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Priming of Reach and Grasp Actions by Handled Objects

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Pictures of handled objects such as a beer mug or frying pan are shown to prime speeded reach and grasp actions that are compatible with the object. To determine whether the evocation of motor affordances implied by this result is driven merely by the physical orientation of the object's handle as opposed to higher-level properties of the object, including its function, prime objects were presented either in an upright orientation or rotated 90° from upright. Rotated objects successfully primed hand actions that fit the object's new orientation (e.g., a frying pan rotated 90° so that its handle pointed downward primed a vertically oriented power grasp), but only when the required grasp was commensurate with the object's proper function. This constraint suggests that rotated objects evoke motor representations only when they afford the potential to be readily positioned for functional action.

Keywords: action representations, dorsal-ventral stream interactions, hand action representations, motor affordances

It is well known that handled objects like beer mugs and frying pans evoke hand action representations even when such affordances are not demanded by task requirements (e.g., Handy, Grafton, Shroff, Ketay, & Gazzaniga, 2003). A host of theoretical issues emerges in relation to this interesting phenomenon, including questions involving the nature of spatial attention drawn to an object's handle, and perhaps more fundamentally, the nature of the motor affordances elicited by an object. The classic notion of a *simple affordance* (Gibson, 1986) refers to a perception-action loop that has nothing to do with the actor's knowledge of the object nor with his or her goals (see McGrenere & Ho, 2000). Turner (2005) provides the informative anecdote of an orangutan interacting with a claw hammer inadvertently left in its enclosure. The animal picked up the object, moved it about, then immediately used the claw of the hammer to scratch the walls of the enclosure and some minutes later used the head of the hammer to strike various surfaces. The orangutan, it would seem, had perceived directly how to use the hammer. The notion of a simple affordance has been substantially revised since being introduced by Gibson. According to Norman's (1999) influential definition, an affordance is bound to past knowledge as well as current perception of the object, hence the term *perceived affordance*. The distinction between simple and perceived affordances is clarified by another example from Turner. An American tourist exiting a "slam-door" train in Britain was unable to open the door because she did not understand that in such carriages, there is no interior door handle. To open the door requires first opening a window, then reaching outside to use an exterior handle. Thus, in the Gibsonian sense, the door afforded opening, but the perceived affordance, given this person's background, did not lead to the required action.

Because of the subtle distinctions inherent in the notion of affordance, it is of great interest to clarify the nature of the hand action representations automatically elicited by familiar handled objects like a teapot. For example, the handle of the object could evoke an action representation directly, without regard to functional properties of the object. Symes, Ellis, and Tucker (2007) referred to this affordance as a *pure physical affordance*, meaning an affordance driven solely by the structural properties of an object in a particular orientation. A substantial number of publications on handled objects tacitly adopts this view of affordances; the image of a handled object, oriented to the left or right, is assumed to induce an action representation on the side of the body aligned with the handle. These studies, relying on tasks that require left or right key-press responses, demonstrate spatial correspondence effects in which a response is speeded when the object's handle is aligned with the response hand (e.g., Pellicano, Iani, Borghi, Rubichi, & Nicoletti, in press; Phillips & Ward, 2002; Tucker & Ellis, 1998; Vainio, Ellis, & Tucker, 2007). Taken at face value, handle alignment effects would seem to indicate that the affordance generated by the object is based on the particular left or right orientation of the handle (Tucker & Ellis, 1998). The insight offered by these experiments, however, is constrained by the methodology involved in left-right key presses. We know only that side of responding is affected by the position of the handle, not whether the affordance includes a reach and grasp component nor even whether the action representation specifically involves hands as effectors. Indeed, in a number of instances, spatial alignment effects are produced when responses are carried out using the feet or two fingers of the same hand (e.g., Phillips & Ward, 2002;

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Symes, Ellis, & Tucker, 2005; Vainio et al., 2007). These latter results imply that what is being measured is a spatial representation having to do with the relative location of the object's handle, not with a specific hand action representation (for related arguments, see Bub & Masson, 2010, and Cho & Proctor, in press).

