

# Pouring or chilling a bottle of wine: an fMRI study on the prospective planning of object-directed actions

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**Abstract** This fMRI study investigates the neural mechanisms supporting the retrieval of action semantics. A novel motor imagery task was used in which participants were required to imagine planning actions with a familiar object (e.g. a toothbrush) or with an unfamiliar object (e.g. a pair of pliers) based on either goal-related information (i.e. where to move the object) or grip-related information (i.e. how to grasp the object). Planning actions with unfamiliar compared to familiar objects was slower and was associated with increased activation in the bilateral superior parietal lobe, the right inferior parietal lobe and the right insula. The stronger activation in parietal areas for unfamiliar objects fits well with the idea that parietal areas are involved in motor imagery and suggests that this process takes more effort in the case of novel or unfamiliar actions. In contrast, the planning of familiar actions resulted in increased activation in the anterior prefrontal cortex, suggesting that subjects maintained a stronger goal-representation when planning actions with familiar

compared to unfamiliar objects. These findings provide further insight into the neural structures that support action semantic knowledge for the functional use of real-world objects and suggest that action semantic knowledge is activated most readily when actions are planned in a goal-directed manner.

**Keywords** Action planning · Action semantics · Objects · Goals · Grips · Superior parietal cortex

## Introduction

Our capacity to use tools and objects is often considered one of the hallmarks of the human species (Johnson-Frey 2003; Lewis 2006). Although chimpanzees may occasionally use tools, this ability turns out to be very limited and rigid (e.g. using stones to open nuts; Biro et al. 2003; Hayashi et al. 2005). In contrast, humans have the remarkable capability to use objects in a flexible fashion (cf. van Elk et al. 2009) and to combine multiple objects in complex actions. For instance, while in a restaurant you might want to pour your partner a glass of wine in which case you would probably grasp the wine bottle closer to the bottom in order to facilitate a pouring action. On the other hand, if the goal were to chill the wine, you would need to hold the bottle close to the top to facilitate the insertion of the bottle into an ice bucket. In either case, a particular goal leads to the selection of an appropriate way of grasping the object that is critically dependent on action semantic knowledge about an object's functional properties.

As the example illustrates, many of our actions are guided by action semantic knowledge whereby higher-level action goals (e.g. pouring a glass of wine) determine the selection of lower-level action features (e.g. grasping

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the wine bottle at the lower side). Several recent theoretical views have proposed that our ability to perform complex actions relies on the hierarchical organization of the motor system and that action goals are an organizing feature of action planning (Cooper 2002; Grafton and Hamilton 2007; Rosenbaum et al. 2007). According to this view, actions consist of sequences of motor primitives brought together to achieve a desired goal (e.g. making coffee; Grafton and Hamilton 2007). In support of this view, behavioral studies have shown that both humans and monkeys plan their actions in a way that allows them to end the action in a comfortable end-posture, which is known as the end-state comfort effect (Cohen and Rosenbaum 2004, 2011; Weiss et al. 2007; Chapman et al. 2010). For instance, subjects tend to grasp objects in a different way when they are required to rotate the object upside down compared to when they are required to put the object away (Herbort and Butz 2011).

Anticipatory action planning relies on the use of a predictive model that takes into account the final goal of the action and the movement constraints of the body (Wolpert et al. 1998; Wolpert and Ghahramani 2000). Several studies have shown that the parietal and prefrontal cortex play an important role in instantiating the predictive model and in representing the final goal of an action. For instance, apraxic patients with parietal lesions showed an impairment in selecting the appropriate handgrip for grasping inverted tools (Sunderland et al. 2011). In addition, these patients had difficulties with recognizing object-related gestures (Buxbaum et al. 2007; Kalenine et al. 2010) and did not show the same anticipatory motor-response during the observation of object-directed actions as healthy subjects (Fontana et al. 2011). Furthermore, recent neuroimaging studies have shown that planning a sequence of movements to achieve a desired end-state relies on activation in prefrontal brain areas, whereas selecting movements based on a specific grip type enhanced activation in the parieto-occipito sulcus (Majdandzic et al. 2007; van Schie and Bekkering 2007).

Although these studies provide insight into the neural mechanisms underlying anticipatory action planning, an often overlooked aspect in the domain of motor control is that many actions require the use of semantic knowledge. Knowing what to do with a wine bottle is something that cannot be inferred solely on the basis of an object's spatial features (Gibson 1979). It involves associating an intended goal (e.g. pouring wine into a glass) with a specific way of grasping the object (i.e. grasping the bottle at the lower side)—a process that requires semantic knowledge. Your partner would be quite surprised if you grasped the wine bottle near the base and then moved it toward the bucket, and even more surprised if wine was poured into it. The importance of semantic knowledge for planning actions

with multiple objects becomes unmistakably clear in patients with the action disorganization syndrome (ADS) or apraxia, who often fail to combine objects in a meaningful fashion, thereby resulting in incorrect action sequences (e.g. spooning butter in one's coffee instead of on one's bread; Rumiati et al. 2001; Schwartz 2006). Behavioral studies underline the importance of semantics for action planning. For instance, it was found that a concurrent semantic task interfered more strongly with grasping objects than a concurrent visuospatial task (Creem and Proffitt 2001). Furthermore, it has been shown that planning meaningful actions with objects results in a priming effect for words that were congruent with the intended end location of the action (Lindemann et al. 2006; van Elk et al. 2009). Together these studies provide behavioral support for the importance of semantic knowledge for successful action planning.

