late sensory processing (150–300 ms)—Similar to the results of the previous time window, there were no reliable effects of or interactions with Relatedness for either *taxonomic* or *skilled use* action pairs. There was a marginal Relatedness by Anteriority

interaction for *skilled use* action pairs ($p = 0.06$). However, follow up comparisons revealed no Relatedness effect in either the anterior or the central-posterior region ($ps > 0.2$). For *grasp-to-move* action pairs, the effect of Relatedness continued to be reliable [$F(1,23) = 4.12$; $p = 0.05$], but now jointly interacted with Anteriority and Electrode [$F(10,230) = 3.49$; $p = 0.01$]. Follow up comparisons showed that the Relatedness effect was only reliable over anterior [$F(1,23) = 6.58$; $p < 0.05$], but not central-posterior electrode sites ($p = 0.3$).

Semantic processing (300–500 ms)—Consistent with prior literature (McPherson and Holcomb, 1999), for *taxonomic* pairs, there was a robust Relatedness effect [$F(1,23) = 30.93$; $p < 0.0001$], which jointly interacted with Anteriority and Electrode [$F(10,230) = 6.9$; $p = 0.0001$]. Follow-up analysis showed reliable Relatedness effect in both regions [anterior: $F(1,23) = 16.88$; $p < 0.0005$; central-posterior regions $F(1,23) = 30.17$; $p < 0.0001$], with larger effects over the back of the head. For the two action pairs, the Relatedness effect was also reliable [*grasp-to-move*: $F(1,23) = 9.33$; $p < 0.01$; *skilled use*: $F(1,23) = 6.43$; $p < 0.05$]. For *grasp-to-move* action pairs, the Relatedness effect did not interact with Anteriority ($p = 0.2$). However, when examined in each region, the Relatedness effect was only reliable in the anterior region [$F(1,23) = 9.65$; $p = 0.005$] and was marginal in the central-posterior region ($p = 0.08$). For *skilled use* action pairs, there was a reliable Relatedness by Anteriority interaction [$F(1,23) = 6.71$; $p < 0.05$], with the effect being reliable only in the anterior region [$F(1,23) = 9.22$; $p < 0.01$], but not in the central-posterior region ($p = 0.3$).

To more directly compare the relative size of effects as well as the distributional difference among the three types of relatedness conditions, mean amplitude *differences* in the N400 time window were measured for each related condition and its corresponding unrelated condition. These were subjected to an ANOVA with factors of Relation Type (taxonomic vs. skilled use vs. grasp-to-move), Anteriority (anterior vs. central-posterior), and Electrode (as already described). The results showed a main effect of Relation Type [$F(2,46) = 4.02$; $p < 0.05$] that interacted with Anteriority [$F(2,46) = 5.25$; $p < 0.05$]. Follow up analysis performed in anterior and central-posterior regions separately showed a reliable Relation Type effect only in the central/posterior region [$F(2,46) = 8.32$; $p < 0.01$] (in the anterior region $p = 0.6$), with reliably more N400 reduction for the taxonomic relation than either of the two action relations [taxonomic vs. skilled use: $F(1,23) = 11.41$; $p < 0.005$; taxonomic vs. grasp-to-move: $F(1,23) = 7.43$; $p = 0.01$] and no difference between skilled use and grasp-to-move action relations ($p = 0.4$). Thus, whereas all conditions elicited an effect in the N400 time window over anterior regions, the N400 effect for taxonomic pairs extended into (and indeed was larger in) centro-posterior regions, as is typical of N400 effects in prior work looking at taxonomically related stimuli (e.g., review in Kutas and Federmeier, 2011).

Summary and comparisons across time windows—To summarize the results so far, we replicated the taxonomic priming effect reported in the prior literature (McPherson and Holcomb, 1999; and see Kutas and Federmeier, 2011 for a review), with no priming in the two sensory time windows (0–150 ms and 150–300 ms), but reliably less negative N400s to related than to unrelated conditions. The N400 effect was widespread, but was maximal over central-posterior electrode sites. For action relations, we observed priming effects in the sensory time windows only for the “grasp-to-move” action pairs. These effects started out

widespread but became reliable only over anterior sites in the late sensory time window. We observed N400 priming effects for both types of action relatedness conditions. However, the N400 effects for both “skilled use” and “grasp-to-move” conditions were distributed differently from the effect for the “taxonomic” condition and were reliable only in the anterior region.