Neurophysiological evidence, in fact, is not consistent with the assumption that handled objects aligned with one or the other hand give rise exclusively to limb-specific action representations. During the motor preparation phase, and even during the movement phase, cells in the dorsal premotor cortex (PMd) of the monkey are tuned for directionality of the movement for both arms despite the fact that the monkey is required to respond with one arm exclusively and the other arm is immobilized (Cisek, Crammond, & Kalaska, 2003). This striking outcome led Cisek et al. to infer that ". . . a major component of the neural activity in PMd specifies reaching movements at an abstract level of movement planning independent of the effector which will be used to perform the reach" (p. 936). Their proposal is consistent with other findings in the neurophysiological literature (e.g., Shen & Alexander, 1997; Wise & Murray, 2000).

The implication of these studies is that a substantial part of action representations elicited by handled objects is limb-independent. These action representations must surely include a reach and grasp component, and we have already seen compelling neurophysiological evidence that this component most likely is programmed at a relatively abstract level that is hand independent. A methodology is required that provides further insight into the nature of this component of an action representation. In a previous paper, we used color as a cue to direct subjects to make a left or right reach and grasp action on a response element (Bub & Masson, 2010). A picture of a handled object was presented in a color that served to cue the left or right hand. The object's handle was oriented to the left or right, and the hand action was either congruent or incongruent with the reach and grasp action associated with the colored object. For example, a vertically oriented closed grasp is congruent with a teapot but incongruent with a frying pan. Consistent with the neurophysiological evidence for hand independent motor representations, we showed that congruency effects (faster responding when a congruent action was cued) were independent of whether or not the response hand was aligned with the object's handle.

Here, we are concerned with the nature of the affordance induced by images of handled objects presented either in a canonical orientation or rotated away from their conventional upright position. This manipulation of orientation is intended to address a fundamentally different question than previous work on handle alignment effects based on key-press responses. Alignment effects, as we have noted, can reflect only competition between the left and right hand as response options, and so by their very nature, cannot yield insight into the type of hand action representation evoked by the image of an object deviating from its conventional upright position. Consider, for example, a frying pan with its handle pointing upward. This image invites a vertically oriented power grasp as a simple affordance, but the result of carrying out that action does not conform to the grasp commensurate with the pan's proper function. How do the orientation and function of an object jointly contribute to its perceived affordance? In the next section, we describe the methodology we have developed to clarify the nature of reach and grasp action representations automatically evoked by objects in different orientations.

Measuring Affordances to Objects in Canonical and Rotated Orientations

We will use the term affordance to be consistent withNorman's (1999) conceptualization. The notion of a perceived affordance as described by Norman depends on the prior history of interaction with an object, and also on its shape and current orientation relative to the actor. How do we determine what affordance is elicited by the object in a particular position? Aside from key-press responses, a previous approach used in the literature on perceived affordances has been to contrast the type of grip (power versus precision) as the response in tasks requiring judgments about a target object (e.g., Ellis, Tucker, Symes, & Vainio, 2007; Tucker & Ellis, 2001). Target-compatible grip responses (e.g., a power grip to a hammer) are executed more rapidly than incompatible responses (e.g., a power grip to a grape). A limitation of this method is that it offers no ready way to distinguish the same grip type (e.g., power) that varies with respect to the orientation of the wrist. If we wish to know whether a beer mug on its side evokes the affordance typically associated with the object versus the affordance invited by the rotated image of the object, then we need some way of determining which of these two action representations (a vertically versus a horizontally oriented grasp) has been elicited. In addition, a response that does not require programming and executing a reach and grasp action may not be sensitive to dynamic components of the action representation afforded by an object.

We describe a procedure intended to produce visuomotor priming of a reach and grasp action carried out shortly after viewing a handled object. This methodology allows us to determine whether the motor affordance automatically generated by the image of a handled object in an unusual orientation differs from the affordance typically associated with the object. Subjects were trained to make a speeded reach and grasp response to one of two response elements (depending on a visual cue) placed directly in front of them (Figure 1a). One response was applied to a vertically oriented handle (as in a teapot), whereas the other fit a horizontally oriented handle (as in a frying pan). Subjects were cued to respond by means of a picture of a hand shaped and oriented to fit the target response (Figure 1b). Subjects were practiced on this simple visually guided task until cued responding was rapid and accurate. After training, subjects made speeded reach and grasp responses directly following a visual prime. The priming event consisted of a picture of a handled object displayed for a brief interval before the onset of the response cue (Figure 1c). Handled objects generate motor representations that can automatically influence reach and grasp responding (Bub & Masson, 2010). Based on this evidence, we assume that the handled object in our task evokes representations that serve as the motor priming event. If the visually guided reach and grasp action to the response element is sensitive to these recently evoked motor representations, then we should observe priming effects defined by the relationship between the depicted object and the cued response.