Still, the neural mechanisms supporting the retrieval of action semantics and the process whereby action semantics guides the selection of goals and grips are not well understood. In the present study, we used a novel motor imagery paradigm whereby goals and grips for planning an object-directed action were selected based on action semantic knowledge. Participants were required to imagine planning an action in which a central object (e.g. a wine bottle) had to be moved toward a target object (e.g. a wine glass). The effect of action semantics on the selection of goals and grips was investigated by manipulating the familiarity of the objects involved (i.e. subjects' experience with using these objects). Familiarity has a strong influence on how effectively semantic knowledge is used in language and other cognitive processes (Connine et al. 1990; Montaldi et al. 2006). Similarly, semantic knowledge of an object's functional properties is highly dependent on prior physical experience, and object familiarity may influence the ease whereby inferences are made about the goal or the grip for using the object (Tessari and Rumiati 2004; van Elk et al. 2009; van Elk et al. 2010b). Thus, in the present study, we manipulated the familiarity of the objects involved, by including both familiar and unfamiliar objects. Familiar objects are typically used in a daily fashion (e.g. a knife or a toothbrush), whereas unfamiliar objects are only used occasionally (e.g. a pair of pliers, a soup ladle). As a consequence, semantic knowledge about the use of objects is probably more easily activated when planning actions with familiar compared to unfamiliar objects.

To assess the importance of action semantics for selecting both action goals and action grips, we manipulated the mode of action planning, by instructing subjects to plan an action based on goal- or grip-related information (for a similar manipulation, see: Majdandzic et al. 2007; van Schie and Bekkering 2007). In case of a 'goal cue',

subjects were required to indicate how they should grasp a specific object in order to move it to a pre-specified goal. In the case of a ‘grip cue’, subjects were instructed to indicate whether they would move the central object to the left or the right target object, given a pre-specified way of grasping the central object. As previous studies have shown a distinction between brain areas supporting action planning based on goal- or grip-related information (Majdandzic et al. 2007; van Schie and Bekkering 2007) in the present study, we expected a similar differentiation between brain areas involved in representing the goal or the grip of an action. More importantly, given the notion that action semantics entails both grip- and goal-related knowledge (van Elk et al. 2008), it was expected that object familiarity modulates the strength of activation in brain areas representing action goals (such as the anterior prefrontal cortex) and action grips (such as the inferior parietal lobe and the parieto-occipital sulcus).

## Materials and methods

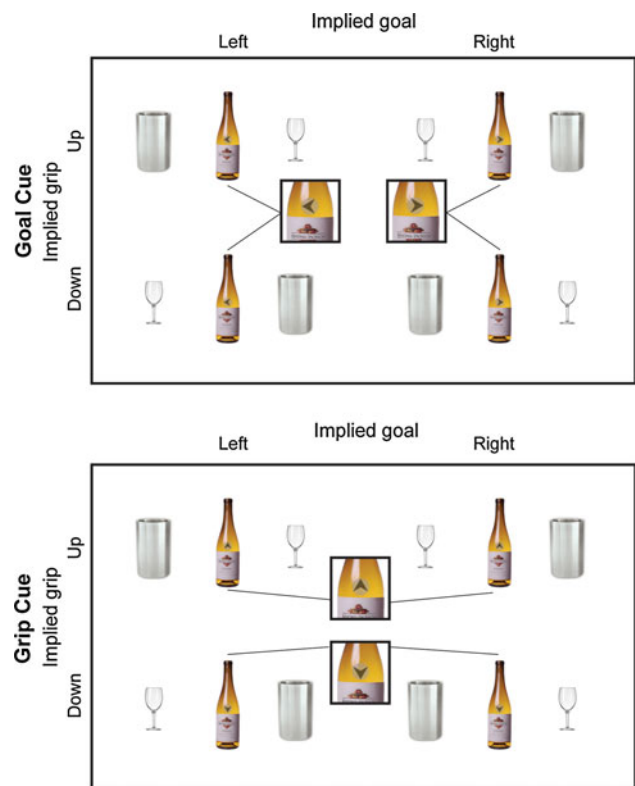
### Subjects

In total, 18 subjects participated in the experiment (7 women, mean age = 19.8 years) who received 60 USD for participation. Data from 2 subjects were excluded from the analysis because of performance at chance level. Subjects declared themselves through informal verbal inquiry to be right-handed. All subjects gave informed written consent in accordance with the guidelines from the Human Subjects Committee, Office of Research, University of California, Santa Barbara. The study was conducted in accordance with the declaration of Helsinki.

### Stimuli

Stimuli consisted of pictures representing a central object (e.g. a wine bottle) placed between two target objects (e.g. a wine glass and a wine bucket; see Fig. 1). As stimuli, 14 different object pairs were selected. Each object could be grasped in two separate ways (e.g. a wine bottle can be grasped at the upper or lower side), and each grasp type was associated with a different target object (e.g. moving the bottle to the wine glass or to the wine bucket; see Table 1).