Given that the “grasp-to-move” condition elicited effects in early time windows, it is unclear whether the effect seen for this condition in the N400 time window represents a persistence of the pattern observed in the sensory time windows or a new influence of the action relation. Although there is no definitive way to answer this question, we performed two analyses to assess whether the effect pattern in the N400 was similar in size to that observed in the earlier time window (suggesting the possibility of persistence) or whether the effect was augmented in size (suggesting a new influence). First, we statistically compared the N400 time window (300–500 ms) with the immediately preceding sensory time window (150–300 ms). Second, we measured peak amplitude differences between the earlier positive peak (P2) and the later negative peak (N400) for each relation type. These analyses were conducted on data recorded over anterior regions, where the N400 effects were observed for the action conditions. For both the *taxonomic* and the *skilled use* conditions, we expect reliable time-window differences and peak-to-peak effects, showing the emergence of an N400 effect. A similar pattern in the *grasp-to-move* condition would provide evidence for an N400 effect in this condition as well; lack of such augmentation leaves open the possibility that the effect for this condition reflects a continuation of the earlier pattern in the waveform.

Direct time window comparison—To compare the size of the relatedness effect between the N400 time window and the preceding late sensory time window, for each relation type, an ANOVA was conducted on the mean amplitude difference between the related and unrelated condition with factors of Time Window (150–300 vs. 300–500 ms) and Electrode (the 11 anterior electrode sites). The results revealed significant Time Window effects for both *taxonomic* and *skilled use* conditions [taxonomic: $F(1,23) = 16.22$; $p = 0.0005$; skilled use: $F(1,23) = 14.43$; $p < 0.001$], reflecting larger amplitude differences in the N400 time window than in the earlier window. However, for the *grasp-to-move* condition, there was no evidence that the amplitude differences changed across the two time windows ($p = 0.8$).

Peak-to-peak analysis—Peak amplitude differences between the earlier positive peak (P2) and the later negative peak (N400) were measured as the difference between the local maximum (most positive voltage value that had more negative values both earlier and later within the time window) and following local minimum between 100 and 500 ms post-stimulus onset from anterior electrodes. To avoid spurious peaks from high frequency noise, for this analysis waveforms were additionally filtered with a 5 Hz low pass filter. These peak amplitude differences were then tested using an ANOVA with factors of Relatedness and Electrode for each relation type separately. The results showed reliable Relatedness effects for the *taxonomic* [$F(1,23) = 11.24$; $p < 0.005$] and *skilled use* condition [$F(1,23) = 6.7$; $p < 0.05$] with smaller effects peak to peak (suggesting facilitated N400 responses) in the related than in the unrelated conditions. By contrast, again, there was no reliable Relatedness effect

for the *grasp-to-move* condition ($p = 0.7$), suggesting that the size of the N400 elicited by the related and unrelated conditions was not different once effects on the P2 had been taken into account.

The results of the time window comparisons and the peak-to-peak analyses thus provided complementary evidence for an N400 effect in the taxonomic and skilled use conditions. However, for the *grasp-to-move* condition, these analyses showed that effects in the N400 time window were not augmented compared to the pattern seen in the earlier time windows, leaving open the possibility that the pattern in this condition reflects a continuation of the earlier effect rather than an N400 facilitation *per se*.

Discussion

The present study took advantage of the multidimensional characteristics of ERPs to test whether “grasp-to-move” and “skilled use” actions influence different aspects of object processing. Our results showed that priming effects due to shared grasp-to-move and skilled use actions were different in time course and functional characterization.

