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Grasp Representations Depend on Knowledge and Attention

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Seeing pictures of objects activates the motor cortex and can have an influence on subsequent grasping actions. However, the exact nature of the motor representations evoked by these pictures is unclear. For example, action plans engaged by pictures could be most affected by direct visual input and computed online based on object shape. Alternatively, action plans could be influenced by experience seeing and grasping these objects. We provide evidence for a dual-route theory of action representations evoked by pictures of objects, suggesting that these representations are influenced by both direct visual input and stored knowledge. We find that that familiarity with objects has a facilitative effect on grasping actions, with knowledge about the object's canonical orientation or its name speeding grasping actions for familiar objects compared to novel objects. Furthermore, the strength of contributions from each route to action can be modulated by the manner in which the objects are attended. Thus, evocation of grasping representations depends on an interaction between one's familiarity with perceived objects and how those objects are attended while making grasp actions.

Keywords: grasping, attention, working memory, object recognition, experience

Visual objects that we merely view and attend to can trigger motor processing. Even pictures of manipulable objects, which by their nature cannot be grasped, engage a variety of motor cortical regions, including areas of the parietal and prefrontal cortex (Chao & Martin, 2000; Grèzes & Decety, 2002; Handy et al., 2005; Handy, Tipper, Schaich Borg, Grafton, & Gazzaniga, 2006). Such activation occurs even when the task does not require thinking of how an object might be handled. This evidence has led to the claim that objects automatically evoke *motor affordances* (e.g., Caligiore, Borghi, Parisi, & Baldassarre, 2010), a term originally coined by Gibson (1979) to denote possible actions invited by physical objects in relation to an observer's physical capabilities. The extension of the term *affordance* to incorporate motor activation induced by depicted objects raises a number of interesting questions. What kind of motor representations are evoked by pictured objects? More specifically, do pictures trigger motor representations associated with an object's identity? Alternatively, might the shape of an object rather than its identity give rise to the online analysis of possible actions? Some evidence based on functional imaging research favors the latter possibility. Handy et al. (2006) found greater activation of the motor cortex when observers lacked any direct experience with the pictured objects. Using functional MRI, these authors compared the impact of two different kinds of objects on motor regions: objects that were frequently grasped (door knobs) versus objects for which observers reported no motor experience (artificial rock climbing holds). Cortical activity associated with these two types of object was assessed relative to a baseline condition involving pictured objects—car tires—that presumably do not elicit any unimanual grasp response. The novel objects elicited more activity in the left motor, premotor, and parietal cortex. By contrast, pictures of door knobs triggered no such response in visuomotor regions. Interestingly, for experienced climbers who were familiar with rock climbing paraphernalia, no increased activity in visuomotor areas was found for any of the object types. Handy et al. inferred that motor activity reflected analytic processes for how to interact with an object, processes that are no longer necessary once visuomotor associations are learned. Van Elk, Viswanathan, van Schie, Bekkering, and Grafton (2012) likewise reported that in a motor-imagery task, unfamiliar objects yielded greater activation in motor regions than did familiar objects.

This evidence notwithstanding, we assume that under suitable task conditions stored knowledge must also play a role in the evocation of motor presentations induced by pictured objects. Consistent with this assumption, Gentilucci (2002) has shown that familiar objects evoke experiences of habitual interactions with the

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objects, which can influence the reach kinematics of a grasp action. Herbort and Butz (2011) reported that habitual actions contribute to the choice of a grasp used to rotate an object, overriding the posture more commensurate with the intended goal of the movement. Actions made to familiar objects are also influenced by competition between conceptual knowledge of an object's function as well as encoding of its structural properties (Jax & Buxbaum, 2010). There are also neural differences when viewing novel objects for which subjects have learned a functional use, as opposed to objects they have merely grasped and manipulated (Creem-Regehr, Dilda, Vicchrilli, Federer, & Lee 2007). These studies suggest that stored knowledge about an object can impact actions made upon those objects.

Neuropsychological evidence lends further support to the claim that both conceptual knowledge and directly perceived structural properties of an object contribute to the programming of reach-and-grasp actions. Apraxic patients are specifically impaired in accessing stored knowledge of grasp postures (Buxbaum, Sirigu, Schwartz, & Klatzky, 2003; Randerath, Li, Goldenberg, & Hermsdörfer, 2009) but can readily demonstrate the hand shape needed to lift (though not use) an object. Conversely, in optic ataxia, unfamiliar objects are less accurately grasped than familiar objects (Pisella et al., 2000).

The notion that more than one source of information may contribute to motor priming effects is fully compatible with a dual-route model of action described by Yoon, Heinke, and Humphreys (2002; also see Riddoch, Humphreys, & Price, 1989). According to this account, two separate mechanisms determine action selection. The direct visual route depends on an object's shape and an analysis of its structural parts (such as graspable handles). The semantic route involves knowledge that is more abstract and can be activated by information such as an object's name. Importantly, the vision-to-action route is dependent on direct visual input, whereas both pictures and names of objects can activate the semantic route.

A key assumption behind the dual-route model is that task demands can alter the contribution of a particular route to action selection. In particular, semantically driven selection of action can override or preempt the contribution of the direct route (and vice versa). For example, when subjects are required to produce actions to words under response deadline conditions, errors indicate a reliance on conceptual rather than visual properties of the referenced object (Rumiati & Humphreys, 1998). Neuropsychological evidence offers additional support for the notion that task set can preempt or minimize the contribution of the direct route in favor of the semantic route. A striking example is provided by Randerath et al. (2009). They required neurological cases with apraxia to grasp handled objects (e.g., a hammer) under two task conditions: (a) manually transport the object into a container or (b) demonstrate how the object is normally used. When the object was presented so that the handle pointed away from the subject, it was possible to observe the following remarkable dissociation. For the transport task, the hand was correctly rotated to produce a normal functional grasp (e.g., the hand would be rotated to grasp a hammer by the handle). By contrast, the use task elicited nonfunctional grasps for the same objects. A rotated hammer might trigger an attempt to stir with the object, and the hand was not correctly oriented to grasp the handle. We infer that the task of merely transporting the object emphasized the direct route which, given the object's structural properties, yielded a grasp action directed toward the handle. The instruction to use the object, however, demanded retrieval of actions driven by the semantic route, which can be selectively impaired in cases of apraxia (e.g., Sirigu et al., 1995). An attempt to use the object invoked the damaged semantic route, preempting the contribution of the intact direct route.

In what follows, we describe and implement a methodology to distinguish between different kinds of motor influence on speeded reach-and-grasp actions. We examine the influence of stored knowledge by introducing pictures of novel objects that subjects have had no previous experience seeing or grasping. As noted previously, structural and conceptual knowledge can impact the programming of grasp actions. For novel objects, there are structural properties that can be used to shape grasping actions, but there is no conceptual knowledge. In contrast, motor representations generated by familiar objects can be influenced by their structural properties as well as conceptual knowledge, such as semantic or functional knowledge. We compare the effect of familiarity on grasp actions in Experiments 1 and 2.