Half of all central objects were relatively familiar, whereas the other half of all objects was relatively unfamiliar (see Table 1). The classification of objects was based on a test in which a group of subjects who did not participate in the fMRI study were asked to rate the centrally presented objects on a 5-point scale according to their familiarity (‘How familiar is the object represented in the



**Fig. 1** Example stimuli used in the experiment. Target stimuli consisted of pictures representing an *arrow* superimposed on a central object and two target objects. In the case of a Goal Cue (*upper panel*), the *arrow* was pointing to the left or the right target object, thereby specifying to which object the central object should be moved. In the case of a Grip Cue (*lower panel*), the *arrow* was pointing to the upper or lower side of the central object, thereby specifying at which side the central object should be grasped. The implied goal of the action could be the left or the right target object (i.e. left and right side of each panel) and the implied grip of the action could be a grip at the upper part or lower part of the central object (i.e. upper and lower side of each panel)

picture? In other words: how often do you use an object like this?'). Based on the familiarity ratings, half of all objects were classified as relatively familiar (mean familiarity rating = 4.8), whereas the other half of all objects was classified as unfamiliar (mean familiarity rating = 2.1).

A cue was superimposed on the central object, consisting of a black arrow. In the case of a *goal cue*, the arrow was pointing to the left or the right object, and in the case of a *grip cue*, the arrow was pointing to the upper or lower side of the central object (see Fig. 1). Goal cues indicated to which target object the central object should be moved and thereby implied a specific way of grasping the central object (i.e. at the upper or lower side). Grip cues indicated at which part the central object should be grasped and thereby implied that the central object should be moved to one of the target objects.

**Table 1** Central objects and target objects used in the experiment

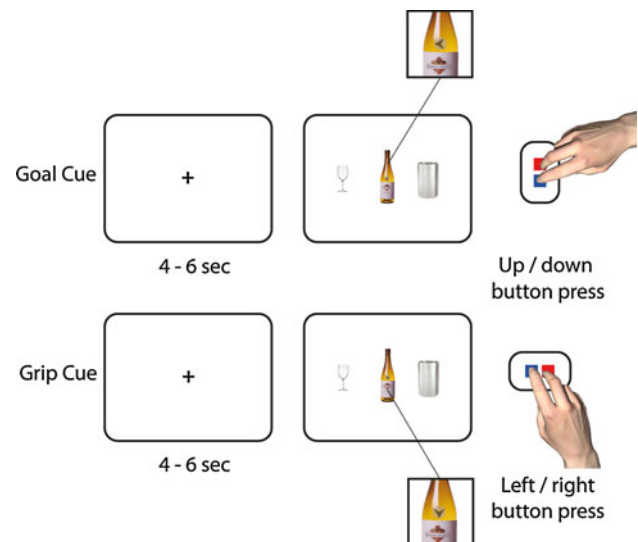
Objects	Target object 1	Target object 2
<i>Familiar</i>		
Wine bottle	Wine glass	Wine bucket
Cola can	Glass	Car
Spoon	Cornflakes	Kitchen utensil rack
Corkscrew	Wine bottle	Beer bottle
Knife	Butter	Knife tray
Toothbrush	Toothpaste	Toothbrush holder
Spatula	Pan	Cutlery stand
<i>Unfamiliar</i>		
Soup ladle	Pan	Suspension rail
Sports bottle	Cup	Bicycle holder
Vinegar bottle	Salad	Oil/vinegar set
Pliers	Open end plier holder	Wood plier block
Hammer	Nail	Tool utensil rack
Ancient key	Antique lock	Key holder
Charcoal	Blackboard	Box of charcoal

The upper panel represents familiar objects and the lower panel represents unfamiliar objects. The middle column and right column represent the associated target objects for each central object

The location of the target objects was counterbalanced, such that in half of all pictures, each grasp type was associated with a movement toward the left target object, and in the other half of all pictures, the grasp type was associated with a movement toward the right target object (see Fig. 1). Thus, for each object pair, 8 different pictures were created according to the following design: Action Cue (goal vs. grip), Implied Goal (left vs. right) and Implied Grip (up vs. down).

#### Experimental design and procedure

Each trial started with the presentation of a fixation cross after which a picture appeared on the screen (see Fig. 2). During *grip blocks*, subjects observed a ‘grip cue’ (i.e. arrow pointing to the upper or lower part of the central object) and made an inference about the goal of the action (i.e. deciding whether they would move the central object to the left or right target object). In contrast, during *goal blocks*, subjects observed a ‘goal cue’ (i.e. an arrow pointing to the left or the right target object) and made an inference about the grip of the action (i.e. deciding whether they would grasp the central object at the upper or lower side). Thus, during *grip blocks*, subjects responded by making a left or a right button press, and during *goal blocks*, the response box was rotated 90° to allow subjects to respond with an up or down button press (see Fig. 2). Subjects always responded with the index and middle finger of their right hand. If subjects did not respond within 3,000 ms after picture onset, the next trial was initiated.