We argue that the priming effects emerging from this procedure are specific to the planning and execution of motor representations and are not simply due to the perceived compatibility between the

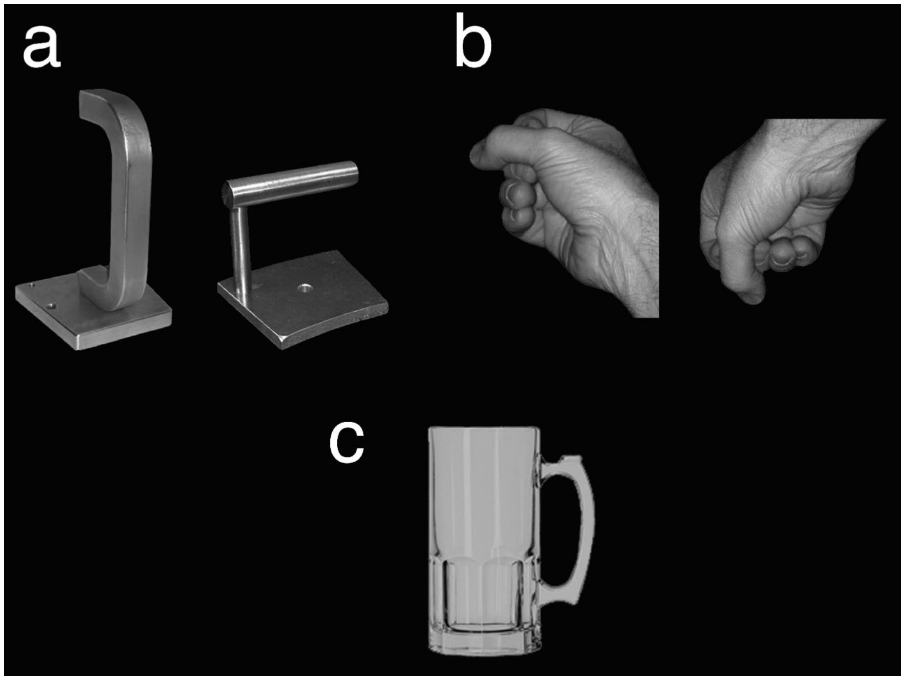

Figure 1. Response elements and sample stimuli used in the experiments. (a) Two response elements were positioned directly in front of the subject, affording either a vertically or horizontally oriented grasp. (b) One of two pictured hand cues were used to signal the target action for a trial. (c) An example prime object shown in normal orientation.

prime object and hand cue (a form of stimulus-stimulus compatibility, as opposed to stimulus-response compatibility). In support of this claim, we note a recent study by Girardi, Lindemann, and Bekkering (2010), in which subjects were shown a priming picture consisting of a hand and an object, and were required to make a power or precision grasp to classify the object as manmade or animate. When the size of the object was consistent with the required grasp (e.g., precision grasp to classify a needle as manmade), the response was faster. The magnitude of this priming effect depended on whether the pictured hand was positioned to grasp the object. This dependency disappeared when the object and hand were spatially separated rather than depicted as interacting. This result implies that stimulus-stimulus compatibility effects, obtained when the hand and object were spatially arranged to imply interaction, no longer occur once the interactive spatial arrangement between hand and object is violated. In our experiments, the prime object and hand cue are temporally separated (i.e., they appear sequentially, not simultaneously, so they do not create the impression of an interaction). In addition, the location of the hand cue, if superimposed on the object prime, would not appear to be in the correct position for interacting with the object. Therefore, it is unlikely that the priming effects are due to the perceived compatibility between object prime and hand cue. Rather, the influence of the object occurs at the level of planning and executing the cued reach and grasp response.

We assume that motor representations evoked by a picture of a graspable object will affect a cued action depending on whether the object and cued action require the same grasp orientation or different grasp orientations. We define a cued action as *congruent* with the prime object when the action and the object's handle are in the same orientation (e.g., a closed grasp with the wrist vertically oriented and an upright beer mug). An action is *incongruent* when its orientation conflicts with that of the object's handle (e.g., a closed grasp with the wrist horizontally oriented and an upright beer mug). If the depicted object evokes hand action representations that affect the cued reach and grasp response, then performance of the cued action should be depend on whether the action is congruent with the orientation of the object's handle: a congruent grasp should be speeded relative to an incongruent grasp.