In Experiments 3 and 4, we examine a second influence that depends on the depicted form of an object, which varies according to the object's orientation. To lift a typically oriented spray can, for example, requires a closed grasp with the palm held vertically. The same object rotated 90° from upright is grasped with the palm maintained in a horizontal rather than a vertical position. The difference between action representations triggered by upright versus rotated objects is of special interest. An implemented version of the dual-route model (Yoon et al., 2002) has no mechanism for dealing with motor representations induced by rotated objects, a theoretical gap explicitly acknowledged by the authors. Nevertheless, we can safely assume that the conceptual route generates action representations determined by a rotated object's typical (i.e., canonical) orientation. The image of a spray can, for example, rotated 90° from upright will trigger a closed grasp with the palm held vertically, the lift action typically associated with the object.

The nature of the action representation generated by the direct route in response to a rotated object is less straightforward. The model includes stored perceptual representations that are activated by the parts of an object in their corresponding spatial locations (Yoon et al., 2002). This representation is centered on the main component of the object. Presumably under suitable task demands, a rotated object—even a novel one with little or no conceptual properties—will trigger motor representations based on a previously experienced canonical rather than depicted form. Additional processes would be invoked to generate actions determined by the object's perceived orientation. We establish that this is indeed the case.

Our methodological approach elucidates how motor representations triggered by a pictured object can influence speeded reach-and-grasp actions. Subjects attend to the object while carrying out a cued power or precision grasp varying in wrist orientation (vertical/horizontal), applied to one of four response elements (see Figure 1). The object itself is not predictive of the cued action. Motor representations evoked by the object can be congruent or incongruent with the cued grasp, inducing priming effects on speeded responses. Elsewhere, we have argued that such priming effects, occurring when the subject carries out cued reach-and-grasp actions, reflect constituents of real-world actions rather than abstract supramodal codes (Bub, Masson, & Kumar, 2017). The

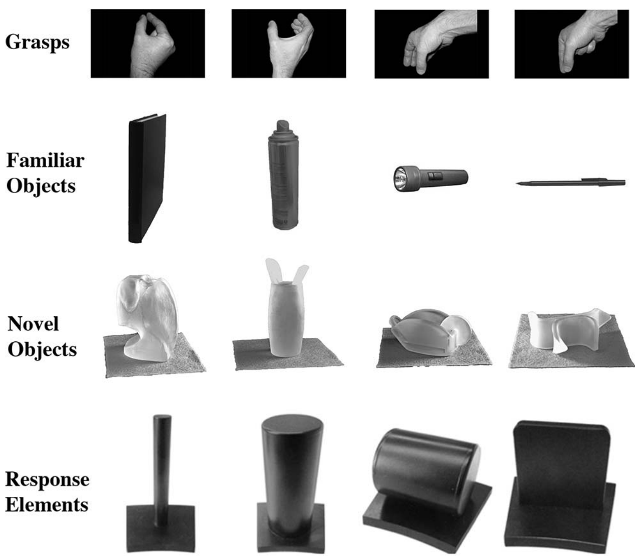

Figure 1. Grasps and the familiar and novel objects that correspond to them. Grasp types are horizontal pinch, horizontal grasp, vertical grasp, and vertical pinch; familiar items are a book, a spraycan, a flashlight, and a pen. Four novel objects were chosen based on the intersubject agreement for their associated volumetric grasp. The response elements are fitted onto the graspasaurus apparatus.

evidence described in the present article will be found consistent with this claim.

As we have already suggested, a familiar object can trigger stored motor representations based on previous experience and in addition, the object's perceived form can also generate priming effects. By performing a reach-and-grasp action while identifying a pictured object, the executed action may be jointly controlled by the dorsal stream, which ensures an accurate grasp of the physically present response element, and the ventral stream which represents information about actions that are automatically triggered by the pictured object. Prior work has shown that the kinematics of grasp actions can be affected in just this way (Till, Masson, Bub, & Driessen, 2014). Under the right task conditions, we assume that both these influences will contribute separately to priming effects.

Experiment 1

Here, we directly compare motor priming effects for pictures of familiar and novel objects. Subjects were briefly shown an object prime followed by the picture of a hand representing a power or precision grasp with the wrist oriented vertically or horizontally. The hand posture served as the cue to produce a specific grasp applied to one of four response elements. On 25% of the trials, after the reach-and-grasp action was made, subjects were asked to identify the object prime, so they had to attend to the item's identity and hold it in working memory. An equal congruency effect for familiar and novel objects would provide evidence that grasping representations are driven mainly by the online analysis of a visual form. If stored knowledge and experience also contribute to motor priming effects, we should observe a familiarity advantage; a larger congruency effect should be obtained for familiar than novel objects. If that result occurs, it is also of interest whether novel objects show any congruency effect at all.

Method

Subjects. Forty undergraduate students at Vanderbilt University (M_{age} = 21.1; 24 female, 16 male) participated in Experiment 1 for course credit. Sample size was determined by a power analysis based on an effect size from a similar experiment reported by Bub, Masson, and Cree (2008, Cohen's dz = 0.995). Assuming the effect size for novel objects is roughly half that of familiar objects, the sample size necessary to detect such an effect with a power of 0.9 at an alpha of 0.05 is roughly 36. Another 30 subjects performed a norming study to select the novel objects. All subjects were right-handed and had normal or corrected to normal visual acuity. This study was approved by the Vanderbilt Institutional Review Board (Protocol 120041).

Stimuli. Four familiar objects used by Bub et al. (2008) were chosen that correspond to four grasps: horizontal grasp, horizontal pinch, vertical grasp, and vertical pinch (see Figure 1). To select unfamiliar objects that would not remind subjects of familiar objects and whose volumetric grasps clearly corresponded to each of the four target grasps, a set of 12 objects was created out of clay. A norming study was conducted in which subjects memorized arrays of four objects on a table with a 3 × 3 grid. Memory for the positions was tested by clearing the table and having the experimenter place each object in front of the subject, who was then asked to position object in its original location. On each trial, the experimenter noted which, if any, of the four target grasps was used to pick up each object (whether they remembered the location was not of interest). The procedure was repeated three times for each object and subjects were then asked whether each object resembled a real life item and what could be its possible function. Four objects were chosen that had complete agreement across subjects with respect to chosen grasp and that were reported not to resemble any real object. These objects were then rendered in Plexiglas and photographed (see Figure 1).

Procedure. Subjects were seated in a chair in front of the grasping apparatus. Touching any part of response elements on the apparatus would record a reaction time (RT) for the completion of the grasp. The response elements are fitted in a frame and are placed along an arc such that each one was equidistant from the spacebar. The order of the four response elements along the apparatus was held constant for each subject but was randomized between subjects. Figure 2 shows a subject in front of the experimental setup.