Action priming effects due to shared “grasp-to-move” action features were reliably obtained as more positive responses on sensory potentials. There were also priming effects in the N400 time window, although follow-up analysis suggested no clear augmentation in this time window beyond the difference already obtained in the earlier sensory time windows. By contrast, shared “skilled use” action features yielded no appreciable priming effects during sensory processing, showing the first evidence of priming only during the N400 time window, with reduced negativity for primed related to unprimed object pictures. For both action conditions, the topography of the N400 effect differed from that obtained for the control condition. Instead of the widespread (centro-posterior maximum) N400 priming effect seen here – and in prior work – for the taxonomic pairs, the effect in the N400 time window for both types of action-based relation was only reliable over anterior scalp regions. We next discuss our interpretations of these effect patterns.

Faster-rising activation of grasp-to-move than skilled use action information: P1 priming effect

Consistent with eye-tracking findings showing a faster-rising activation time course for “grasp-to-move” relative to “skilled use” action attributes (Jax and Buxbaum, 2010; Lee et al., 2013, 2014), our results showed that early aspects of object processing were influenced by “grasp-to-move” action attributes, with more positive responses to primed than unprimed objects starting in the P1 window and continuing onto subsequent components. These data thus further specify that the fast-rising “grasp-to-move” action attributes modify early visual processing of objects, providing supportive evidence for the 2AS + theory (Buxbaum, 2017).

The P1 component is an early exogenous sensory potential generated in the extrastriate visual cortex (Clark et al., 1994). Enhanced P1 amplitudes have been seen during perception of ‘attention-grabbing’ stimuli such as fearful vs. neutral faces (e.g., Pourtois et al., 2005), reward-associated visual features (Hickey et al., 2010), stimuli appearing in a validly cued location (Hillyard et al., 1998), or, under certain circumstances, the location where a tool

recently appeared (Handy et al., 2003). Larger P1s in these conditions have been suggested to reflect attention modulation on sensory gain that aids early visual processing (for more discussion, see Hillyard et al., 1998 for spatial attention and Taylor, 2002 for object-specific attention).

Previous work has suggested that primed visual features draw more attention and are more accessible (Lu and Proctor, 1995; Smith et al., 2003; Warren, 1972). Critically, it has been noted that, at least in the case of fearful faces, only visual information that is available rapidly can have a timely influence on P1 (Pourtois et al., 2005). The enhanced P1s to “grasp-to-move” primed objects in the present study thus showed that, despite statistically equivalent rated global visual prime-target similarity among the related conditions, only “grasp-to-move”, but not “skilled use”, action attributes are apprehended during early visual processing in a manner that can affect attention through priming.

Grasp-to-move priming effects were also seen during the subsequent time window (150–300) encompassing the P2 and N300 components, likely cascading from or triggered by the P1 attention effect. Part of the normal response to visual stimuli, the P2 has been shown to be enhanced by feature-based attention (Luck and Hillyard, 1994; Luck and Kappenman, 2013). The N300, on the other hand, has been thought to reflect higher-order visual categorization processes enabled by interactive, recurrent feedback between brain areas mediating object identification and visual structural processing, especially the system that represents the global shapes of objects and their parts, regardless of size, orientation, or spatial location of local contours (Schendan and Kutas, 2007). As the graspable parts of objects in ‘grasp-to-move’ pairs are invariably quite similar in shape (e.g., paint roller and flashlight; shoe brush and call bell), we can speculate that visual attention is biased by the grasp-to-move attributes of the prime, thereby enhancing contour processing for the graspable parts of the target (via increased sensory gain). As a consequence, the shape similarity of the graspable parts of prime and target objects may facilitate the visual categorization process, leading to a reduced N300 response.

