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RESEARCH ARTICLE

Observing functional actions affects semantic processing of tools: evidence of a motor-to-semantic priming

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Abstract Recent evidence shows that activation of motor information can favor identification of related tools, thus suggesting a strict link between motor and conceptual knowledge in cognitive representation of tools. However, the involvement of motor information in further semantic processing has not been elucidated. In three experiments, we aimed to ascertain whether motor information provided by observation of actions could affect processing of conceptual knowledge about tools. In Experiment 1, healthy participants judged whether pairs of tools evoking different functional handgrips had the same function. In Experiment 2 participants judged whether tools were paired with appropriate recipients. Finally, in Experiment 3 we again required functional judgments as in Experiment 1, but also included in the set of stimuli pairs of objects having different function and similar functional handgrips. In all experiments, pictures displaying either functional grasping (aimed to use tools) or structural grasping (just aimed to move tools independently from their use) were presented before each stimulus pair. The results demonstrated that, in comparison with structural grasping, observing functional grasping facilitates judgments about tools' function when objects did not imply the same functional manipulation (Experiment 1), whereas worsened such judgments when objects shared functional grasp (Experiment 3). Instead, action observation did not affect judgments concerning tool–recipient associations (Experiment 2). Our findings support a task-dependent influence of motor information on high-order conceptual tasks and provide further insights into how motor and conceptual processing about tools can interact.

Keywords Functional actions · Structural actions · Tool objects · Semantic judgment · Motor knowledge · Action observation

Introduction

Several studies have shown that both visual and lexical processing of objects trigger incidental activation of motor actions directed toward the objects (Glover 2004; Tucker and Ellis 1998, 2001). Conversely, programming either power or precision grasping actions facilitates visual processing of objects associated with a congruent grip (Bekkering and Neggers 2002; Craighero et al. 1999; Symes et al. 2008). Such lines of evidence suggest that the neural representation of objects and of their related actions is tightly coupled (Helbig et al. 2010).

Objects are associated with multiple actions according to the actor's goal (Ansuini et al. 2006, 2008). Tools in particular are related to two distinct classes of actions: (1) "structural" or "volumetric" actions intended to hold, displace, or transport objects, in which hand shaping for grasping is driven by objects' structure and spatial location; (2) functional actions, aimed to use objects according to their functional properties. Access to conceptual knowledge about objects' function is necessary for activation of functional actions, to configure prehensile postures best fitting subsequent skilled movements (Buxbaum et al. 2006; Buxbaum and Kalénine 2010; Frey 2007). Both structural and functional actions seem to be elicited by processing tool pictures and tool names, as well as action sentences (Bub et al. 2008; Bub and Masson 2010; Jax and Buxbaum

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2010). However, as clearly shown by Creem and Proffitt (2001), most normal subjects spontaneously tend to select a functional grasping when requested to grab a tool without any specific purpose. This automatic selection of functional actions is reduced when subjects are engaged in a concurrent semantic verbal task but not in a spatial task, suggesting that semantic processing is implied in formation of the functional grasping (Creem and Proffitt 2001).

Several studies also suggest that activation of tool-related action knowledge affects visual recognition as well as lexical–semantic processing of objects. For instance, Myung et al. (2006) showed that lexical processing of target object words was speeded when subjects were primed with words denoting objects that shared the same functional action pattern with the targets. Similarly, Helbig et al. (2006) showed that accessing functional action representations facilitates object visual recognition. In their study, naming pictures of target objects was faster when subjects were presented with prime images of objects activating actions congruent rather than incongruent with the targets. Similar findings have been obtained when Helbig et al. (2010) used video clips showing congruent or incongruent functional gestures instead of static objects. More recently, Lee et al. (2014) required subjects to select target objects in a visual array, while they were presented with auditory sentences referring to either structure-based (“picking up”) or function-based (“using”) actions directed to target objects. By tracking subjects’ ocular movements, Lee et al. (2014) found that spoken verbs expressing functional actions favored target identification.

Evidence supporting that functional action knowledge contributes to objects recognition led Campanella and Shallice (2011) to investigate whether such information should be considered as a semantic feature of objects. In a word-to-picture matching task performed under time pressure, Campanella and Shallice (2011) observed that subjects needed more time to identify target objects when these were presented along with distractors sharing the same functional manipulation features (“distance” effect) and that their performance worsened after repeated presentations of the same target–distractor pairs (negative serial position effect). Because both the distance and the negative serial position effects can be found in patients suffering from semantic access disorder, the authors proposed that functional manipulation knowledge could be considered as an actual semantic dimension.

Overall, the reviewed studies suggest that functional action representations are strictly linked to (or are indeed part of) objects’ lexical–semantic representation. However, there are two limitations of these studies. First, most authors, but Helbig et al. (2010), assessed activation of action-related information by using other object-related stimuli as a prime (e.g., picture or name). Second, the above studies investigated influence of motor knowledge on recognition of object identity only (i.e., naming objects or identifying objects among others). If a tight relationship between motor and conceptual knowledge exists, then it could be predicted that activation of functional action features of an object should in turn activate all semantic attributes within the conceptual representation of that object. This would affect performance in higher-order tasks, requiring elaboration of objects’ semantic properties. Moreover, such an effect should be weaker (or absent) when structural rather than functional manipulation features are activated.