Subjects were trained to make reach-and-grasp responses to pictured hand cues corresponding to the elements on the response apparatus (shown in Figure 1). They then received a sequence of 32 practice trials and 240 critical trials in which a picture of one of the eight objects was shown for 300 ms, followed by a hand cue. Subjects made the cued response onto the appropriate response element as quickly as possible. To ensure that subjects attended to the displayed objects, for 25% of the trials, there was a visual matching probe that appeared after the grasp action was completed. Subjects were told to indicate which object had been presented on that trial. To do this, they selected the relevant object from a display of the eight critical objects (labeled A–H) shown on the computer monitor. Each object was shown 30 times over the

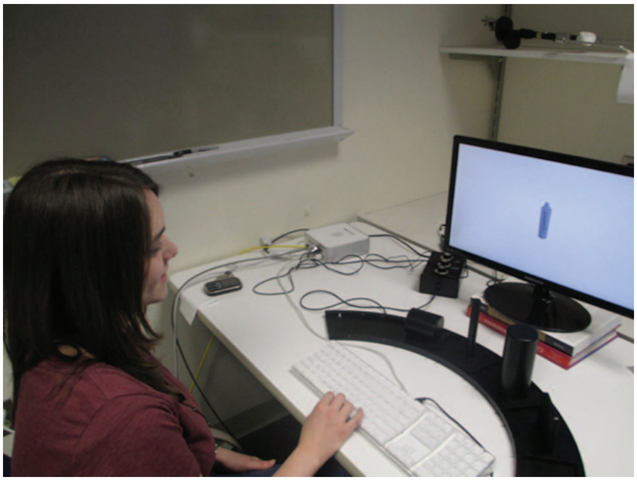

Figure 2. Picture of the experimental setup. See the online article for the color version of this figure.

critical trials, with congruent object-action pairs occurring on 50% of the trials. We analyzed response time to grasp the response element.

Results

Total grasping times less than 250 ms and greater than 2,400 ms were eliminated (0.5% of responses, as recommended by Ulrich & Miller, 1994). Incorrect responses were also removed (1.8% of responses).

As can be seen in Figure 3, congruency effects were obtained for both familiar and novel objects but the congruency effect was larger for familiar objects. This pattern is reflected in a 2 × 2 analysis of variance (ANOVA) performed on mean grasping times, with Congruency (congruency, incongruent) and Object Type (familiar, novel) as within-subjects factors. There was a main effect of Congruency, $F(1, 39) = 66.5$, $p < .0001$, $\eta_p^2 = 0.63$, with faster RTs for congruent than incongruent trials (1,093.3 ms vs. 1,130.6 ms). The congruency advantage was present for both familiar, $F(1, 39) = 58.3$, $p < .0001$, $\eta_p^2 = 0.58$, and novel objects, $F(1, 39) = 19.5$, $p < .0001$, $\eta_p^2 = 0.33$. There was also an interaction between Congruency and Object Type, $F(1, 39) = 12.18$, $p = .0012$, $\eta_p^2 = 0.24$, with a larger congruency effect for familiar compared to novel objects. Of particular note is that the mean for incongruent trials was similar for both novel and familiar objects. Thus, RTs for incompatible object-grasp combinations were the same regardless of novelty. Therefore, the factor driving congruency differences is found in the RTs for congruent trials, with shorter RTs for familiar congruent trials compared to novel congruent trials.

Discussion

Here, we replicated the congruency advantage for volumetric grasps for familiar items (Bub et al., 2008) and extended it to a set of novel objects that were never experienced outside of the screen presentations during the experiment itself. These results suggest that volumetric grasps can be primed and that shape information computed online is used for both familiar and novel objects to drive this priming. In addition, there is evidence that familiar objects provide access to stored knowledge about volumetric grasps, as evidenced by greater priming familiar than for novel objects.

Experiment 2

Consistent with prior work (Bub et al., 2008), we found congruency effects for volumetric grasps with familiar objects and we extended these results by finding congruency effects for volumetric grasps of novel objects. When the object's identity was held in working memory during the grasp, we found congruency effects for novel objects, suggesting that action representations evoked by shape perception were engaged even for objects that had never been encountered before. This result supports the idea that online volumetric grasps can be evoked by the perception of object shape alone (Bub & Masson, 2010; Bub et al., 2008; Buxbaum & Kalenine, 2010). In addition, familiar objects elicited larger congruency effects than novel objects, revealing that stored motor representations for these objects had a further influence on volumetric grasps.

Based on the dual-route model of action (Yoon et al., 2002), the visual match-to-sample probe in Experiment 1 directs attention to the object's structure and visual form, so action plans are impacted by current and direct visual input. However, the congruency effect for familiar objects was greater than that for novel objects, which we attribute to the additional contribution of the semantic route accessible only for familiar objects. We assume that the nature of attention to a depicted object will likewise modulate the relative influence of the direct and semantic routes on cued reach-and-grasp actions. We explore this possibility in Experiment 2.

In Experiment 1, the object was viewed in the context of a match-to-sample task, and priming was significantly greater for familiar than novel objects. This is consistent with the assumption that priming effects that occur when attention is directed to the shape of familiar objects were based on the combined activation of both the semantic and direct routes. How might we elicit a greater reliance on semantically driven motor priming and reduce attention to an object's structural properties? According to a connectionist implementation of the dual-route model, task-induced reliance on local semantic units filters out competing activation of

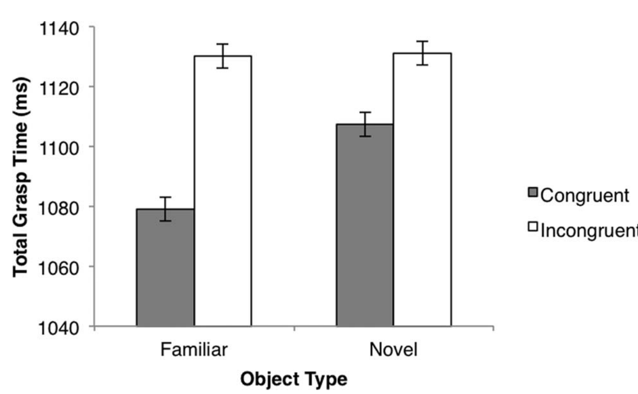

Figure 3. Mean total grasp time for familiar and novel objects based on congruency. Error bars represent 95% confidence intervals for the congruency effect, for familiar and unfamiliar objects separately.

structural units corresponding to an object's shape (Yoon et al., 2002). We have already argued that actions generated to the name of an object are based on semantic rather than visual attributes. Therefore, attending to the name of a depicted object should presumably enhance the impact of the semantic route on the cued action and weaken the effect of the direct route.

If this line of reasoning is correct, then the priming effect triggered by familiar objects should be reduced when attention to the object is encouraged by a naming rather than a match-to-sample task. But how should the change in probe task affect the priming effect induced by novel objects? Naming of newly learned objects recruits a large network of brain areas including the left frontotemporal and cerebellar cortex (Grönholm, Rinne, Vorobyev, & Laine, 2005). Nonetheless, because of the minimal amount of conceptual knowledge available for novel objects, grasping representations may continue to depend on their visual form. Accordingly, we predicted that the magnitude of the priming effect induced by novel objects should be unaffected by the change in task set.