Semantic facilitation for objects following action-related objects: N400 priming effect

The N400 component is part of the default response to a wide range of potentially meaningful stimuli (e.g., including words, pictures, faces, and sounds). The amplitude of the N400 has been shown to be sensitive to a variety of item-level and context-level semantic factors, with reduced amplitudes interpreted as evidence for facilitated semantic processing (Federmeier and Laszlo, 2009; Kutas and Federmeier, 2011; Kutas and Hillyard, 1980). The present study used the better-understood taxonomic condition as a reference for the N400 action semantic effect of interest. Taxonomically related pairs were members of the same semantic category, sharing abstract semantic attributes and context/event-associations but very few sensory-motor attributes (e.g., garden shears and watering can; French press and tea infuser; bongo drums and oboe). Replicating prior findings, we found a robust semantic-category-based N400 priming effect, showing reduced N400s to objects following taxonomically related objects than unrelated objects (McPherson and Holcomb, 1999). Also consistent with prior findings, this N400 effect was widespread, encompassing central parietal and anterior scalp regions. N400 semantic priming effects are taken to reflect eased

processing of semantic attributes of the target object due to prior activation of shared information from the prime object (see Kutas and Federmeier, 2011 for a more detailed discussion of the mechanisms reflected by the N400 component).

We then used the N400 response as a tool to assess the influence of action information on semantic processing for objects. Our results showed that, in contrast to the selective action priming effect from “grasp-to-move” actions in the sensory processing time windows, N400 responses were facilitated by both “grasp-to-move” and “skilled use” action relations. However, the size of the effect observed in the “grasp-to-move” condition for the N400 time window was not different from the effect observed in the preceding sensory processing window (as revealed in the time window analysis), and was no longer reliable when the difference in the preceding time window was taken into account (as revealed in the peak-to-peak analysis), raising the possibility that it is a continuation of the earlier effect pattern.

The robust and reliable N400 priming effect for “skilled use” object pairs is consistent with theoretical views of “skilled use” action attributes in “two route” approaches (Buxbaum, 2017; Jeannerod et al., 1995a). In the 2AS + account, for example, “skilled use” action knowledge is considered part of semantic memory, including multisensory and motor memories accumulated when using objects or observing others using them. It is hypothesized that, over multiple exposures, action attributes that are constant across these instances (such as the kinematic tool use trajectory, how one’s body looks and feels as it moves in a certain tool use action, etc.) is extracted, constituting manipulation knowledge. With this knowledge, a “hammering” gesture can be identified regardless of the recipient of the action and the size of the stroke or grip.

These views that “skilled use” action knowledge is stored in long term memory and shaped by action experiences are corroborated by recent behavioral and imaging findings (Rüther et al., 2014; Yee et al., 2013). For example, object-use observation was found to lead to increased activation in the object representation network including IFG, SMG, and angular gyrus during later object viewing (Rüther et al., 2014). The activation time course of “skilled use” action attributes is slower and longer-lasting (Jax and Buxbaum, 2010; Lee et al., 2013; Valyear et al., 2011), typical of semantic memory (e.g., Damian and Als, 2005). In addition, the magnitude of overt action deficits in apraxia is associated with the degree of slowing of incidental activation of skilled use information from objects (Lee et al., 2014). These data all suggest that manipulation knowledge may be a component of object semantic representations. The evidence from these studies, however, is indirect. In showing priming effects on the N400, a well-established electrophysiological signature of access to long-term memory, the present study is among the first to provide evidence that “skilled use” action attributes constitute a part of the semantic representations of objects.

The N400 priming effect in the sensory-motor mediated “skilled use” action conditions differed in scalp topography from that seen in the taxonomic condition, wherein the shared semantic features were less sensory-motor dependent. With a distributed source, the N400 has been taken to reflect coordinated activity across the semantic network as meaning features are accessed in response to incoming sensory information (Federmeier and Laszlo, 2009; Kutas and Federmeier, 2011; Kutas and Hillyard, 1980). As brain regions involved in