How would rotating the object prime modulate its effect on the cued grasp action? A simple (possibly, naive) answer is that the evoked affordance is driven only by the handle in a particular orientation, not by any more elaborate principle that takes the function of the object into account. If this assumption is correct, we would expect the following outcome. Consider the difference in affordance between the two versions of the beer mug shown in Figure 2. The beer mug in its canonical orientation should prime a closed grasp with a vertically oriented wrist, making the congruent action faster than the incongruent action. Now consider the beer mug in the rotated orientation. This object, simply based on the orientation of the handle, affords a closed grasp with the palm facing downward. We defined this grasp as congruent because it fits the orientation of the object's handle, even though it is not the grasp typically associated with the object. Thus, our classification of a grasp as congruent or incongruent is based simply on the visual appearance of the object's handle (e.g., a horizontal closed grasp is congruent with a rotated beer mug). If the visually based affordance underlies priming of the grasp response, then rotated

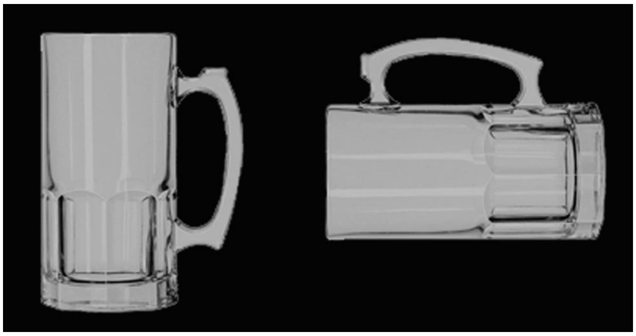

Figure 2. An example prime object shown in normal and rotated orientation were the rotation places the object in an F-commensurate position for a right-handed observer.

objects should show the same effect as normally oriented objects. This prediction is based on the assumption that the priming effect of a handled object is due entirely to the handle's orientation (horizontal versus vertical), without regard to higher level influences such as knowledge of the functional properties of the object. The reason that this view is likely to be over-simplistic is that actions on objects invariably entail outcomes, and considerable evidence indicates that such outcomes are automatically evaluated, even when they are irrelevant to task performance (e.g., Creem & Proffitt, 2001; Hommel, 1993; Kiesel & Hoffmann, 2004).

An important aspect of the affordance automatically evoked by a tool or utensil may be the inclusion of an anticipated effect—the goal state of the action triggered by the object. Massen and Prinz (2007) have demonstrated that precuing the target-movement mapping for a tool benefits performance. The target-movement mapping associated with a tool or utensil is the relationship between the hand action applied to the object and the outcome of this action. Subjects were required to touch one of two targets with a lever pivoting around one of two possible points that when momentarily active, determined the direction of motion (up or down). Precuing a pivotal point (and therefore the target-movement mapping) led to enhanced performance, whereas no such benefit was found if only the spatial location of the target was precued. These authors infer that subjects represent tools and their associated target-movement mappings in a similar way to the representation of elementary stimulus-response mappings. If their assumption is correct, then the perceived affordance of a handled object rotated from its upright position would include the outcome of the grasp applied to the current orientation, which in turn will depend on properties of the object having to do with its function. For example, a horizontally oriented beer mug affords a closed grasp with the palm facing downward, but the outcome of this grasp depends on the location of the mug's opening. If it is at the top of the hand (near the thumb), then the mug will be positioned for drinking; but if the opening is at the bottom of the hand, then the mug will be positioned for storage.

We infer, then, that the perceived affordance evoked by the handled object must include information about the outcome of the action. Indeed, Rosenbaum, Cohen, Meulenbroek, and Vaughn (2006) reviewed considerable evidence showing that how an object is grasped does not depend merely on its immediate appearance, but also on the ultimate goal of the actor. Our claim is that even automatically evoked affordances may include anticipated effects of actions, based on repeated experience dealing with the conventional use of an object. In other words, the possibility exists that the affordance automatically evoked by a handled object is modulated by a history of functionally interacting with an object.