To test this hypothesis, we investigated whether observed functional and structural grasping actions can differently influence semantic judgments based on conceptual properties, such as objects’ function or association with typical recipients. The possible effects of bottom-up activation of functional versus structural action knowledge were assessed in three experiments. In Experiment 1 healthy subjects were required to judge whether pairs of tools requiring different functional handgrips could be used to achieve similar action goals, i.e., whether they accomplish the same purpose (e.g., a straight razor and an electric razor). Immediately before each pair, static images of hands grabbing one of the paired objects (hereafter: “target objects”) with either functional or structural grasp were presented (prime stimuli). In Experiment 2, the same prime conditions as in Experiment 1 were used, but participants were required to judge whether presented tools were correctly paired with possible recipients for actions they typically carry out (e.g., a squeegee and a glass window). In other terms, Experiment 2 required participants to process objects for a thematic relation (i.e., for co-occurrence of objects within the same event schema; Kalénine and Bonthoux 2008; Kalénine et al. 2009; Mirman and Graziano 2012; Schwartz et al. 2011; Tsagkaridis et al. 2014). Both experiments entailed retrieving conceptual knowledge about tools’ function (i.e., what an object is for) and tapped conceptual processing of objects beyond mere identification. In line with our working hypothesis, we expected to observe a better performance after observation of functional rather than structural grasping actions in both tasks. Finally, in Experiment 3 the same judgment task as in Experiment 1 was used to assess whether the possible effect of functional motor knowledge can be disrupted when pairs of objects to be judged have different functions but share similar functional grasping postures. In this last case, knowledge about functional manipulation had to be decoupled from knowledge about objects’ function, and an interference effect, rather than a facilitation, could be expected.

Three features of our experimental setup are worth underlining. Across all experiments, we used the same “target” objects (and related prime stimuli), whereas we varied

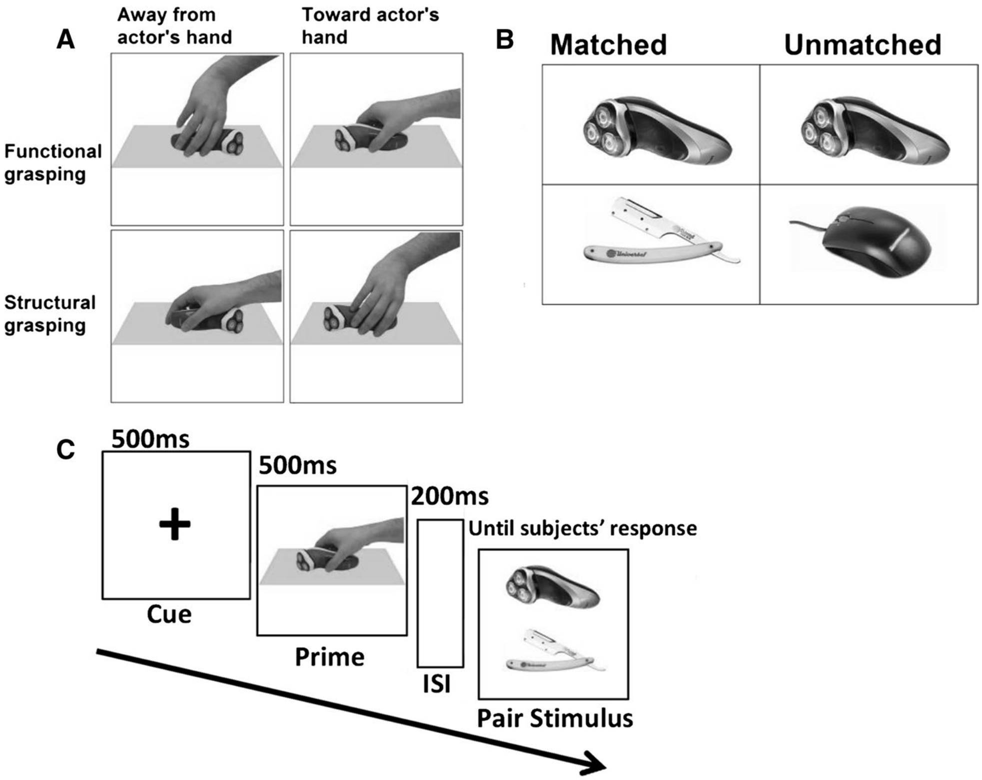

Fig. 1 **a** Examples of prime stimuli associated with target objects. One picture was produced for each combination of two object orientations (away, toward the actor) and two grasp types (functional, structural). **b** Examples of stimulus pairs employed in Experiment 1: matched pairs included a target object (e.g., an electric razor) coupled with an object having similar function and different manipulation (e.g., a straight razor), whereas unmatched pairs included a target object coupled with an object having different function and different manipulation (e.g., a PC mouse). **c** Sequence of events in experimental trials (the same sequence was used in all the experiments)

only the second objects within the pairs. This choice was intended to reduce possible sources of variability across experiments related to differences in employed objects and primes. Moreover, in the prime stimuli we varied the orientation of the objects (and consequently the trajectory of actor's reaching movements) to assess the possible role of factors related to kinematic properties (i.e., the trajectory) of the observed action; we expected that such features did not modulate participants' performance, whereas functional versus structural grasp actions would do it. Last, judgments required in all the experiments did not overtly refer to motor knowledge, in order to address the specific question whether functional motor information can influence processing of objects' semantic features outside the motor domain.