semantic processing are non-identical across different stimulus types (Huth et al., 2016; A. Martin, 2007), N400 scalp distributions have also been shown to vary. Here, unlike the widespread scalp distribution of the N400 taxonomic priming effect, the N400 action priming effect was more anterior and focal. Similarly anterior N400 responses have been seen in other action-related manipulations. For example, in one recent study (van Elk et al., 2010), participants viewed an object picture, and, after a short interval, moved the corresponding object to a pre-specified body part, rendering the action meaningful (e.g. moving a magnifying glass towards the eye) or meaningless (e.g. moving a cup towards the eye). Picture-locked ERPs showed an anteriorly-focused N400 difference between the meaningful and meaningless actions. Moreover, when an additional word was presented between picture display and action execution, larger N400s were found over anterior sites to object-incongruent than to object-congruent words only when the actions were meaningful. For example, in the case of moving glasses towards the eyes, N400s were more negative to the object-incongruent word ‘mouth’ than to the object-congruent word ‘eyes’; however, no such effect was found for the case of moving a cup towards the eyes (van Elk et al., 2008). Finally, Bach et al. (2009) presented pictures of a tool (e.g., a key) and a potential target object of the action (e.g., a keyhole) in succession, and found N400 effects from function mismatch versus match between the tool and its target object (e.g., inserting a screwdriver versus a key into a keyhole) regardless of tool-target presentation order.

Note that there are important differences in the measured constructs and methodology between the present study and these studies (Bach et al., 2009; van Elk et al., 2008, 2010). First, the stimuli in these aforementioned studies did not permit distinctions between “grasp-to-move” and “skilled use” action attributes. Furthermore, whereas the current design focused on the action semantics of one particular object, effects in van Elk’s and Bach’s studies reflect a joint effect of accessing object-related action attributes, processing the relation between objects, and in some cases even preparing and planning for action. Finally and most importantly, whereas action preparation and execution were either depicted or required in these studies, only objects were explicitly presented in the present study. These differences may help explain the N400 scalp distributions that differed somewhat across the studies (ranging from frontal-central in, e.g., van Elk et al., 2010 to more clearly frontal, as in the current study). More generally, however, the relatively anterior N400 action-related priming effects seen in the present study and related previous studies suggest that access to action semantics (Bach et al., 2009; van Elk et al., 2008, 2010; also see Leshinskaya and Caramazza, 2016 for a discussion) may differ from access to semantic information with weaker relationships to sensory-motor attributes, such as seen in the taxonomic conditions here (see also Kalénine and Buxbaum, 2016; Tsagkaridis et al., 2014).³

A frontal effect was also observed in the N400 time window for the “grasp-to-move” condition, but its nature is less clear. In contrast to “skilled use” actions, “grasp-to-move” actions have been linked to a bilateral dorso-dorsal stream that computes object affordance in relation to current visual information (e.g., shape, size, and position with respect to the

³N300 effects tend to have an anterior distribution, similar to that observed here. However, such effects have been linked to the processing of global structural similarity, which was controlled here, and also tend to obtain earlier (before about 350 ms). Thus, it seems most likely that these are N400 effects with an anterior distribution, as also seen in prior studies using objects.

actor), and hence have been considered to be less connected with object semantic representations than are “skilled use” attributes (e.g., Poliakoff et al., 2007; also see Buxbaum and Kalénine, 2010 for a review). In the present data, lack of augmentation in the size of the relatedness effect in the “grasp-to-move” condition between the N400 time window and the preceding time window (as revealed in the time window and peak to peak amplitude analyses) leaves open the possibility that this was simply the continuation of the earlier effect pattern.

Alternatively, it is possible that there is indeed an N400 action priming effect for the grasp-to-move condition as well. Such a result might be predicted on accounts that posit interactivity between earlier sensory and later semantic action processing stages. Some previous data are consistent with such interactivity. For example, Shibata et al. (2009) showed that the relationship between hand shape and the shape of an object to be grasped is used by observers to make sense of the details of cooperative interpersonal actions. Feedback from object representations to “grasp-to-move” actions has also been reported by Jeannerod and colleagues (Milner et al., 1999), who showed that an optic ataxic patient with dorsal stream lesions made significant grasping errors with novel three-dimensional shapes, yet improved markedly when objects of the same shape and size were familiar. In light of these findings, the N400 semantic facilitation from “grasp-to-move” action attributes observed in the present study could be due to cascading information between the two classes of actions—with facilitated processing of the earlier-rising “grasp-to-move” attributes in turn facilitating processing of “skilled use” attributes and other aspects of semantics.