Consider again a beer mug rotated 90° counterclockwise from its canonical orientation for a right-handed observer. The appearance of the beer mug in this case is consistent with a horizontally oriented closed grasp not only because of the position of the handle, but because the object as a whole when grasped in this way could be made ready for its typical function after a simple wrist rotation. Now consider the same object but mirror reflected and rotated 90° clockwise (see Figure 6). The handle is horizontally oriented as before and at face value affords the same right-handed grip: A closed grasp with the palm facing downward. The eventual result of this action, however, would be a beer mug with the open end facing downward unless the wrist undergoes an uncomfortable and awkward rotation to place the beer mug in its conventional orientation. Thus, presenting the image of an object in one or the other of these two rotated views does not lead to equivalent affordances if the notion of affordance includes the end-state of an implied action. We will term a grasp as *F-commensurate* when that action results in an outcome that preserves the typical function of the object. For example, a right-handed closed grasp with the palm facing downward is F-commensurate with the rotated object depicted in Figure 2. A grasp is *F-incommensurate* when the outcome leads to the object being oriented in such a way as to require an awkward or even bizarre wrist adjustment to implement its function (as with the rotated view in Figure 6). We have argued that handled objects may yield priming effects consistent with the orientation of the handle when the cued grasp is F-commensurate. The question of great interest is whether primes also evoke F-incommensurate affordances. If commensurability matters, then higher level knowledge such as the functional properties of an object must play a role in shaping the automatic evocation of motor representations in combination with the affordance determined by the handle.

In addition to our enquiry into the influence of F-commensurability on motor representations automatically generated by handled objects, we examine the durability of the prime's influence by using a short interval between the prime object and the cued reach and grasp action in the first two experiments, but a longer interval in Experiment 3. Our interest in the duration of the priming effect is linked to an influential account of the neural mechanisms determining actions to manipulable objects. This account is founded on a distinction between (a) a dorsal stream that processes transient visual input from the target object to derive the metrics needed for a response, and (b) a ventral stream that derives a more stable representation of object identity that is maintained in memory (Goodale & Milner, 1992; Goodale & Milner, 2004; Milner & Goodale, 2006; Milner & Goodale, 2008). Jax and Rosenbaum (2009) have raised the possibility that dorsally driven priming effects are short-lived, and so are measurable only when a sufficiently brief interval (less than a second) occurs between prime and target. If the priming effects we report are indeed fleeting, then the evidence would be consistent with the claim that the motor representations automatically generated by the image of a handled object include a contribution from the dorsal stream. The relationship between F-commensurability and the action representation afforded by a handled object is therefore of relevance to the ongoing debate on the interaction between memory-based and visually-guided influences during the programming and execution of a reach and grasp action. We return to this important issue in the final discussion.

Experiment 1

In Experiment 1, subjects responded to a visual cue by making a reach and grasp action on one of two response elements placed directly in front of them. The visual cue was preceded by a picture of a handled object that, when presented in its canonical orientation, afforded either an action congruent with the cued response or an incongruent action. For example, a beer mug in its normal orientation (Figure 1) affords a closed grasp with a vertically oriented wrist and the same cued action is then congruent with that affordance. In the incongruent condition, the cued action is a closed grasp with the palm oriented downward. When the beer mug is presented in a rotated view (Figure 2), we define the congruent action as the one that fits the depicted view of the object (closed grasp with horizontally oriented wrist) rather than the action consistent with its canonical orientation. Thus, what we deem as the congruent action matches the affordance of the object in its present orientation and therefore should yield a faster response than the incongruent action if priming is based on action representations corresponding to the presented viewpoint. This is an interesting hypothesis because a plausible alternative possibility is that priming of the cued action is mediated entirely by the identity of the object rather than its current viewpoint. In that case, a rotated object would prime the action typically applied to the upright object, not the action that fits the depicted orientation of the handle.

To ensure that subjects attended to the prime object, in Experiment 1A they were required to name the prime at the end of the trial. Given that this task encourages identification of an object prime at an abstract conceptual level, the possibility that action representations are generated conforming to an object's canonical orientation regardless of its depicted orientation may be favored. In Experiment 1B, we required subjects to report the orientation of the prime (upright or rotated) at the end of each trial, rather than the prime's identity. Attending to orientation could emphasize the canonical form of the object because it serves as the standard for comparison. If, despite task demands that emphasize the canonical form of the object, it is the depicted view that determines the nature of the affordance, then the priming effect clearly would favor the visible image rather than a memory-based representation of how an object typically is grasped.