Experiment 1

Method

Participants

Twenty-nine undergraduate students (12 males; mean age = 24.3 years; SD = 3.4), naïve to the purposes of the study, took part in the experiment after having provided their informed consent. All the participants were right-handed healthy subjects with normal or corrected-to-normal vision. All procedures were run in concordance with the Declaration of Helsinki and approved by the local ethics committee.

Experimental stimuli and procedure

The prime stimuli were colored pictures portraying a hand grabbing a target object (laid on a horizontal plane) with either functional or structural grasping. For each target object, four prime stimuli were built by combining two objects orientations (handle pointing toward or away from the actor's hand) with two grasp types (functional or structural). Prime stimuli had a size of 600 × 600 pixels and a visual angle of 6.6° at a viewing distance of 65 cm (see Fig. 1a).

Stimuli consisted of 36 pairs of colored object pictures. Objects in a pair were matched in size and were aligned along the horizontal axis of a blank square having the same overall size of the prime stimuli. In matched pairs, the 18 "target" tools were coupled with 18 objects sharing the same function but not the same functional manipulation (e.g., a nail clipping and nail scissors; a hair butterfly clamp and a hair clip). In unmatched pairs, the "targets" were coupled with 18 objects having different function and functional handgrip (e.g., a nail clipping and a house key; a hair butterfly clamp and a fork; see Fig. 1b for an example of stimuli and "Appendix" for a complete list). Target objects were on top of the pair in half of the stimuli.

To ascertain that objects were correctly paired according to the above criteria, an independent group of 10 undergraduate students rated similarity of functional grasp as well as similarity of function for each pair. Both evaluations were carried out by means of five-point Likert scales, with 1 indicating "absolutely different" and 5 indicating "absolutely similar." Mean ratings for both handgrip and function evaluations were submitted to a Wilcoxon signed-rank test. Matched and unmatched pairs obtained similar, very low ratings on action similarity (mean ratings $= 1.79$ and 1.76 respectively; $p = .759$), whereas matched pairs were given significantly higher scores on function ratings (mean $= 4.02$) than unmatched pairs (mean $= 1.01$; $p = .005$).

Each of the 36 pairs was presented four times during the experiment, for a total of 144 trials; the four presentations of each stimulus pair were preceded by one of the associated prime stimuli. The presentation order was pseudorandomized to satisfy the following conditions: (1) a given pair was never repeated until all 36 pairs were presented, and (2) the order of prime stimuli preceding each pair was counterbalanced between subjects.

We carried out stimulus presentation on a 17-in. monitor screen as well as data collection (accuracy and response times, RTs) by Superlab 4.0 software.

Participants sat on a comfortable chair facing the monitor, with their feet resting on a foot keyboard and their hands with palms facing down on their legs. Subjects were asked to judge whether objects in each pair served the same functional purpose (i.e., they could be used to achieve a similar goal). To avoid any response compatibility effect related to manual responses (Tucker and Ellis 1998), subject were instructed to respond as fast and accurately as possible "yes" or "not" by pressing the right or left pedal on the foot keyboard (response pedals inverted for half participants). Each trial began with a central fixation cross (500 ms), followed by a prime stimulus (500 ms). Then, after a 200-ms interstimulus interval (blank screen), paired stimuli were presented until participants provided their response (see Fig. 1c). To ensure that participants paid attention to the prime stimuli during the entire duration of the experiment, 16 catch trials (about 11 % of the total) were included, in which the prime stimuli depicted a hand pointing to the target object. Participants were instructed not to respond on the subsequent pair when the hand pointed to objects without touching them.

Results and comment

The data analysis was performed by SPSS v.19 (IBM). Percentage of correct responses was very high (>95 %) across all conditions. A preliminary Spearman rank correlation analysis between participants' accuracy rate and mean RTs in all experimental conditions revealed a significant negative correlation between speed and accuracy ($r_{s(232)} = -144$, $p = .028$). This ruled out a speed–accuracy trade-off, allowing us to perform further statistical analyses on RTs only.