**Fig. 2** Overview of the experimental setup and procedure. In goal blocks subjects were presented with a picture representing a goal cue (i.e. *arrow* pointing to the left or right target object). Based on the goal cue subjects were required to indicate at which part they would grasp the central object (i.e. at the upper or lower side), in case they should move it towards the specified target object. For instance, in case of the *arrow* pointing to the wine glass, the correct response would be to press the down button, as the wine bottle needs to be grasped at the lower side in order to pour wine in the glass. In grip blocks subjects were presented with a picture representing a grip cue (i.e. *arrow* pointing to the upper or lower part of the central object). Based on the grip cue subjects were required to indicate to which target object they would move the central object (i.e. left or right target object), in case they grasped it at the indicated side. For instance, in case of the *arrow* pointing towards the lower side of the wine bottle, the correct response would be to press the left button, as grasping the bottle at the lower side allows pouring wine in the glass

In total subjects performed one grip block and one goal block, each consisting of 200 trials. Block order was counterbalanced between participants. A pseudorandom trial ordering specified by an m-sequence (Buracas and Boynton 2002) ensured a counterbalanced stimulus presentation over the experiment. Trials were separated by a variable interval of 4 or 6 s (2–3 TRs), and the onset of the picture was pseudorandomly jittered in steps varying between 0 and 1,000 ms in 100 ms steps. Every 50 trials visual feedback was given about the subject’s performance for 10 s. At the beginning of the experiment outside the scanner, the task was carefully explained and the different object pairs were visually presented to ensure that the participant would recognize each of the objects used.

During the experiment, we recorded subjects’ EEG as well by means of an MRI compatible EEG system (Brain-Amp MR, Brain Products). Unfortunately, the EEG signal was too distorted by gradient, pulse, ECG and ocular artifacts to be used for subsequent analysis. Therefore, we only report the fMRI data here.

## Behavioral data and analysis

Behavioral analysis focused on reaction times and error rates. Trials in which the subject made an incorrect response or missed trials were discarded from reaction time analysis. Reaction times and error rates were averaged per condition and subject and were analyzed using a repeated measures ANOVA with the factors Action cue (Goal cue vs. Grip cue) and Familiarity (Familiar vs. Unfamiliar objects).

## MRI recording and analysis

Images were acquired on a Siemens 3T Magnetom Trio system with a 12-channel phased-array head coil. Functional images were acquired using a T2-weighted echo-planar gradient-echo imaging sequence (repetition time [TR] = 2,000 ms; echo time [TE] = 30 ms). Each volume consisted of 37 slices acquired parallel to the anterior-posterior commissure plane (interleaved acquisition; 3 mm with 0.5 mm gap;  $3 \times 3 \times 3$  mm in-plane resolution). After the functional runs, a high-resolution T1-weighted sagittal sequence image of the whole brain was acquired (TR = 15 ms; TE = 4.2 ms; FA = 9; FOV = 256 mm).

Statistical analyses were conducted using SPM8 software (Wellcome Department of Cognitive Neurology, London, UK). Preprocessing steps involved realignment, correction for motion and differences in slice acquisition time, spatial normalization and smoothing with an isotropic Gaussian kernel of 8 mm full-width at half-maximum. Anatomical normalization to MNI space was performed by coregistration of the functional images with the anatomical T1 scan. To minimize the effect of signal changes due to movements, we used the robust weighted least-squares algorithm (rWLS) that inversely weights each image by the inverse of its variance (Diedrichsen and Shadmehr 2005).

First-level fMRI analyses were performed for each individual subject according to the GLM. The fMRI time series for both blocks was fitted in one statistical model, with four regressors (and their temporal derivatives) according to the four possible combinations of action cues (goal cue vs grip cue) and object familiarity (familiar vs. unfamiliar). Regressors of no interest included: incorrect and missed responses, button press responses and performance feedback. After estimation, beta values were taken to the second level for random effects analysis to obtain a population estimate for the effects of action cues and object familiarity. Reported activations are at  $p < .05$  corrected at the cluster level for multiple comparisons using an auxiliary (uncorrected) voxel threshold of  $p < .001$ .

## Results

### Behavioral results

Behavioral data are represented in Fig. 3. Overall, subjects made errors in 9.3% of all trials and subjects missed responses in 1.4% of all trials. The analysis of error rates revealed a main effect of Object,  $F(1, 15) = 20.6$ ,  $p < .001$ ,  $\eta_p^2 = 0.58$ , reflecting more errors for unfamiliar (6.2%) compared to familiar objects (3.1%). In addition, a marginally significant interaction was observed between Action cue and Object,  $F(1, 15) = 4.4$ ,  $p = .055$ ,  $\eta_p^2 = 0.23$ , reflecting relatively more errors for unfamiliar objects in response to goal cues.

For the analysis of reaction times, a main effect of Familiarity,  $F(1, 15) = 26.7$ ,  $p < .001$ ,  $\eta_p^2 = 0.64$ , reflected faster responses to familiar (1,280 ms) compared to unfamiliar objects (1,352 ms). Although a tendency was observed for faster responses to goal cues (1,278 ms) compared to grip cues (1,353 ms), the effect of Action cue did not reach statistical significance,  $F(1, 15) = 3.4$ ,  $p = .09$ ,  $\eta_p^2 = 0.18$ .