Method

Subjects. Forty-five undergraduate students at Vanderbilt University (M_{age} = 21.9; 28 female, 17 male) participated in this experiment for course credit. We aimed to recruit 40 subjects as in the previous study but more subjects signed up than anticipated. All subjects were right-handed and had normal or corrected to normal visual acuity.

Procedure. Subjects underwent a short training regimen where they learned the names of the four novel objects they would see during the grasping phase of the experiment. Each of the four objects was assigned a random nonsense label out of a pool of eight names (awg, cax, div, goz, keb, mog, pif, ror). The training consisted of three phases. Throughout the training, the task was to press the first letter of the object's name. In the initial training phase, the object would appear with a name label (32 trials, each object appears eight times). In the second stage, object appeared without a label but corrective feedback was given if an incorrect letter was pressed (120 trials). In the third stage, objects appeared without labels and without corrective feedback (80 trials). Subjects needed to pass a 90% accuracy threshold to complete training or else they would redo the second stage.

The grasping phase was similar to Experiment 1 with a few exceptions. For each trial, subjects saw an object for 300 ms followed by a hand cue. As before, subjects were to make the hand gesture onto the appropriate response element. After 25% of trials, subjects were prompted to type the first letter of the object's name.

Results

We used the same exclusionary criterion as in Experiment 1, removing trials faster than 250 ms and slower than 3,000 ms (0.5% of responses removed). Incorrect responses were also removed (1.6% of responses removed).

In this experiment, both familiar and novel objects showed congruency effects of similar magnitude, and grasp times were overall longer for novel than familiar objects (see Figure 4). This pattern is supported by the results of a 2 × 2 ANOVA performed on mean grasping times, with Congruency (congruency, incongruent) and Object Type (familiar, novel) as within-subjects factors. There was an overall congruency advantage, $F(1, 44) = 53.5$, $p < .0001$, $\eta_p^2 = 0.55$, as well as a main effect of Object Type, $F(1, 44) = 32.5$, $p < .0001$, $\eta_p^2 = 0.45$, with overall faster RTs for familiar objects. However, there was no Congruency × Object Type interaction, $F(1, 44) = 0.006$, $p = .94$, $\eta_p^2 = 0.00$, suggesting that the amount of priming for familiar and novel objects was the same.

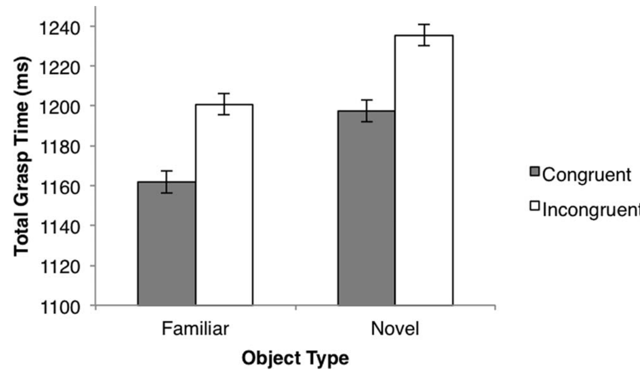

Figure 4. Experiment 2 mean reaction time data. Error bars represent 95% confidence intervals for the congruency effect, for familiar and unfamiliar objects separately.

To examine whether the congruency effects in Experiments 1 and 2 were comparable, we ran a cross-experiment comparison using a 2 × 2 × 2 ANOVA with Experiment (1, 2) as a between-subjects factor, and Congruency (congruent, and incongruent), and Object Type (familiar and novel) as within-subject factors. There was a significant interaction between Experiment, Congruency, and Object Type, $F(1, 83) = 6.25$, $p = .01$, $\eta_p^2 = 0.07$, with a greater congruency effect in Experiment 1 for familiar objects than novel objects (see Figure 5) and with equivalent congruency effects in Experiment 2 for both familiar and novel objects. Further, the congruency effect for novel objects was the same as Experiments 1 and 2, $F(1, 83) = 1.44$, $p = .23$, $\eta_p^2 = 0.017$, so the priming for novel objects was equivalent despite the changes in the probe task. In contrast, there was a significant difference between the priming for familiar objects between experiments, $F(1, 83) = 8.3$, $p = .005$, $\eta_p^2 = 0.89$, with more priming in Experiment 1 than Experiment 2. Thus, the Experiment × Congruency × Object Type interaction was driven primarily by a difference in familiar-object priming between the two experiments.

Discussion

In Experiment 1, when subjects attended to the visual form of objects, we established that volumetric grasps could be primed by novel as well as familiar objects. This indicates that motor priming can be triggered by shape-based information alone. However, the priming was larger for familiar objects, suggesting that previous experience with objects also had an impact on grasping representations. We inferred that the visual match-to-sample probe task recruited motor representations based on both the semantic and direct routes.

In Experiment 2, we were interested in measuring grasping representations when the task demands placed greater emphasis on

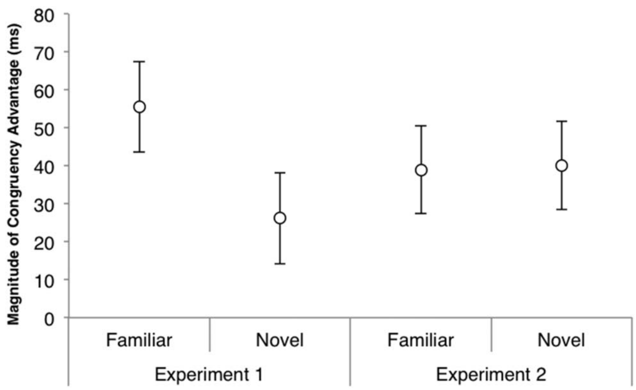

Figure 5. Comparison of congruency effects in Experiments 1 and 2. Error bars represent 95% confidence intervals.

the semantic route to action. To this end, subjects were taught name labels for novel objects. In the grasping task, we used a name label probe on 25% of trials, to ensure that subjects attended to the labels. As we conjectured, this manipulation should activate the semantic route to action for familiar objects and diminish the contributions from the direct visual route. In contrast, there is little to no semantic knowledge for the novel objects, so we predicted that action representations for these objects should reflect mostly the visual route to action.

These predictions are confirmed in the results of Experiments 1 and 2. The level of priming for novel objects was the same between the two experiments, and this likely reflects activation of the visual route to action. Thus, the main difference in priming between the two experiments was for familiar objects, and because for familiar objects there was no need to teach names in Experiment 2, the only difference accounting for this result is the different attentional probe. In Experiment 1, the probe task emphasizes the object's shape, and in addition, the larger priming for familiar over novel objects suggests an additional contribution from stored knowledge. Attending to the shape of a familiar object evokes a contribution from both the direct and semantic routes to motor priming effects. In Experiment 2, attention to the name rather than the shape of the object encouraged a greater reliance on semantically driven motor representation, filtering out the contribution of the object's depicted form (Yoon et al., 2002). Thus, priming for familiar objects was now equivalent to that of novel objects.