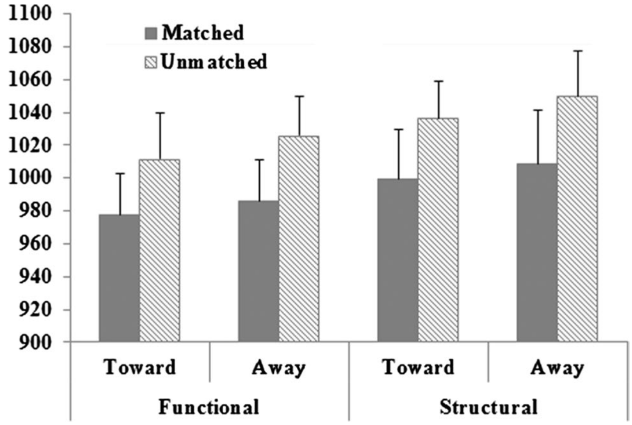

Fig. 2 Mean RTs in all conditions of Experiment 1 (*error bars* displaying SE): participants responded significantly faster on matched than on unmatched pairs and on pairs preceded by functional than by structural primes (see text)

Trials with RTs beyond the 95th and below the 5th percentile were discarded from analysis. On participants' correct RTs, a 2 × 2 × 2 ANOVA for repeated measures was carried out, with pair type (matched, unmatched), prime condition (functional, structural), and objects' orientation (toward, away from the actor) as within-subject factors. Mean RTs for all condition are plotted in Fig. 2. The analysis revealed a significant main effect of pair type [$F_{(1,28)} = 11.532$; $p = .002$; $\eta^2 = .292$], as the subjects responded faster on matched (mean $= 992.725$, SE $= 26.464$) than on unmatched pairs (mean $= 1030.984$, SE $= 22.538$). The main effect of prime condition was also significant [$F_{(1,28)} = 4.422$; $p = .045$; $\eta^2 = .136$], due to faster responses when pairs were preceded by functional (mean $= 1000.242$, SE $= 22.752$) than by structural primes (mean $= 1023.467$, SE $= 26.233$). The effect of objects' orientation (toward: mean $= 1006.084$, SE $= 23.540$; away: mean $= 1017.625$, SE $= 24.763$) was not significant [$F_{(1,28)} = 2.963$; $p = .096$; $\eta^2 = .096$]. No interaction resulted to be significant (all $p > .1$).

Overall, semantic relationships between objects in matched pairs led to faster judgments in comparison with semantically unrelated objects. More importantly, we observed a modulation of prime condition on subjects' performance: Observing functional grasping actions determined faster semantic judgments about tools' function in comparison with observing structural

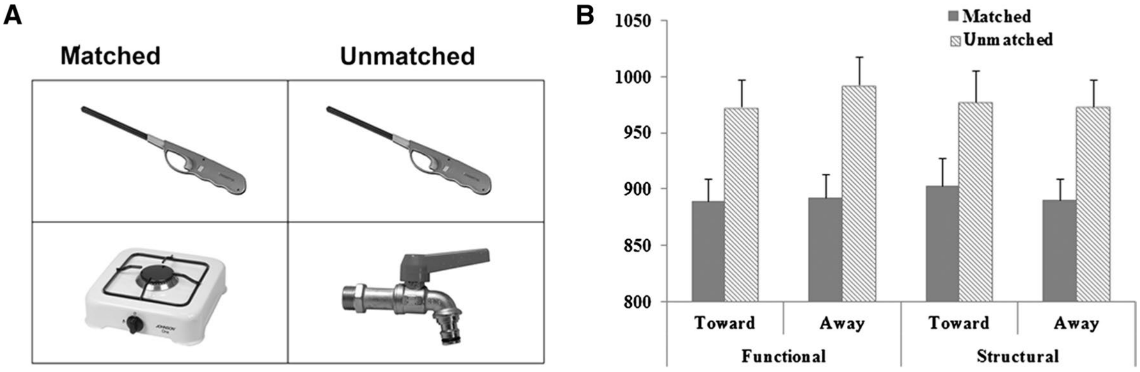

Fig. 3 **a** Examples of pair stimuli employed in Experiment 2: in matched pairs target objects (the same as in Experiment 1) were coupled with appropriate recipients, whereas in unmatched pairs they were coupled with implausible recipients. **b** Mean RTs in all conditions of Experiment 2 (*error bars* displaying SE): participants responded significantly faster on matched than on unmatched pairs (see text)

actions. Therefore, manipulation knowledge would facilitate not only object naming and visual recognition, i.e., basic levels of conceptual processing, as shown in previous studies (Helbig et al. 2006, 2010; Myung et al. 2006, 2010), but also retrieval of specific semantic features about objects (i.e., their function). Different from previous studies in which the object recognition was favored by presenting other object-related stimuli evoking similar manipulation patterns (i.e., by priming motor knowledge), in the present experiment the objects included in each pair did not share the same manipulation movements. Our findings thus provide the first evidence that motor representations can enhance access to semantic properties outside the motor domain. In other terms, observing functional actions can activate motor knowledge, and this would facilitate access to conceptual representations concerning the target objects.