### fMRI results

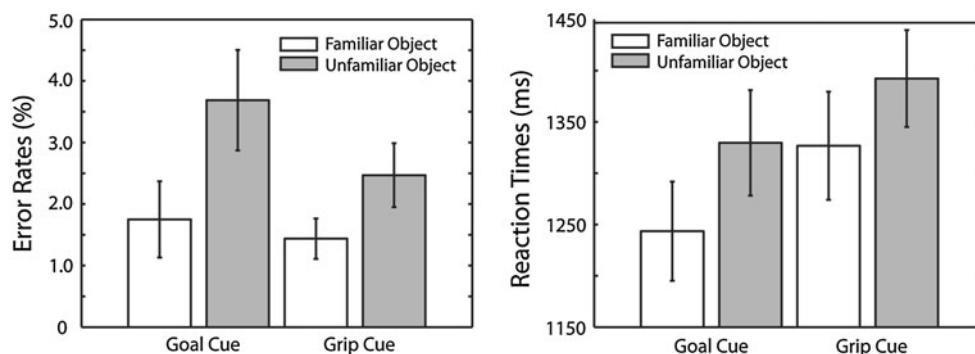
First to identify task-related brain activation, all conditions were compared relative to baseline. It was found that performing the experimental task resulted in increased activation in bilateral occipital, parietal, premotor areas, the insula and anterior prefrontal areas (see Fig. 4).

Comparing trials in which subjects made an inference about the goal compared to the grip of the action did not yield any significant difference, when corrected for multiple comparisons.

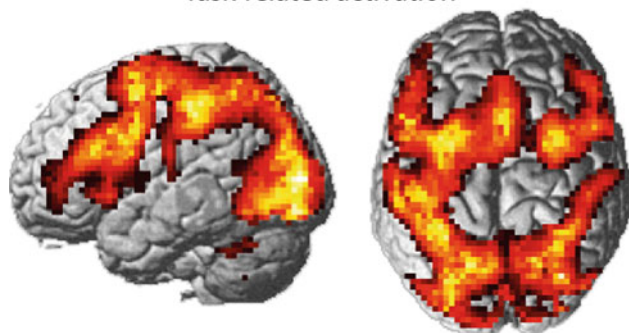
When comparing trials in which familiar objects compared to unfamiliar objects were presented, we observed increased activation in the anterior prefrontal cortex (MPF) extending to the anterior cingulate cortex, the right supplementary motor area (SMA) and the posterior cingulate (see Fig. 5a). Comparing trials in which unfamiliar objects were presented compared to familiar objects revealed increased activation in the bilateral superior parietal lobe (SPL), the right inferior parietal lobe (IPL) and the right insula (see Fig. 5b). The left and right SPL fall within the probability range (40–70%) of Brodmann Area (BA) 7a (Eickhoff et al. 2005). The right IPL falls within the probability range (30–60%) of human intraparietal area 3 (hIP3). A complete list of activated brain regions is represented in Table 2.

Finally, we were interested in the question whether the effects of Object familiarity were modulated by the type of action inference that was made (i.e. making an inference about the goal or the grip). When corrected for multiple

**Fig. 3** Behavioral results. The left graph represents error rates and the right graph represents reaction times for goal cues (left side of graph) and grip cues (right side of graph) in response to pictures representing familiar objects (white bars) or unfamiliar objects (gray bars). Error bars represent standard errors



Task-related activation



**Fig. 4** Task-related brain activation. Brain rendering showing areas commonly activated during the experimental task compared to baseline. All clusters are significant at  $p < .05$ , FWE-corrected for multiple comparisons

comparisons, the interaction between Action cue and Object did not reach statistical significance.

Using a region of interest (ROI) analysis based on the averaged activation estimates for each of the areas that were found significant for the main effect of Object familiarity, an interaction was observed between Object familiarity and Action Cue in the right IPL,  $F(1, 15) = 4.8$ ,  $p < .05$ . This interaction reflected that the effect of Object Familiarity in this area was stronger for goal cues compared to grip cues (see Fig. 5). No interaction effects were observed in the other ROIs. Please note that this ROI analysis was conducted for explorative purposes only and to determine whether the strength of activation in areas responsive to Object Familiarity, was modulated by the orthogonal factor of Action Cue.