Awareness of action attributes during object processing

In addition to our main findings, our results also revealed that, compared to taxonomic information, participants were much less aware of the action similarity of the primed-target pairs. Whereas the majority of the taxonomically related pairs were judged as related (92%), action-related pairs were mostly judged as unrelated, similar to the other two unrelated conditions (judged as unrelated: Skilled use related: 60%; Grasp-to-move related: 77%; Action unrelated: 89%; Taxonomically unrelated: 68%).

The effects of interest in the present study (early sensory visual potentials and N400s) are obligatory responses to visual and potentially meaningful stimuli (Kutas and Federmeier, 2011; Luck, 2013; Luck and Kappenman, 2013). These responses have been shown to be robust regardless of conscious awareness (P1 and N1: Koivisto and Revonsuo, 2003; Sergent et al., 2005; N300: Eddy et al., 2006; N400: Zhou et al., 2016; Stenberg et al., 2000). Based on these findings, we do not believe that the ERP patterns observed here depend upon conscious detection of prime-target similarity. Instead, our findings suggest that action similarity is processed by the brain despite not always being consciously accessible.

It might be suggested that objects similar in action are judged as unrelated because action is not always processed consciously. On classic two-route accounts of visual processing, reach and grasp actions mediated by the bilateral dorsal visual stream operate on currently-viewed structural characteristics of objects, and are largely inaccessible to consciousness (Goodale and Milner, 1992, 2013; Milner and Goodale, 1995; Jeannerod et al., 1995b). More recent evidence indicates, however, that skilled use actions are mediated by relatively more ventral

regions (the “ventro-dorsal stream”), are strongly left-lateralized, and are consciously accessible (e.g., Ishibashi et al., 2016; M. Martin et al., 2016; Tobia and Madan, 2017; see Binkofski and Buxbaum, 2013; for discussion). One possibility is that the relatively low probability of detection of action similarity results from a cognitive bias to rely upon “taxonomic” features such as function and appearance as well as typical “thematic” features such as location (e.g., “kitchen”) and temporal events (e.g., “birthday”) in categorization tasks (see Mirman et al., 2017 for review). The relatively stronger explicit awareness of attributes such as function, appearance, and location as compared to action attributes may be due, in turn, to the benefits and importance of the former in communication, naming, and perhaps “inner speech” (e.g., both bongo drums and oboe can be labeled as instruments; both pillow and comforters can be labeled as bedding). Explicit categorization may be more difficult and of less communicative value for the majority of the action related pairs, particularly for the grasp-to-move pairs.

Conclusion

Clarifying current accounts of the characteristics and time course of activation of action information during object processing, our data showed that action attributes associated with manipulable objects affect both early visual sensory and later semantic processing for objects even under circumstances in which execution or preparation of object-directed actions is not required. These data add to the accumulating evidence that perception and action are not independent from each other (Amazeen and DaSilva, 2005; Goodale and Haffenden, 2003; Mahon et al., 2007) and that action attributes contribute constitutively to object representations (A. Martin, 2007; Yee et al., 2013). More critically, with data from well-characterized ERP components, our findings provide direct evidence that “grasp-to-move” and “skilled use” action attributes contribute to different aspects of object processing. While “grasp-to-move” action attributes may play a role in attentional enhancement of visual object characteristics, “skilled use” action attributes are a component of distributed multimodal semantic object representations.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

Acknowledgments





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Appendix A. Supplementary data





Supplementary data related to this article can be found at <https://doi.org/10.1016/j.neuroimage.2017.11.045>.

Appendix

(A). Examples for Action pairs. Each column lists a target and its corresponding “grasp-to-move”, “skilled use”, and unrelated primes. Readers are referred to the Materials section for how items were arranged and presented for each participant.

	Example set #1	Example set #2	Example set #3	Example set #4	Example set #5
Action pair targets					
Grasp-to-move related primes					
Skilled use related primes					
Unrelated primes					

(B). Examples for Taxonomic pairs. Each column lists a target and its corresponding related and unrelated primes. Readers are referred to the Materials section for how items were arranged and presented for each participant.