Interestingly, the effect of functional action observation was not modulated by object orientation. In prime stimuli wherein the objects were directed away from actor, functional grasping was achieved by rotating the hand to direct the thumb toward the functional part of objects (see Fig. 1a). This resulted in an awkward rotation of the wrist, but is consistent with observations on normal subjects (Creem and Proffitt 2001) and complies with the end-state comfort effect (Cohen and Rosenbaum 2004; Janssen and al. 2011), whereby actions are planned so as to term movements in the most comfortable posture for intended goal. We can thus suggest that the lack of effect of object orientation is consistent with the idea that participants did not pay attention to the path followed by actor's hand, but to the interaction between hand and object.

Experiment 2

Method

Participants

Thirty-one undergraduate students (ten males; mean age = 24.7 years; SD = 2.9), naïve to the purposes of the study, took part in the experiment after having provided their informed consent. All the participants were right-handed healthy subjects with normal or corrected-to-normal vision; none of them had taken part in Experiment 1. All procedures were run in concordance with the Declaration of Helsinki and approved by the local ethics committee.

Experimental stimuli and procedure

Experimental design, apparatus and procedures were the same as in Experiment 1, but in this case the "target" objects were coupled with their typical recipients (e.g., a gas lighter and a gas cooker) in matched pairs, whereas they were coupled with implausible recipients (e.g., a gas lighter and a faucet) in unmatched pairs (Fig. 3a; see "Appendix" for a detailed list). An independent group of 10 healthy students rated pairs for pertinence of object-recipient coupling (from 1 = "completely appropriate" to 5 = "completely inappropriate"). Ratings showed significantly higher scores for matched pairs (mean = 4.75) than for unmatched pairs (mean = 1.12; $p = .005$, Wilcoxon signed-rank test).

In the present experiment, subjects were required to judge as fast and accurately as possible whether each object was paired or not with an appropriate recipient, i.e., to judge "action-based thematic relatedness of object pairs" (Tsagkaridis et al. 2014).

Results and comment

Percentage of correct responses was very high (>95). The same correlational analysis as in Experiment 1 was conducted to explore the relationships between accuracy and RTs. We observed a significant negative correlation ($r_{s(248)} = -148$, $p = .024$), allowing us to rule out a speed–accuracy trade-off.

After the same data-cleaning procedure as in Experiment 1, participants' correct RTs were submitted to a 2 × 2 × 2 ANOVA for repeated measures, with pair type (matched, unmatched), prime condition (functional, structural), and objects' orientation (toward, away from the actor) as within-subject factors. Results are plotted in Fig. 3b. The main effect of pair type was significant [$F_{(1,30)} = 35.052$, $p < .001$; $\eta^2 = .556$] because responses were faster on matched (mean = 893.233, SE = 19.429) than on unmatched pairs (mean = 979.085, SE = 22.999). Neither prime condition (functional grasp: mean = 936.575, SE = 19.521; structural grasp: mean = 935.743, SE = 21.259) [$F_{(1,30)} = .011$, $p = .918$; $\eta^2 = .000$] nor objects' orientation (toward: mean = 935.330, SE = 21.201; away: mean = 936.988, SE = 19.768) [$F_{(1,30)} = .035$, $p = .853$; $\eta^2 = .001$] were significant. Likewise, no interaction reached significance (all $p > .1$).

Such data showed that, as in Experiment 1, judgments were faster for related stimuli than for non-related pairs, consistent with a facilitation effect likely due to semantic relatedness. However, the crucial finding in Experiment 2 was the observation that judgments on object-recipient pairs are not sensitive to primes triggering motor knowledge. Matching tools with recipients might require more abstract inferential reasoning than function judgment (assessed in Experiment 1), since objects can be coupled with several plausible recipients (for instance, scissors could be used to cut paper, cloth, hair, and so on; Garcea and Mahon 2012), and can be even used on untypical recipients to achieve purposes outside their usual function (e.g., a coin can be used as a screwdriver; Goldenberg and Spatt 2009). Such inference would constrain influence of motor processing on high-order semantic processing to specific conceptual properties (such as object function), but further studies are needed to clarify this issue, provided that we used both manipulable and non-manipulable items as recipients. Such heterogeneity might have introduced an unwanted variability in RTs, but it was necessarily implied by our choice of keeping fixed the "target" objects (some of which had a non-manipulable object as typical recipient) across all the experiments of this study. Further research on the precise relationships between motor knowledge and processing of thematic relations appear to be necessary, also because action-based thematic relations are thought to be the most salient links among manufactured object concepts (Kalénine and Bonthoux 2008; Kalénine et al. 2009; Tsagkaridis et al. 2014).

Experiment 3

Method

Participants

Thirty-four right-handed healthy undergraduate students (14 males; mean age = 23.9; SD = 3.3) with normal or corrected-to-normal vision were recruited. They all were naïve to the purposes of the study and gave their informed consent before participating to the experiment; no subject had participated in previous experiments. All procedures were run in concordance with the Declaration of Helsinki and approved by the local ethics committee.