Our goal in Experiment 1 was to determine whether an action afforded by a handled object is determined by the depicted orientation of the handle or by the orientation in which the object typically is experienced and used. Ruling out the second possibility would imply that the perceived view of an object is an important contributor to the evoked affordance. The question would remain, however, as to whether this affordance depends entirely on the depicted orientation. We have raised the conjecture that action representations automatically evoked by an object, although depending partly on the object's current orientation, may also include higher-level information about the outcome of an action. Thus, an object rotated to an F-commensurate viewpoint may afford a grasp consistent with the orientation of the handle because the outcome of the grasp, following a simple wrist rotation, would result in the object being positioned for normal use. In Experiment 1, all rotated objects were displayed in an F-commensurate orientation. We leave for later the interesting question of whether affordances yielded by objects in this orientation are also elicited by objects presented in an F-incommensurate orientation.

Method

Subjects. Forty-eight undergraduate students at the University of Victoria participated in the experiment for extra credit in a psychology course. Half of these subjects participated in Experiment 1A and the other half were tested in Experiment 1B.

Materials. Two grasp actions associated with handled objects, one with the wrist oriented vertically and one with the wrist oriented horizontally, were selected (see Figure 1). A grayscale digital photograph was taken of a hand shape consistent with each action. These photographs were used to cue target hand actions. Digital photographs of four handled objects, two corresponding to the vertical grasp (beer mug and teapot) and two corresponding to the horizontal grasp (frying pan and cylindrical flashlight) posed in the canonical orientation for use with the right hand, were selected to serve as prime objects. A second digital image for each prime object was created by rotating the canonical image 90° to produce primes for the rotated-prime condition. The rotation was counterclockwise for the beer mug and teapot, but clockwise for the frying pan and flashlight. These rotations resulted in an orientation that we refer to as permitting an F-commensurate grasp. That is, even though the object was not in its canonical orientation, the dominant hand could still be used to grasp it by its handle and with a simple wrist rotation the object would be returned to its canonical orientation, ready for use. When displayed on a computer monitor viewed from 50 cm, the prime objects fit within a square 11.4° high and wide, and the hand cues fit within a square 6.9° high and wide. Mirror image versions of each object and hand cue were created for use with left-handed subjects.

Procedure. Instructions and stimuli were presented on a color monitor controlled by an Apple Mac Pro desktop computer. Subjects were seated with the forefinger of the dominant hand depressing a key mounted on a response box at the start of each trial. A response apparatus containing the elements shown in Figure 1 was placed between the response box and the computer monitor. The response elements were mounted side by side on a curved base and this apparatus was connected to the computer. The relative positions of the elements was counterbalanced across subjects. When cued, the subject lifted the dominant hand from the start position and reached forward to grasp the response element that was associated with the cued grasp. Contact with the response element disrupted a weak electrical field which signaled to the computer the completion of the response action.

A testing session began with 28 training trails in which a hand cue was presented with no prime and the subject responded as quickly as possible by grasping the associated response element. Each of the two actions was cued 14 times in a randomly ordered sequence. Subjects were then shown the four prime objects as the experimenter named each one. The objects were then shown one more time and the subject named each in turn. This phase was intended to ensure that subjects were familiar with the prime objects and could identify them from their photographs.

Eighteen blocks of 16 trials each was then presented, in which an object prime was followed by a hand cue and subjects performed the cued hand action as quickly and as accurately as possible. Each block consisted of a randomly ordered presentation of the 16 combinations of prime object (4), object orientation (2), and hand cue (2). The first two blocks were treated as practice trials, and the remaining 16 blocks (256 trials) were critical trials. Subjects were informed that on some trials, objects would be rotated relative to their normal view, but that this would not alter the task requirements of making the cued hand action. After completing the grasp response, the subject then named the prime object that was shown on that trial (Experiment 1A) or reported whether that object was upright or rotated (Experiment 1B).