These results demonstrate that action representations are reliant on an interaction between one's familiarity with a set of objects and the manner in which the objects are attended. The action representations for familiar objects receive contributions from both the visual and semantic routes, but the contributions from each can be modulated by task demands. When the task involves attention to the depicted visual form of objects, there are contributions from both the visual and the semantic routes. When the task involves name labeling, the impact of the visual form is diminished, but the semantic route still impacts grasping actions. For novel objects, the manner by which the objects are attended has a minimal impact, and we infer that the direct visual route is the primary contributor to action representations for these objects.

In the next set of experiments, we are interested in further exploring the interaction of experience and the dual routes to action by manipulating the objects' orientation.

Experiment 3

How might the effects we studied in Experiments 1 and 2 change if the prime object is shown in an unfamiliar orientation? The question is directly relevant to the distinction we raised at the outset, between the grasp representation associated with the typical (i.e., canonical) orientation of an object and the grasp computed directly from its depicted form. We have assumed that the representation of a canonically oriented grasp can be generated from conceptual or associative knowledge of a familiar object. In addition, though, both familiar and novel objects can have an especially salient orientation determined by structural factors like perceived stability. Consistent exposure to a particular orientation may also contribute to an object's canonical representation (for additional factors, see Blanz, Tarr, & Bülthoff, 1999).

The goal of Experiments 3 and 4 was to distinguish between priming effects induced by the canonically oriented grasp and the grasp invoked by the object's depicted orientation. As noted above, the grasp posture determined by our conceptual knowledge of a spray can is presumably linked to its typical (canonical) orientation, and this representation may be engaged even when the object is shown in a new orientation. What of the grasp posture triggered by novel objects, which presumably is generated without access to stored conceptual knowledge? The direct route assembles actions online from the depicted form of the object. For example, a horizontal spray can, in accordance with its perceived orientation, would afford a closed grasp with the palm facing downward. We will demonstrate, however, that under suitable task conditions novel objects, can also elicit grasp representations based on their canonical orientation, regardless of an object's perceived orientation (e.g., Walker, Kennedy, & Berridge, 2011). The depicted and canonical representations of a novel object may coexist simultaneously and indeed, we will find that task demands can induce observers, at the point of recall, to emphasize one or the other type of representation (Marsolek, 1999; Walker et al., 2011).

Consider again the task of attending to a novel object displayed as a prime just before the occurrence of a cued reach-and-grasp action. Assume that attention to the object is ensured by requiring subjects to carry out a match-to-sample task after producing the cued action (cf. Experiment 1), with the choice items in their canonical orientation. Let the image of a priming object appear upright on some trials and on others, rotated 90° from upright. For upright primes, the grasp posture associated with the canonical representation of the object matches the grasp posture activated by the depicted view. These two sources of activation should contribute jointly to motor priming effects. The semantic route contributes to the activation of canonically based action representations when objects are familiar, but novel objects can invoke only the direct route. The outcome, as we have seen in Experiment 1, would be greater priming for familiar compared to novel objects.

For rotated primes, the grasp posture matching the object's depicted view conflicts with the posture determined by its canonical representation. Which of these contributes to motor priming effects? The answer will depend on the relative weights assigned to the canonical and depicted representations. From the perspective of the motor system, we can think of the object (presented first as a prime and then a short time later as the target in a match-to-sample task) as undergoing a spatial transformation from a rotated to an upright orientation. Paraphrasing an argument by Walker et al. (2011), the usefulness of a grasp posture that conforms to the perceived orientation of the object depends on there being nothing to suggest that its orientation will change relative to the observer. Absent such a constraint, there is less value in maintaining a high level of access to the motor codes induced by the object's depicted view. Under these task conditions, we infer that it is the canonical representation of an object rather than its depicted view that triggers the motor features responsible for priming effects.

Method

Subjects. 40 undergraduate students at Vanderbilt University (M_{age} = 19.0 years, 28 female, 12 male) participated in this experiment for course credit. All subjects were right-handed and had normal or corrected to normal visual acuity.

Stimuli. For the purposes of using rotated primes, we use two grasps: a vertical grasp and a horizontal grasp, and chose two objects that fit each grasp type. Additionally, we created two new novel objects for this experiment (see Figure 6).

Procedure. The basic procedure was the same as in Experiment 1, with a few exceptions. The graspasaurus had two response elements corresponding to a vertical grasp and a horizontal grasp. The order of the two response elements was changed for each subject. Before the grasping trials, subjects saw two hand cues and were shown by a research assistant which cue corresponded with which response element. To familiarize the subjects with the objects, each of the eight objects (four novel, four familiar) were shown on the screen individually for 2 s.

Figure 6. Familiar and novel objects with their respective hand gestures. For vertical grasps, the familiar objects are a spraycan and a soap dispenser. For the horizontal grasp, the familiar objects are a flashlight and stapler. See the online article for the color version of this figure.

Figure 7. An example of the hand cue embedded within the object prime. The object is rotated 90° to the left. See the online article for the color version of this figure.

For the experiment, subjects held the spacebar down to start a trial. Then, an object was displayed with a superimposed hand cue (see Figure 7). The subject lifted their hand off of the spacebar to grasp the response element corresponding to the hand cue and the experimenter coded the accuracy of the grasp on a separate keypad, pressing 1 if the subject grasped the correct response element and 0 if they did not. On 25% of trials, an array of eight objects was shown 500 ms after the grasp was made. There were letters corresponding to each object, and the subject typed in the letter that corresponded with the object shown during the trial. The probes were meant to ensure that subjects attended to the objects throughout the experiment, but they also made the canonical form salient throughout the experiment.

Rotated primes showed objects rotated 90° to the left or 90° to the right in the picture plane. For critical trials, each object picture (Eight objects × Three rotations) was presented equally often with each hand gesture, resulting in 48 prime-hand combinations. Each of these combinations was presented seven times in random order, resulting in 336 total trials. The crucial factors are Object Type (novel, familiar), Prime-Action Congruency (congruent, incongruent), and Prime Orientation (upright, rotated left, rotated right). This arrangement yields 28 observations per subject for each critical condition.

Here, congruency was coded on the canonical rather than the depicted form. We define congruency in this fashion to determine whether the priming elicited is based on previous experience for canonical object orientations. Thus, priming of the depicted form of the object would be implied by a negative priming effect.

Results

We removed trials with response times shorter than 250 ms or longer than 2,250 ms (0.5% of responses removed). Incorrect responses were also removed (0.4% of responses removed).