Experimental stimuli and procedure

Experimental design, apparatus and procedures were the same as in Experiment 1. The only variation regarded the 18 unmatched pairs, in which target tools were coupled with objects having different functions but requiring functional actions similar to those of the targets (e.g., a nail clipping and a junior stapler; a hair butterfly clamp and a clothes peg; Fig. 4a and see "Appendix" for a list). Again, in a preliminary study on an independent sample of ten students, we ascertained that matched pairs (the same used in Experiment 1) obtained a higher score on function similarity ratings (mean = 4.04) with respect to unmatched pairs (mean = 1.44; $p = .005$), whereas unmatched pairs obtained a significantly higher score than matched pairs on grasp similarity rating (mean ratings = 4.38 and 1.79 respectively; $p = .005$, Wilcoxon signed-rank test).

Results and comment

As in previous experiments, the accuracy of subjects' responses was high (>95 %) and was negatively correlated with RTs ($r_{s(272)} = -280$, $p < .001$), ruling out a speed–accuracy trade-off. Thus, further analyses were limited to RTs.

After the same data-cleaning procedure as in previous experiments, a 2 × 2 × 2 ANOVA for repeated measures was performed on participants' correct RTs, with pair type (matched, unmatched), prime condition (functional, structural), and objects' orientation (toward, away from the actor) as within-subject factors. Mean RTs in all condition are reported in Fig. 4b. Subjects responded

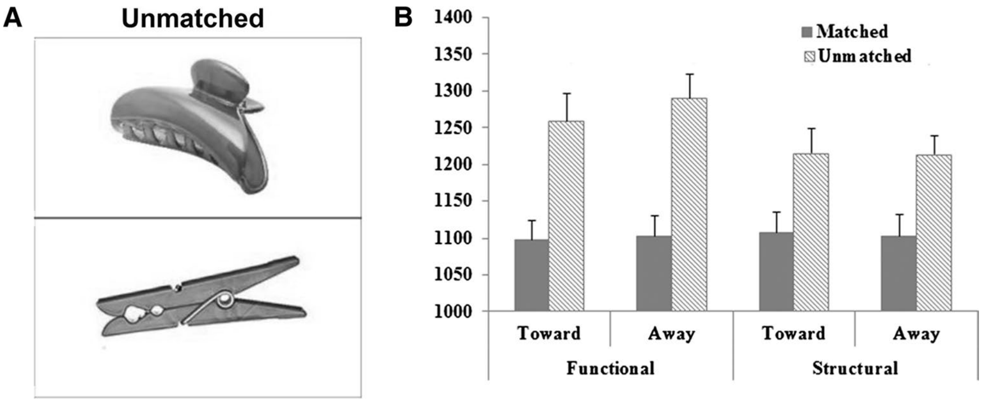

Fig. 4 **a** Examples of unmatched pairs used in Experiment 3, in which target objects were coupled with objects having different function but similar manipulation (matched pairs were the same as in Experiment 1). **b** Mean RTs in all conditions of Experiment 3 (*error bars* displaying SE): participants responded significantly faster on matched than on unmatched pairs, and on unmatched pairs preceded by structural primes than on unmatched pairs preceded by functional primes (see text)

faster on matched (mean = 1102.717, SE = 25.413) than on unmatched (mean = 1244.825, SE = 25.621) pairs [$F_{(1,33)} = .84.386$, $p < .001$; $\eta^2 = .719$]. Prime condition approached significance [$F_{(1,33)} = 3.202$, $p = .083$; $\eta^2 = .088$] since subjects responses were slightly slower when a functional prime (mean = 1187.451, SE = 27.084) rather than a structural prime (mean = 1160.090, SE = 23.790) was presented, whereas the effect of objects' orientation was not significant (toward: mean = 1170.20, SE = 26.95; away: mean = 1177.422, SE = 23.663) [$F_{(1,33)} = .388, p = .538$; $\eta^2 = .012$]. Importantly, there was a significant interaction between prime condition and pair type [$F_{(1,33)} = 6.181$, $p = .018$; $\eta^2 = .158$]. Bonferroni-corrected post hoc comparisons revealed that on unmatched pairs participants' RTs were slower in functional (mean = 1274.988, SE = 31.567) with respect to structural prime condition (mean = 1214.661, SE = 25.466; $p = .025$), whereas prime conditions did not differ from each other on matched pairs (functional: mean = 1099.915, SE = 25.778; structural: mean = 1105.519, SE = 26.543) ($p > .1$). No other interaction was significant (all $p > .1$).

As in Experiment 1, observing functional actions affected subjects' performance on semantic judgments about object function, but in this case the effect consisted in slowing down participants' responses for pairs in which objects had different functions but shared the same functional manipulation (unmatched pairs). These findings would suggest that activation of common motor representations shared by two objects can have a competitive effect with respect to processing of non-motor features of objects. In both Experiment 1 and Experiment 3, the results show that motor knowledge affects semantic judgments. However, differently from Experiment 1, in the present Experiment 3 observation of functional grasping actions did not facilitate semantic judgments for matched pairs, in which objects had not the same manipulation pattern. One could suggest that the intermingled presentation within the same experiment of trials in which motor knowledge exerts a confounding effect (i.e., unmatched pairs) with trials in which motor knowledge has a facilitation effect (i.e., matched pairs), might have reduced the positive cueing effect of primes depicting functional actions. In other terms, since our experimental setup was intended to induce a conflict between motor and conceptual processing, it seems plausible that activation of motor knowledge exerted a sort of an inverse priming effect on object semantic elaboration in all trials of Experiment 3 (where we observed generally longer RTs than in Experiment 1). This issue will be addressed further in the general discussion.