## Discussion

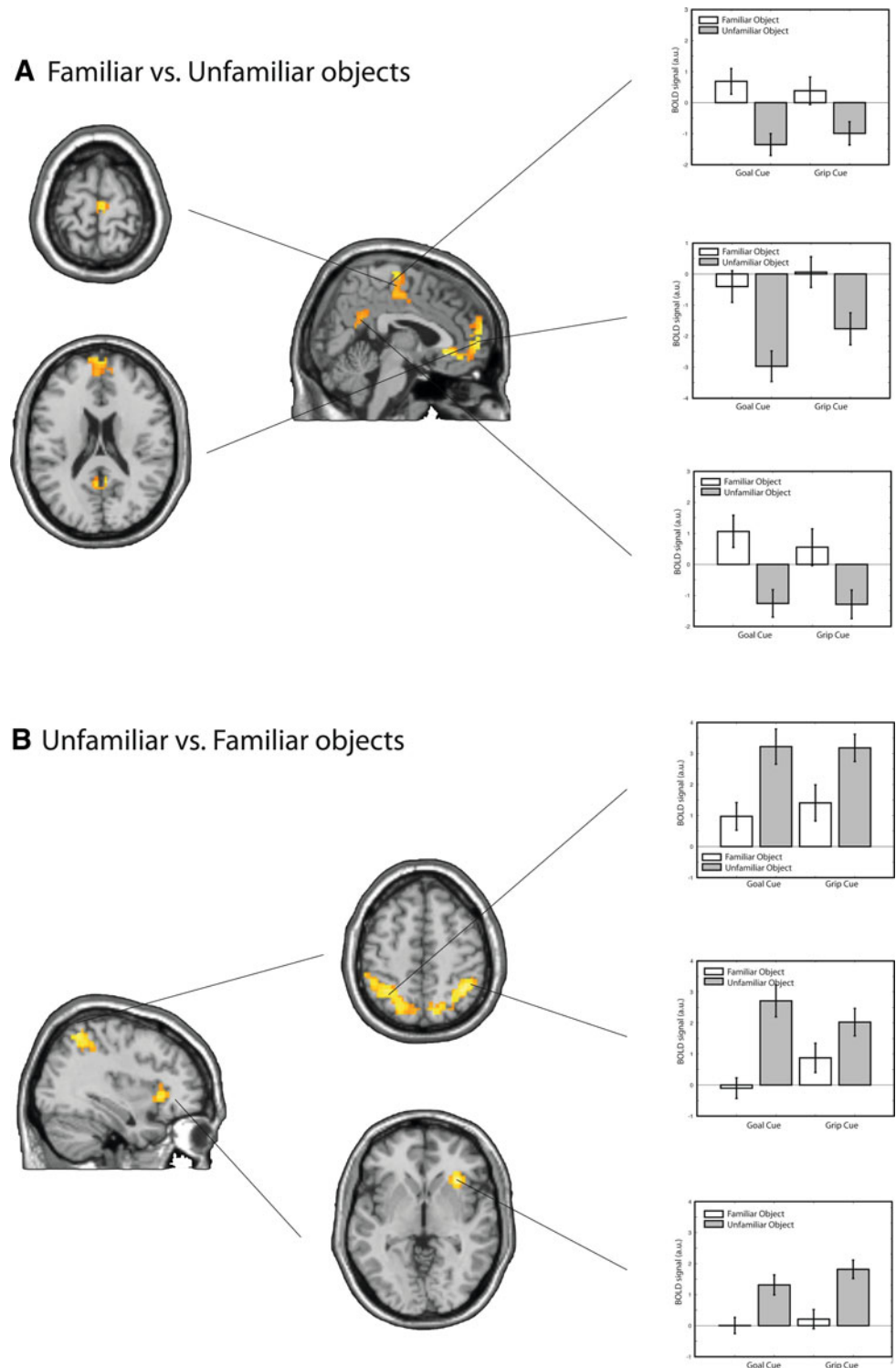
We used a motor imagery paradigm in which participants were required to imagine planning object-directed actions. We manipulated the familiarity of the objects involved by including both familiar (e.g. a toothbrush) and unfamiliar objects (e.g. a pair of pliers). In addition, we manipulated the type of action inference that was made: subjects were

required either to select the appropriate grip type given a pre-specified goal (Goal cue) or to select the goal of an action given a specific grip type (Grip cue).

We found that planning actions with unfamiliar compared to familiar objects was slower and was associated with increased activation in parietal brain areas. The faster responses to familiar compared to unfamiliar objects are in line with studies on action planning, showing a comparable advantage for planning familiar compared to unfamiliar actions (Tessari and Rumiati 2004; van Elk et al. 2009; van Elk et al. 2010b), and with studies on semantic dementia, showing an advantage for familiar objects in the retrieval of action semantics (Lambon Ralph et al. 1998). The reaction time advantage reflects that action planning was easier in the case of familiar objects, likely because action semantics could be more easily activated. In contrast, for unfamiliar objects, the activation of action semantics took more effort, as reflected in slower reaction times.

The planning of actions with unfamiliar objects was associated with increased activation in the bilateral superior parietal lobes (SPL) and the right inferior parietal lobe (IPL). Several studies have shown that the parietal lobe plays an important role in instantiating a predictive model of an upcoming action and in representing the grip of an action in relation to its end location (Wolpert et al. 1998; Wolpert and Ghahramani 2000). For instance, whereas healthy participants typically adjust their handgrip according to the consecutive use of an object (Cohen and Rosenbaum 2004; Weiss et al. 2007; Chapman et al. 2010; Cohen and Rosenbaum 2011), apraxic patients with parietal lesions showed an impairment in selecting the appropriate handgrip for grasping inverted tools (Sunderland et al. 2011). In line with these findings, in a recent study, it was found that activation in the right IPL and superior parietal cortex selectively increased with greater demands on prospective grasp planning (e.g. simple grasping vs. grasping to rotate; Marangon et al. 2011). Finally, studies in monkeys have shown that grasping neurons in the IPL fire selectively depending on the final goal of the action (e.g. grasping to eat or place; Fogassi et al. 2005; Bonini et al. 2010). Thus, the stronger activation in IPL and SPL

**Fig. 5** Brain activation modulated by Object Familiarity. **a** Brain areas that were significantly more activated for familiar compared to unfamiliar objects overlaid on the standard MNI brain. The left picture represents a sagittal view of activation in medial brain areas, encompassing the medial prefrontal cortex (MPF) extending to the anterior cingulate cortex (ACC), the right supplementary motor area (SMA) and the posterior cingulate cortex (PCC). The right pictures represent an axial view of SMA (*upper picture*) and MPF and PCC activation (*lower picture*). **b** Brain areas that were more strongly activated for unfamiliar compared to familiar objects overlaid on the standard MNI brain. The left picture represents a sagittal view of the right hemisphere representing activation in the right insula (rIns) and the right superior parietal lobe (SPL). The right pictures represent an axial view of bilateral IPL/SPL activation (*upper picture*) and rIns activation. All clusters are significant at  $p < .05$ , FWE-corrected for multiple comparisons. *Bar graphs* on the right represent the BOLD response averaged for each activated region for the different experimental conditions



found in the present study suggests that determining the grip in relation to its end location took more effort when planning actions with unfamiliar compared to familiar objects.