As shown in Figure 8, there was a significant congruency advantage for each condition, as supported by a 2 × 2 × 2 ANOVA with Congruency (congruent, incongruent), Object Type (familiar, novel), and Orientation (upright, rotated) as within-subject factors. For these analyses, we first examined the two rotated conditions (rotated left, rotated right), and found no significant difference between them, $F(1, 30) = 2.34$, $p = .13$, $\eta_p^2 = 0.06$. Thus, we combined the two rotated conditions for further

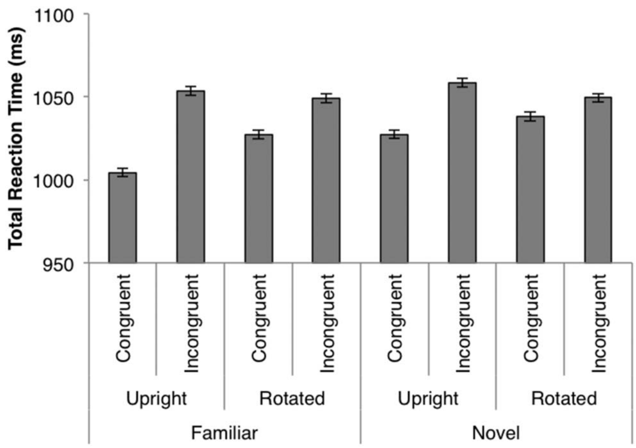

Figure 8. Mean reaction time data for Experiment 3. Error bars represent 95% confidence intervals.

analyses. There was an Object Type × Congruency interaction, $F(1, 39) = 6.33$, $p = .01$, $\eta_p^2 = 0.17$, with stronger congruency advantages for familiar than novel objects (see Figure 9). As in Experiment 1, attending to the object's shape yielded greater priming for familiar objects. Additionally, there was an Orientation × Congruency interaction, $F(1, 39) = 9.40$, $p = .005$, $\eta_p^2 = 0.24$, with more priming found for upright rather than rotated objects, suggesting evocation of grasp representations to the canonical form even when the depicted form is rotated. However, there was no Congruency × Object Type × Orientation interaction, $F(1, 39) = 0.41$, $p = .53$, $\eta_p^2 = 0.014$, suggesting little difference in the magnitude of priming across object type and the objects' depicted orientation.

Discussion

Here, we explored whether grasps made in response to hand cues presented over a task-irrelevant object would depend on an object's depicted view or on the conceptual knowledge of an object's canonical form. To test this possibility, we introduced rotated and upright object primes. For familiar objects we found priming for both orientations, which was nonetheless stronger for upright than rotated objects. Upright objects trigger motor representations based jointly on their canonical representation and depicted forms, and these motor influences combine to generate priming effects. When attending to rotated objects, however, motor representations associated with the canonical form dominated the depicted form, as evidenced by a positive priming effect even when the familiar objects are rotated.

For novel objects, a remarkably similar pattern was observed. For rotated novel objects, we found priming according to the canonical rather than the depicted form. As we already noted, prior work has shown that canonical orientations are formed relatively quickly based on experience (Tarr & Gauthier, 1998) and they likely also depend on how stable a perceived view appears to be from a geometric standpoint (Blanz et al., 1999). In other words, the fact that rotated views of novel objects did not appear to easily rest on a horizontal surface, together with the consistent presentation of the canonical view in the match-to-sample task, likely encouraged rapid access to canonical representations.

Nevertheless, priming for novel objects was smaller compared to familiar objects. This confirms the results of Experiment 1, and suggests that experience and learned conceptual knowledge can influence the strength of grasping representations. Subjects had weaker representations for the canonical form for novel objects compared to familiar objects, resulting in less overall priming.

This study demonstrates multiple types of knowledge that can influence the activation of motor representations from pictured objects. In an upright orientation, the grasp posture associated with an object's canonical form matches the posture assigned to its depicted form, and these representations combine to generate strong priming effects. When objects are rotated, the grasp postures invited by the canonical representation and the depicted form are in conflict, and task demands modulate the outcome of this competition.

Experiment 4

In Experiment 3, attention to the prime occurred via a match-to-sample task carried out directly after a cued reach-and-grasp action, and objects were always displayed for recognition in their canonical orientation. The evidence indicates that under these task conditions, the canonical representation of rotated objects contributed more to motor priming than the object's depicted form. If attention to the prime is determined instead by asking subjects to retrieve a label for pictured objects, we might expect a different outcome.

There is good evidence that novel count nouns (individuated objects that can be counted) assigned to novel objects can generate orientation-independent visual representations that exist together with representation of their depicted forms, and both can be accessed during recall (Walker et al., 2011). Canonical and depicted forms of a rotated object, if concurrently active in working memory, would generate competing motor representations. For example, the rotated object depicted in Figure 7 would trigger both

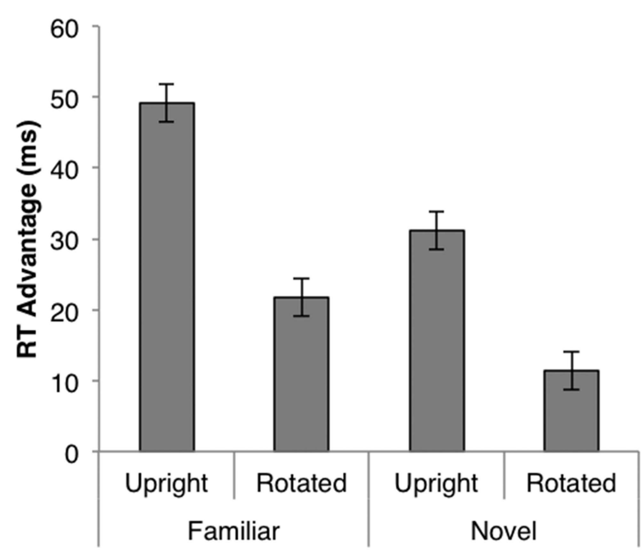

Figure 9. Congruency advantage for Experiment 3. Congruency is defined relative to the object's canonical form. Error bars represent 95% confidence intervals.

a horizontal grasp, based on its depicted form, and a vertical grasp associated with its canonical representation. The net outcome is that no priming effect on the cued reach-and grasp actions would be visible, despite the fact that upright objects clearly yield an effect.

Consider now the impact of rotation on priming induced by familiar objects. Recall that attending to the name of a familiar object yielded motor priming effects that were smaller in magnitude than effects triggered by the match-to-sample task. No such difference occurred for novel objects. We made the reasonable assumption that naming familiar objects placed more weight on the semantic route to action, while at the same time reducing a contribution of the direct route to priming effects. We cannot assume, however, that actions determined by conceptual associations would continue to exert a dominant influence on performance when familiar objects are no longer experienced in their familiar (canonical) orientation. Indeed, evidence suggests that rotation diminishes the availability of grasp actions habitually associated with an object. For example, Riddoch, Edwards, Humphreys, West, and Heafield (1998) observed task-irrelevant grasp actions directed toward the handle of an upright object in a neuropsychological case exhibiting “anarchic hand” syndrome. These competing responses occurred less frequently when the same object was inverted. Similarly, Herbort and Butz (2011) found that habitual actions affected goal directed responses only when the object occurred in its conventional upright orientation. We wish to clarify the nature of priming effects induced by pictures of objects rotated from their typical upright orientation when subjects attend to their names. For rotated novel objects, naming should generate access to both canonical and depicted representations. For familiar objects, rotated objects induce reliance on action representations determined by conceptual associations as well as on the object’s depicted form. At issue for both novel and familiar objects is the net effect of competing motor influences on cued reach-and-grasp actions.