	Example set #1	Example set #2	Example set #3	Example set #4	Example set #5
Taxonomic pair targets					
Related prime					
Unrelated prime					

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	Prime	Target
Skilled use Action Related		
Grasp-to-move Action Related		
Action Unrelated		
Taxonomically Related		
Taxonomically Unrelated		

Fig. 1.
Examples of the experimental stimuli.

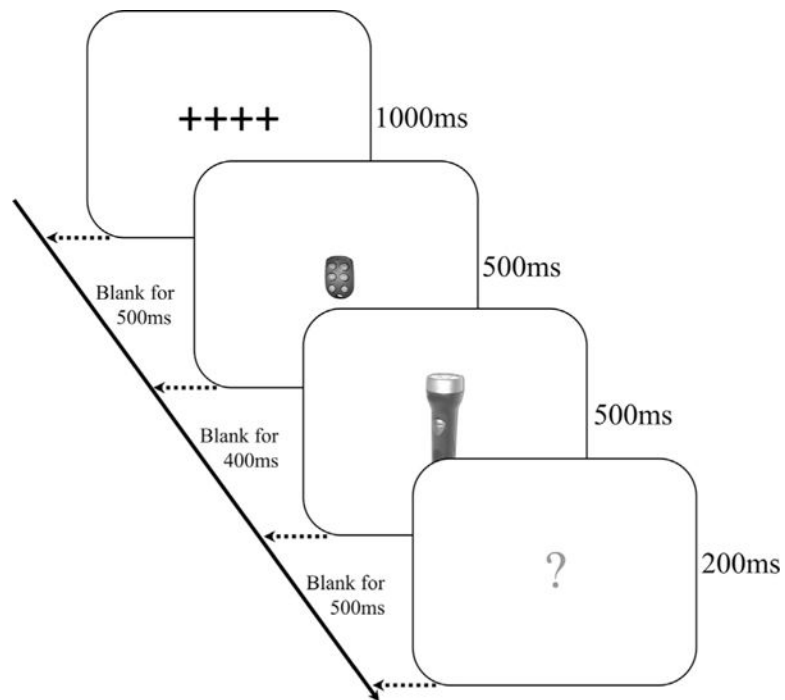
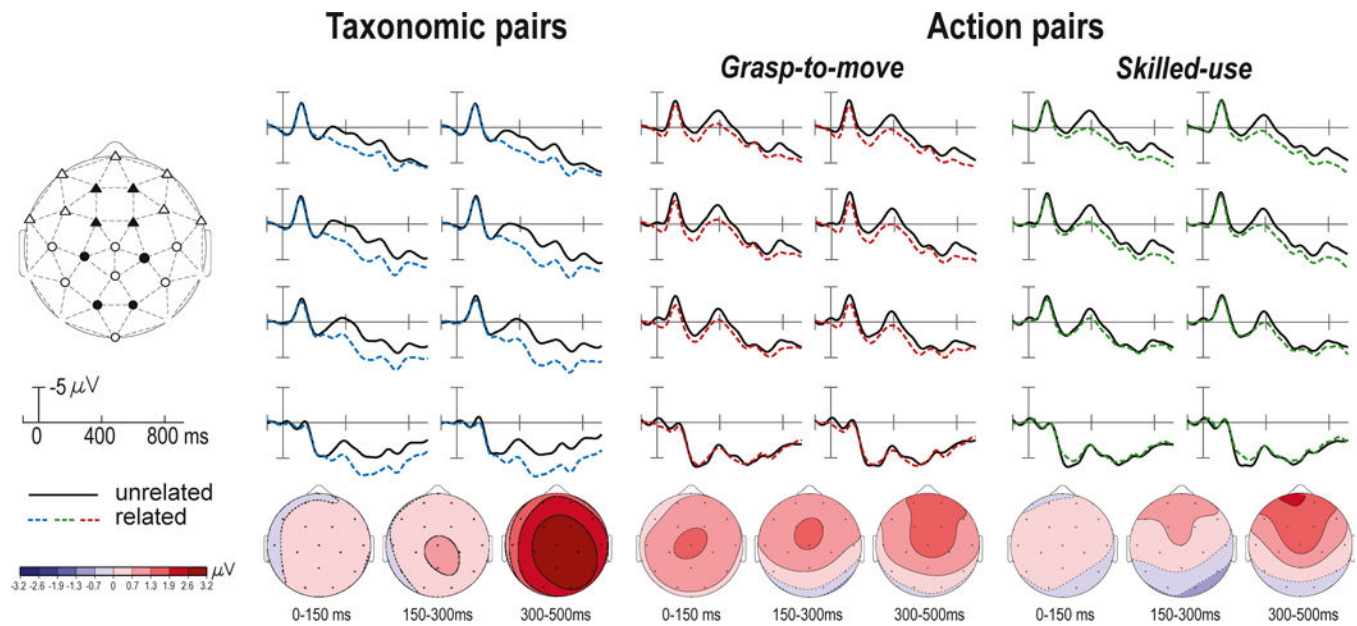