General discussion

We searched for an effect of action observation on two semantic tasks, requiring to judge whether two common tools shared similar functions (Experiments 1 and 3), or to judge whether tools were coupled with appropriate recipients (Experiment 2). A complex pattern of results emerged. We found that observing functional rather than structural actions facilitated function judgments when pairs of tools did not share the same manipulation (Experiment 1). However, observation of functional actions worsened participants' performance on paired tools having different function but similar manipulation (i.e., unmatched pairs; Experiment 3). Moreover, observation of functional grasps did not modulate recipient judgments (Experiment 2). Taken together, such results seem to support our predictions that activation of motor knowledge specific to objects use can affect semantic processing, but also pose several constraints on our hypothesis.

Several lines of evidence suggest that observing others' action lead to coherent activations into one's own motor system (Avenanti et al. 2013; Caspers et al. 2010; Gazzola and Keysers 2009; Rizzolatti and Sinigaglia 2010; but see Hickok 2008), and it has been proven that such motor activation could favor processing of tool identity (Helbig et al. 2010). Our findings expand these results by demonstrating that motor representations triggered by observed actions can also influence performance in high-order semantic tasks. This held true even if we used static hand images instead of videotaped dynamic actions (Helbig et al. 2010; Vingerhoets et al. 2010), in agreement with previous reports demonstrating that static action images can trigger internal action simulation into the observer's motor system (Johnson-Frey et al. 2003; Proverbio et al. 2009; Urgesi et al. 2006). However, observation of functional action would not suffice to modulate processing of a kind of thematic relation, such as the object–recipient association. It remains to be explored whether activation of motor knowledge can modulate other thematic tool properties, such as context of use (see Canessa et al. 2008) or functional relatedness (see Pelgrims et al. 2011).

The function judgment test used in the present study has been adapted from tasks employed in other studies investigating the neural representation of object functional properties (e.g., Andres et al. 2013; Boronat et al. 2005; Pelgrims et al. 2011). Function can be conceived as the "core" conceptual property of tools, and it has been argued that motor information is not necessary to retrieve such high-order conceptual information about objects (Garcea and Mahon 2012). Indeed, conceptual and motor knowledge about tools can dissociate between each other, as evidenced by TMS studies on healthy subjects (Andres et al. 2013; Pelgrims et al. 2011) and by neuropsychological observations on brain-damaged patients. For instance, Buxbaum and Saffran (2002) demonstrated that apraxic patients were impaired in coupling objects according to manipulation, whereas they had spared ability to match objects according to general function. A reverse pattern of impairments has been reported in a patient with bilateral temporal lesions (Sirigu et al. 2002). On these bases, as well as in the light of their own data about independent retrieving of function and manipulation knowledge in healthy subjects, Garcea and Mahon (2012) proposed that an epiphenomenal activation of motor representation occurs once the object-concept has been retrieved.

In recent years, however, several lines of evidence challenging this proposal have been gathered. Neuroimaging studies (Boronat et al. 2005; Buxbaum et al. 2006; Canessa et al. 2008; Chao and Martin 2000; Kellenbach et al. 2003; Yee et al. 2010; for a review see Martin 2007) have highlighted that viewing, recognizing, naming, and categorizing objects activate a distributed cortical network, including the left fronto-parietal areas involved in action representation, as well as the temporal regions concerned with object identity. Moreover, it has been demonstrated that activation of high-order motor information (i.e., functional motor knowledge) triggered by both tool-related primes and observed tool actions favors visual or lexical identification of objects sharing the same motor-related properties (Helbig et al. 2006, 2010; Myung et al. 2006, 2010). In these tasks, tool processing seems to proceed from motor to lexical–semantic representation, supporting the idea of a relevant contribution of motor knowledge in object representation. The results from Experiments 1 and 3 are better consistent with this notion and support the interaction of motor and conceptual systems in high-order cognitive processing.

Results from Experiment 3, however, revealed that motor information activated by observing functional actions slowed access to knowledge about objects' function when pairs of tools to be judged shared the same primed grip. For these items, similarity of objects' functional handgrips interfered with processing of non-motor-related properties of objects; such an interference was so prevalent to reduce the facilitation of observed functional actions on pairs of object matched for function but not for manipulation. This effect is compatible with the idea that objects sharing the same manipulation pattern have overlapping sensorimotor representations (Yee et al. 2010), but would also fit with the proposal that manipulation knowledge is a semantic property itself (Campanella and Shallice 2011). Indeed, it has been proposed that since acquisition of objects' knowledge is mainly grounded on the repeated manual interactions with them, manipulation information, as well as object function, could be a relevant feature for object characterization (Campanella and Shallice 2011; Farah and McClelland 1991; Warrington and McCarthy 1987). In both accounts, to tell apart stimuli according the target property ("function") could be more difficult when stimuli are matched for another relevant feature ("manipulation"). Such inference can imply that motor knowledge can either facilitate or hamper semantic processing depending on the contextual features of the cognitive task.