The finding that motor-related brain areas are differentially involved in imagining familiar compared to unfamiliar actions is in line with previous studies. For instance,

two recent EEG studies showed that the planning and execution of unfamiliar compared to familiar actions was associated with a stronger desynchronization and a subsequent rebound in the beta-frequency band that was localized to parietal areas (van Elk et al. 2010b; Mizelle et al. 2011). In addition, other studies have shown that the observation of unfamiliar tools or the processing of

**Table 2** Overview of regions more strongly activated for familiar compared to unfamiliar objects (upper panel) and for unfamiliar compared to familiar objects (lower panel)

Anatomical region cluster	Local maxima			<i>t</i> -value	cluster size	<i>P</i>
<i>Familiar &gt; Unfamiliar</i>						
Anterior prefrontal cortex	−4	50	13	5.8	418	<.001
Anterior cingulate	2	26	0			
R supplementary motor area	4	−28	65	4.9	94	<.01
Posterior cingulate	−7	−52	22	4.5	92	<.01
<i>Unfamiliar &gt; familiar</i>						
R insula	27	22	8	5.4	84	<.01
L precuneus/superior parietal lobe	−13	−73	36	5.0	394	<.001
R inferior parietal lobe	34	−55	47	4.9	207	<.001
R precuneus/superior parietal lobe	9	−75	47	4.6	124	<.001

For clusters that span several anatomical regions, more than one local maximum is given. All clusters are significant when correcting for multiple comparisons across the whole brain (FWE-corrected)

unfamiliar actions resulted in increased activation in motor-related areas as well (Handy et al. 2006; Beilock et al. 2008; Stapel et al. 2010). Together these studies fit well with the notion that parietal areas are involved in mental imagery of actions and that this process takes more effort in case of difficult actions (for similar findings with the classical hand rotation paradigm, see: de Lange et al. 2005, 2006). Importantly, the effects in parietal areas cannot be attributed to the affordances triggered by simply viewing the objects. Based on the object's affordances, we should expect a stronger activation for familiar compared to unfamiliar objects in parietal areas instead, because the affordances of familiar objects can be more easily perceived than of unfamiliar objects.

In addition to the activation in parietal areas, a stronger activation for unfamiliar compared to familiar objects was observed in the right insular cortex. More specifically, the activation was centered in the anterior part of the insula, a brain region that has strong connections with motor-related areas (Mufson and Mesulam 1982), that is consistently found activated in motor tasks involving the upper and lower limbs (Fink et al. 1997) and that has been associated with a feeling of agency as well (Farrer and Frith 2002; Karnath and Baier 2010). Accordingly, it has been suggested that the insula is involved in generating intentions, based on interoceptive signals regarding the subject's body (Brass and Haggard 2010) and with the subjective feeling of moving (Mutschler et al. 2009). The stronger insular activation for unfamiliar objects could reflect that imagining actions with unfamiliar objects results in a stronger motor imagery process—as reflected in increased parietal activation—accompanied by a stronger feeling of moving.

The planning of actions with familiar objects was associated with increased activation in medial frontal brain areas, such as the superior medial frontal gyrus (sMFG) extending to the anterior prefrontal cortex and the anterior

cingulate. These frontal regions have been associated with the planning of movement sequences (Rowe et al. 2000; Shima and Tanji 2000; Rushworth et al. 2004) and the planning of actions with respect to the intended end location (Majdandzic et al. 2007). In addition, this area supports maintaining a final task goal while processing several subgoals, as for instance in the Tower of London task (Koechlin et al. 1999; Burgess et al. 2000; Sakai et al. 2002). The stronger activation in these regions could reflect that subjects maintained a stronger goal-representation when planning actions with familiar compared to unfamiliar objects.

In the present study, subjects tended to respond faster when imagining an action based on goal-related information compared to grip-related information. This finding reflects that the natural and most efficient way of planning our actions is the case in which we select a grip based on goal-related information (Cohen and Rosenbaum 2004; Rosenbaum et al. 2007). The advantage for goal compared to grip cues is in line with previous studies that have reported a similar advantage for planning actions in terms of the intended end location compared to the grip required for object grasping (Majdandzic et al. 2007; van Schie and Bekkering 2007). However, in contrast to these previous studies in the present study, no general difference in brain activation was found between imaginary actions that were planned based on goal-related information compared to grip-related information. This apparent discrepancy may be related to the specific experimental paradigm and design. In previous studies, participants were required to actually plan and execute real-world actions (Majdandzic et al. 2007; van Schie and Bekkering 2007). In contrast, the present study used a motor imagery paradigm, thereby making it more difficult to control for individual differences in timing and the strategy used for solving the task. In addition, previous studies used novel objects and goal-



and grip-inferences could be based on the objects' affordances. In the present study, goal- and grip-inferences were made about everyday objects and as a consequence required the activation of semantic knowledge, representing the learned association between an object's goal and its associated manner of usage.