Fig. 2.
Illustration of the time course of one experimental trial.

**Fig. 3.**

Grand-average event-related potentials (ERPs) to target objects at 8 representative electrode sites are plotted for taxonomic (Taxonomically related vs. Taxonomically unrelated) as well as for action pairs (Grasp-to-move related vs. action unrelated and Skilled use related vs. action unrelated). Positions of the plotted sites are indicated by filled symbols on the head diagram (nose at top; anterior sites are marked with triangles and central-posterior sites are marked with circles). Negative is plotted up. For illustration purpose, the waveforms were filtered with a low-pass at 8 Hz. The scalp-topography illustrations (bottom) depict the distribution of ERP differences (related minus unrelated condition) in the 0–150 ms, 150–300 ms, and 300–500 ms time windows.

Table 1

Tabulated here are mean values of familiarity and action agreement for primes and targets in all conditions, and mean values for pair-wise action agreement, taxonomic similarity and visual similarity for pairs in all conditions. Standard deviations are shown in parenthesis.

		Action pairs			Taxonomic pairs		
		Skilled use	Related	Grasp-to-move	Related	Unrelated	Unrelated
Primes	Familiarity (1: not at all familiar; 7: very familiar) Action Agreement (proportion out of 1)		5.5 (1.5)	6.2 (0.5)	6.3 (0.5)	6.3 (0.4)	6.3 (0.8)
		Grasp	0.8 (0.2)	0.9 (0.1)	0.9 (0.1)	0.7 (0.2)	0.7 (0.2)
		Use	0.8 (0.2)	0.9 (0.1)	0.8 (0.1)	0.7 (0.2)	0.7 (0.2)
Targets	Familiarity (1: not at all familiar; 7: very familiar) Action Agreement (proportion out of 1)		6 (0.9)	6 (0.9)	6 (0.9)	6.3 (0.6)	6.3 (0.6)
		Grasp	0.9 (0.2)	0.9 (0.2)	0.9 (0.2)	0.8 (0.2)	0.8 (0.2)
		Use	0.8 (0.2)	0.8 (0.2)	0.8 (0.2)	0.8 (0.1)	0.8 (0.1)
Prime-Target Pairs	Pair-wise Action Match (proportion out of 1)	Grasp	0.3 (0.5)	0.9 (0.3)	0 (0.1)	0.3 (0.4)	0.2 (0.4)
		Use	0.9 (0.3)	0.4 (0.5)	0 (0.1)	0.3 (0.5)	0.2 (0.4)
		Taxonomic similarity (1: not at all related; 7: very related) Visual similarity (1: not at all similar; 7: very similar)	1.8 (1.2)	1.6 (0.9)	1.4 (0.7)	5.5 (0.8)	2.3 (1.4)
			2.3 (0.9)	2.7 (1.3)	1.6 (0.7)	2.4 (1.2)	1.5 (0.5)