The present study has two possible limitations. First, our empirical findings cannot rule out that the effect of action observation was mediated by some inferential process about actor's intention, rather than to a direct activation of motor representation for object use. For the purposes of our study, however, it is important to underline that whatever high-order cognitive process occurred, it was triggered by an information that was motor in nature (i.e., an observed motor act), thus reinforcing the idea of an interaction between motor and high-order cognitive processes. A second possible limitation of our study concerns the fact that our prime stimuli contained two sources of motor information, one provided by the observed motor act, and one coming from the object picture itself, that might trigger motor-related properties of objects (Bub et al. 2008; Bub and Masson 2010; Helbig et al. 2006; Jax and Buxbaum 2010). Our experimental design could not tease apart the contribution of motor knowledge evoked by object observation, but our study aimed to demonstrate the critical influence of functional versus structural grasp actions on the semantic task.

Even holding these caveats in mind, our behavioral observations trigger some speculations about the neural mechanisms underlying the observed effects. Neuroimaging studies have highlighted that similar neural substrates are involved in representing tools (Boronat et al. 2005; Canessa et al. 2008; Chao and Martin 2000; Kellenbach et al. 2003; Yee et al. 2010) and tool use (Creem-Regehr and Lee 2005; Johnson-Frey 2004; Johnson-Frey et al. 2005; Lewis 2006). In this cortical network, the inferior parietal cortex seems to play a central role in representing skilled use of objects (Binkofski and Buxbaum 2012; Buxbaum et al. 2006; Frey 2007; Vingerhoets 2014) and is tightly interconnected with a node for conceptual knowledge about tools in posterior temporal areas (Ramayya et al. 2010). Moreover, the inferior parietal cortex is activated during action observation (Caspers et al. 2010; Gazzola and Keysers 2009; Oosterhof et al. 2010; Vingerhoets et al. 2010; Shmuelof and Zohary 2007). Our findings might be compatible with the idea that observation of functional grasping would activate motor schemas relative to learned functional gestures in the inferior parietal cortex, and this would in turn lead to a spreading of neural activation to regions in temporal areas coding for conceptual object properties. Further functional investigations are needed to verify this speculation.

In conclusion, the present results expand knowledge on how motor and semantic information interact. We demonstrated that action observation can activate motor knowledge even during a semantic task not targeting action features of objects and that such information determines different effects as a function of task requirements. Motor processing led to a speeded access to semantic system when objects to be judged did not share their functional actions. On the contrary, motor knowledge interfered with processing of conceptual properties when objects were paired for manipulation features. Therefore, the present study provided a first demonstration of a task-depended "motor-to-semantic priming," that is modulated by the conceptual feature tapped by the task.

Appendix

Lists of objects included in experimental stimuli

Target objects—all experiments	Function judgment—Experiment 1		Recipient judgment—Experiment 2		Function judgment—Experiment 3
	Matched objects	Unmatched objects	Matched items	Unmatched items	Unmatched objects
Gas lighter	Lighter	Screwdriver	Gas cooker	Faucet	Hunting rifle
Coffee pot	Coffee maker	Hairbrush	Coffee cup	Piece of cake	Watering can
Basic corkscrew	Wing corkscrew	Pincers	Cork	Nail	T spanner
White out	Shake 'n squeeze	Spray	Copybook	Blackboard	Soap bubble maker
Paper scissors	Cutter	Bottle opener	Poster boards	Marble sheets	Serving scissor tongs
Hand electric mixer	Stand electric mixer	Vacuum cleaner	Cream casserole dish	Spaghetti dish	Electric iron
Pincer tea infuser	Tea bag	Pipe	Tea cup	Straw bale	Reverse tongs
Squeegee	Glass cleaning cloth	Shaving brush	Glass window	Wardrobe	Paint roller
Hand lens	Field glasses	Stapler	Written sheet	Traffic sign	Hairbrush
Hair butterfly clamp	Hair clip	Fork	Long-haired woman's head	Fingers	Clothes pin
Electric razor	Straight razor	PC mouse	Bearded chin	Feet	Torch
Liquid soap dispenser	Bar soap	Electric iron	Hands	Tongue	Perfume spray
Junior hacksaw	Toolbox saw	Ladle	Pieces of wood	Piece of bread	Slicer knife
Hairbrush	Comb	Ballpoint pen	Woman's hair	Woman's eye	Wall paintbrush
Spray bottle	Toilet cleaner bottle	Hammer	Bathroom sink	Bed	Soldering gun
Nail clipping	Nail scissors	Key house	Finger nails	Long-haired woman's head	Junior stapler
Coffee cup	Small glass	Cake spatula	Lips	Ear	Funnel
Hand stamp	Rubber stamp	Syringe	Ink pad	Ointment tube	Meat pounder

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