Method

Subjects. Thirty-two undergraduate students (M_{age} = 20.2; 25 female, 7 male) at the University of Victoria (British Columbia) participated in this experiment for course credit. Twenty-nine subjects were right-handed and three were left-handed. All had normal or corrected to normal visual acuity. This study was approved by the University of Victoria’s Human Ethics Board (10–147).

Procedure. Subjects learned object names as in Experiment 2. Following this training, they proceeded to the test trials. As in Experiment 3, we used both familiar and novel objects with hand gestures embedded into the objects. The gestures shown could be horizontal or vertical, with four objects corresponding to each gesture. Each object was shown in one of three orientations: upright, rotated 90° to the left, and rotated 90° to the right. This results in 48 critical trial types (Two object types × Two gestures × Four objects × Three orientations). Each trial was shown six times, for a total of 288 trials for each subject.

Subjects pressed a button on a button box to start each trial. As before, objects were shown with hand gestures embedded in them, and the task was to make the gesture onto the corresponding response element. After 25% of trials, subjects were asked to verbally report the object’s name. This probe was meant to ensure that subjects were attending to the object’s name label.

Results

We examined mean RT across subjects (see Figure 10). We removed incorrect responses (0.5%) and trials that were slower than 250 ms and faster than 3,000 ms (0.5% of responses).

For upright objects, the pattern of results replicated Experiment 2, with equivalent priming for familiar and novel objects. For rotated objects, there was no significant priming for novel objects, but there was negative priming for rotated familiar object primes. As in Experiment 3, the two rotated conditions (rotated left, rotated right) show no appreciable difference in priming, $F(1, 31) = 0.13$, $p = .72$, $\eta_p^2 = 0.00$. We entered Congruency (congruent, incongruent) × Object Type (familiar, novel,) and Orientation (upright, rotated) as factors in a 2 × 2 × 2 ANOVA. There was a Congruency × Orientation interaction, $F(1, 31) = 10.91$, $p = .002$, $\eta_p^2 = 0.26$, with more priming for upright than rotated objects (see Figure 11). Additionally, there was a Congruency × Object Type interaction, $F(1, 31) = 4.23$, $p < .05$, $\eta_p^2 = 0.12$, with stronger priming for familiar than novel objects. However, there was no evidence of a Congruency × Orientation × Object Type interaction, $F(1, 31) = 0.20$, $p = .66$, $\eta_p^2 = 0.00$, suggesting similar levels of priming across object type and presented object orientation.

We then examined each individual condition. There was positive priming for the familiar upright, $F(1, 31) = 4.35$, $p = .045$, $\eta_p^2 = 0.12$ and novel upright, $F(1, 31) = 12.2$, $p = .001$, $\eta_p^2 = 0.27$, conditions. However, the priming effects for both objects types were similar in magnitude, $F(1, 31) = 0.78$, $p = .38$, $\eta_p^2 = 0.02$. This pattern is in contrast with Experiment 3, where priming for familiar upright objects was greater than for novel upright objects.

For rotated objects, there was no significant priming for novel rotated objects, $F(1, 31) = 0.55$, $p = .46$, $\eta_p^2 = 0.017$. For familiar rotated objects, there was an effect of congruency in the negative direction, $F(1, 31) = 5.41$, $p = .027$, $\eta_p^2 = 0.148$. Note that negative priming for the canonical form indicates positive priming for the depicted form, so the pattern of priming for familiar rotated objects was toward the depicted form.

We have suggested that the lack of any priming effects for rotated novel objects is the result of two competing motor influ-

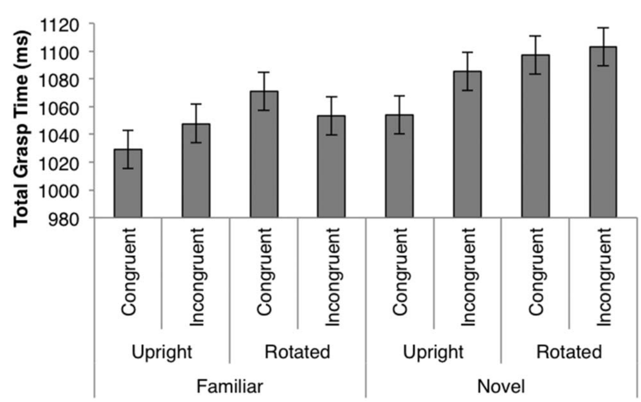

Figure 10. Total reaction time data for Experiment 4. Error bars represent 95% confidence intervals.

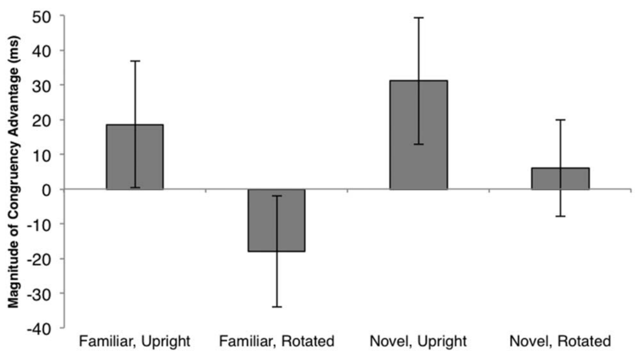

Figure 11. Congruency advantages each condition in Experiment 4. Error bars represent 95% confidence intervals.

ences of equal strength, one based on the object's canonical representation and the other on its depicted form. To obtain further evidence for this claim, we considered the possibility that the relative contribution of these two influences, although equal when averaged across trials (thereby yielding no net congruency effect), varies stochastically from moment to moment. This fluctuation would be reflected in elevated trial-by-trial variation in the congruency effect, which at one instant might favor the depicted view and at another, the canonical representation. Across the full span of trials, then, the congruency effect would fluctuate markedly, even though its overall average impact would be nil. In contrast, under conditions where an overall congruency effect is apparent, the trial-to-trial variability of this effect is due to the net influence of a dominant motor representation operating in the presence of, at most, a weak competitor. For example, for rotated familiar objects the congruency effect favored the depicted view, raising the possibility of weak competition from the canonical representation. Under these circumstances, it follows that a smaller degree of trial-by-trial variability is expected.

To test this argument, we used linear mixed-effects modeling (e.g., Baayen, Davidson, & Bates, 2008) to assess the degree of variability of congruency effects over trials. This type of analysis affords the examination of the consistency of an effect across items, subjects, and/or trials by including individual observations in the analysis, rather than averaging across trials to compute condition means, as is done in a standard analysis of variance. Variation of an effect across units such as items, subjects, or trials is called a *random* effect. Influences of factors that are constant across units are referred to as *fixed* effects. Our specific interest was in the variability of the congruency effect across trials, which pertains to the argument made above. Strongly competing affordances (generated by canonical vs. depicted views of a rotated novel object) should lead to larger trial-to-trial variation in the congruency effect. We applied separate analyses to the response-time data for individual trials with (a) upright primes consisting of familiar objects, (b) upright novel objects, (c) rotated familiar objects, and (d) rotated novel objects. In each analysis, we included an intercept, a fixed effect of congruency, and random effects for subjects and trials, as well as the random effect of congruency across trials. For each analysis, the model estimated parameter values for each of the effects. We anticipated that in the case of rotated novel primes, where no evidence for a congruency effect was obtained, variability across trials would be most apparent, as indicated by a larger parameter estimate for the random effect of congruency over trials.