Interestingly though, the strongest effects of object familiarity in the right IPL were observed when subjects were required to select the appropriate grip based on a goal cue. This finding suggests that action semantics were activated most strongly when planning actions based on goal-related information, which is the default mode of action planning. In contrast, the inverse mode of action planning in which a goal is selected based on grip-related information is less common and accordingly, in this case action semantic information is less strongly activated. Thereby this study provides support for the notion that action semantics are selectively activated, depending on the type of action inference that is made (see also: van Elk et al. 2010a). In addition, the finding that the right IPL was more strongly involved in activating semantic knowledge when planning actions based on goals is in line with the idea that this area represents object-directed actions in terms of their goals. Studies in monkeys have shown for instance that neurons in the inferior parietal lobe (IPL) fire selectively depending on the final goal of the action (e.g. to eat or place; Fogassi et al. 2005; Bonini et al. 2010). In line with these findings, neuroimaging studies in humans have shown that the intraparietal sulcus represents the goal or the outcome of an observed action (Hamilton and Grafton 2006, 2008).

An important question is whether the effects observed for action familiarity could be partly attributed to the ease of responding (i.e. subjects responded faster to familiar compared to unfamiliar objects). Previous studies have localized effects of speed of responding primarily to occipital, supplementary motor and contralateral motor areas to the response hand (Oguz et al. 2003; Mohamed et al. 2004). In contrast, in the present study, the effects of object familiarity were most pronounced in parietal areas and did not appear lateralized with respect to the responding hand. Furthermore, reaction times were modeled as a separate regressor, thereby minimizing the likelihood that the effects in the other conditions can be attributed to differences in button press responses. Finally, although a reaction time difference was observed between goal and grip cues, this difference did not become apparent at a neural level, thereby further supporting that the effects of object familiarity cannot be attributed to differences in responding or response times.

A possible functional mechanism underlying the effects of object familiarity observed in the present study is the ideomotor principle, according to which every action is

represented in terms of the effects it produces (Prinz 1997; Hommel et al. 2001). That is, based on our previous experiences, we have acquired associations between a specific way of grasping an object (e.g. grasping a wine bottle at the lower side) and the associated action effect (i.e. pouring). On this account, action planning involves selecting the required action effect, which in turn activates the associated motor program required for accomplishing the effect (Kunde et al. 2002). The ideomotor principle is closely related to the hierarchical view of the motor system, according to which higher-level action goals determine the selection of lower-level action features (Cooper 2002; Grafton and Hamilton 2007; Rosenbaum et al. 2007). The present study suggests that the ease whereby action goals and grips are selected is strongly determined by the object's familiarity. For familiar objects, the action–effect associations are probably stronger than for unfamiliar objects, simply because we have more experience with using these objects. As a consequence activating these associations during action planning is easier for familiar compared to unfamiliar object pairs.

In our experimental paradigm, we exploited the fact that many objects are associated with multiple target objects and action effects. Based on the frequency of usage, some target objects are probably more strongly associated with a specific object than others. For instance, most people would consider moving a wine bottle to a glass more prototypical than moving a wine bottle to an ice bucket. The present study specifically assessed effects of familiarity by comparing different objects (e.g. a wine bottle vs. a hammer). It remains unknown whether a similar effect of familiarity can be observed when one and the same object is used with a target that is more strongly or less strongly associated with the object (e.g. a wine bottle and a wine glass vs. a wine bottle and an ice bucket). Previous studies have found a differential activation of motor-related brain areas for the observation of incorrect object use (e.g. adding salt instead of sugar to coffee; see: Manthey et al. 2003; Newman-Norlund et al. 2010), suggesting that familiarity between objects may indeed modulate activation in these regions. However, in these cases, the objects used were either completely correct or incorrect. An interesting possibility for future research would be to investigate whether the strength of the association between different objects parametrically modulates the strength of activation in motor-related brain areas.

The present study has implications for the representation of semantic knowledge about objects. On the one hand, it has been argued that semantic knowledge is represented in an 'amodal semantic hub' that is localized to the anterior temporal lobes and that supports the activation of semantic representations in different modalities and for different categories (Patterson et al. 2007; Gainotti 2011). On the

other hand, according to an embodied view of cognition, semantic knowledge is represented in modality-specific brain areas (Beauchamp and Martin 2007; Grafton 2009) and in line with this view, several studies have shown that the processing of manipulable objects is accompanied by the activation in premotor and parietal brain areas (Grafton et al. 1997; Chao and Martin 2000; Grezes et al. 2003; Kellenbach et al. 2003; Vingerhoets et al. 2009). In the present study, we found that the retrieval of action semantics was associated with a stronger parietal activation for unfamiliar compared to familiar objects. The finding that parietal areas, typically associated with high-level action planning, are involved in the retrieval of action semantics is in line with the multimodal account of object knowledge and moreover suggests that the familiarity of the concept determines the strength of activation in these areas as well.

## Conclusions

The present study showed that motor imagery is modulated by the familiarity of the objects involved. Determining the grip in relation to the end location of an action took more effort for unfamiliar objects, as reflected in a stronger activation in parietal brain areas, whereas mental imagery of an action with familiar objects was associated with increased activation in anterior prefrontal brain areas. These findings provide further insight into the neural structures that support action semantic knowledge for the functional use of real-world objects, and suggest that action semantic knowledge is activated most readily when actions are planned in a goal-directed manner.

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