The mixed-effects models were computed using the *lmer* function from the *lme4* package in R. The specification of the mixed-effect model for all of the four conditions and the best-fitting parameter estimates for each condition are shown in Table 1. It can be seen in the first row of numerical entries in the table that only in the analysis of data from trials in which rotated novel objects were the primes was the parameter for the random effect of the congruency across trials greater than zero. In that case, the variance associated with this interaction was estimated to be 666.5. This parameter was estimated to be zero in each of the other three cases. These results clearly are consistent with the proposal that in the case of rotated novel objects, the primes elicited an influence from two competing sources, one associated with its depicted view and another from its canonical representation.

Discussion

In Experiment 2, we found that learning a label for novel objects and being probed to provide those labels throughout the experiment resulted in equal priming for both novel and familiar objects presented in an upright orientation. In Experiment 4, we replicated this result and extended it with a manipulation of the objects' orientation. For rotated novel objects, there is no priming, indicative of a conflict between the learned canonical form and the depicted form. The strengths of these representations appear roughly equivalent, resulting in no priming. Recall that earlier we cited evidence to indicate that novel objects associated with novel count nouns generate representations in working memory associated with both their canonical and depicted forms. Consistent with this idea, the absence of priming for rotated novel objects suggests the possibility of competing action representations. The priming effects obtained for familiar rotated objects favor their depicted form. Thus, it seems that under these task demands, the representation of the canonically oriented form of the object no longer has an overriding influence on the cued grasp action. This outcome is consistent with the proposal by Yoon et al. (2002), who argued that the rapid selection of an action triggered via the direct route can

Table 1
Linear Mixed-Effects Model Specification and Estimated Parameters for Four Priming Conditions in Experiment 4

	Object type and orientation			
	Familiar		Novel	
Effects	Upright	Rotated	Upright	Rotated
Random effects				
Trial Number × Congruency	.0	.0	.0	666.5
Trial number (intercept)	77.4	922.8	1,591.0	92.0
Subject (intercept)	82,524.5	90,768.3	90,360.0	98,078.2
Fixed effects				
Intercept	1,038.5	1,062.2	1,069.3	1,100.0
Congruency	18.8	–16.9	32.2	6.4

Note. Model: Reaction Time ~ 1 + Congruency + (1 | Subject) + [(1 | Trial Number) + (0 + Congruency | Trial Number)]. Parameter values for random effects are variances and for fixed effects parameter values are effect sizes in milliseconds.

effectively block the output of the semantic route when their representations compete.

General Discussion

In this series of experiments, we set out to examine whether grasping representations evoked by pictures of objects are computed online based on object shape or whether stored knowledge and previous experience with objects can aid in reach and grasp actions. To that end, we compared the speed of grasping actions for familiar and novel objects, with the assumption that if stored knowledge affects grasping representations, then it should be reflected in a difference between familiar versus novel object cues. We discovered that the nature of grasping representations is dependent on an interaction between the object familiarity and the manner in which objects are attended and encoded. There are two routes to action involved here: a direct visual route that depends on the current depicted view of an object and a semantic route that involves knowledge of an object's name label and its canonical form.

In Experiment 1, when the probe was a visual match-to-sample, the object's visual form was more salient, resulting in positive priming for familiar and novel objects. This revealed positive priming based on an object's shape even for objects one had no previous experience with. Priming was larger for familiar than novel objects, however, which we interpreted as an additional contribution from the semantic route.

In Experiment 2, when the probe involved naming the objects, the priming was equivalent for familiar and novel objects. Here, the semantic route dominated for the familiar objects because probes were not visual. For novel objects, there is no semantic knowledge, and priming could depend only on the direct visual route, which facilitates action representations based on an online analysis of an object's shape. Although the magnitude of the priming was equivalent for both kinds of objects, the influences are considered to arise from different routes, the semantic route for familiar objects and the direct visual route for novel objects.

In Experiments 3 and 4, we considered another property of an object that could be important to grasping representations, its canonical orientation, the influence of which we could measure by comparing the priming induced by upright and rotated object primes. In Experiment 3, when the probe involved visual matching, we found priming for both upright familiar and novel objects, as in Experiment 1. However, we also found priming of the canonical form for rotated objects, indicating that the representation of the canonical form dominates over the depicted form of objects. Surprisingly, this pattern of results was present even for novel objects, suggesting that a canonical form for these objects is quickly learned under ideal conditions (e.g., when the subjects learn a single view that is also a "good" view). Nonetheless, the canonical view for novel objects appears weaker than that for familiar objects, with less priming overall.

Finally in Experiment 4, we used a name labeling probe with rotated objects. The depicted form of familiar objects exerted the dominant influence on cued grasps actions. For rotated novel objects, however, there was no significant priming, suggesting that the depicted and canonical representations were in conflict and were more equal in strength. Once again, changing the task demands had an impact on which representation prevailed.

In this series of experiments, we demonstrated that stored knowledge can influence grasping representations and that the influence of this knowledge can be modulated by attention to certain object dimensions. We showed that semantic knowledge such as an object's name or visually acquired knowledge such as an object's canonical form can result in different action representations, and the strength of these representations is dependent on the amount of experience one has with those objects. For familiar objects, there are contributions from both the visual and semantic routes, but the contributions of these dual routes can increase or decrease depending on how the objects themselves are attended. The action representations involving novel objects are usually dependent on the direct route to vision because there is no semantic knowledge that can be drawn upon. However, in Experiments 3 and 4, we have demonstrated that people can acquire knowledge such as the canonical form of an object very quickly, and that this canonical orientation influences motor representations evoked by objects. Although the present work showed that even novel objects evoke grasping representations relatively automatically, there still is work to be done to understand the nature of familiar object representations. Using novel objects facilitates this endeavor, as they help clarify aspects of behavior and representations that do not require experience. One open question is the nature of the experience that would be sufficient to produce priming with novel objects that is equivalent to that of familiar objects, in all possible test conditions—in other words, what exactly does it take to turn a novel object into a familiar object?

Finally, we note that our results are pertinent to the following claim. It has been argued that motor representations computed in the act of grasping to lift an object do not rely on access to stored knowledge but rather, are derived online from an object's perceived form (Jax & Buxbaum, 2010). The priming effects we have obtained indicate that a representation of the grasp posture involved in lifting an object is not always limited to its depicted form. Indeed, given that both the familiarity of an object and its canonical orientation play a role in priming effects, it is clear that at least under certain task conditions, stored knowledge is consulted to generate a representation of the grasp posture for lifting an object. Of course, we are referring here to pictured objects rather than solid forms that can actually be grasped. Nonetheless, our results are consistent with a report by Osiurak, Roche, Ramone, and Chainay (2013), who argue that task set determines whether long-term knowledge plays a role in generating a grasp-to-lift action.

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