Each trial began with a fixation cross at the center of the monitor. The subject then placed the index finger of the dominant hand on the response box key, causing the fixation cross to be erased. After a delay of 500 ms, the object prime was presented alone at the center of the monitor for 300 ms. The prime object was then replaced by the hand cue. The cue remained in view until the subject initiated a response by lifting the response hand from its resting position. After grasping the response element, the subject made his or her response to the prime object (naming or classifying its orientation). The experimenter viewed a separate computer monitor that indicated the target response and prime object on each trial and coded each response by keyboard entry as correct or incorrect after each trial.

Results

Errors in making reach and grasp responses (touching the incorrect response element) and errors when reporting the priming object were rare across all the experiments. A large majority of subjects made no errors in most conditions, so we report only the overall error percent and do not report inferential analyses for the error data. For Experiment 1A, the mean error rate for reach and grasp responses was 0.8%, and for naming the object primes the mean error rate was 0.2%. In Experiment 1B, the mean error rate for reach and grasp responses was 0.6% and the mean error rate in reporting the orientation of the prime object was 0.7%.

Response time analyses were handled as follows. First, we report total response time, measured from the onset of the hand cue to completion of the reach and grasp response. Because this measure includes all aspects of responding, it is the most robust measure we have of the possible influence of the prime object on behavior. The second measure we report is movement time, measured from the moment the subject lifted his or her hand from its resting position on the response box until the grasp response was completed. This latter measure comes closest to assessing behavior controlled primarily by the dorsal stream, which governs the execution of visually guided reach and grasp responses. Although movement time is a component of total response time, we assess the influence of primes on this aspect of responding so that we can more directly measure priming of dorsal stream activity.

In both Experiment 1A and 1B, total response times that exceeded 3,400 ms (1,600 ms for the movement-time analysis) were classified as outliers and were excluded from the analyses. This cutoff was established so that within each of the experiments reported here, less than 0.5% of trials were excluded (Ulrich & Miller, 1994). Trials on which a response error was made were also excluded from the response time analyses. Mean correct total response time was computed for each subject as a function of the orientation of the object prime and congruency between the object prime and target action. Congruency was defined by the orientation of the object's handle and the orientation of the hand when making the cued response. For example, when the beer mug was presented as a prime in its rotated orientation so that it appeared lying on its side, the nominally congruent action was a horizontal closed grasp.

Mean total response time for each condition is shown in Figure 3. The pattern of means suggests that a similar degree of priming was produced regardless of prime orientation, such that congruency between the depicted orientation of an object's handle and the required grasp response led to faster responding. The inferential analyses of the data we report used the Bayesian analysis described by Wagenmakers (2007). This analysis estimates the Bayesian posterior odds (using the Bayesian information criterion, BIC) that the observed data favor one model of the data over another (e.g., a model assuming a particular main effect versus a model that assumes no such effect). Wagenmakers reviews the various ad-

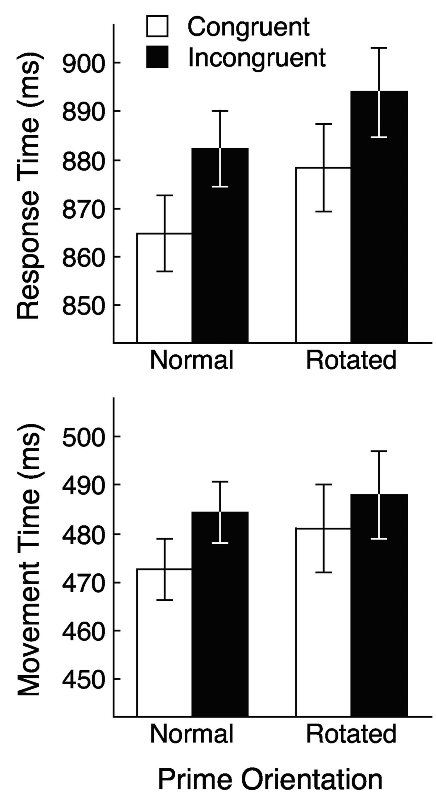

Figure 3. Mean response time in Experiment 1A as a function of prime congruency and prime orientation. The upper panel shows the means for the total response time measure and the lower panel shows the means for the movement time measure. Error Bars represent 95% within-subjects confidence intervals appropriate for evaluating the congruency effect within each orientation condition (Loftus & Masson, 1994; Masson & Loftus, 2003).

vantages of this analysis over standard null hypothesis significance testing (NHST), including the logical problem of drawing inferences about the validity of hypotheses when the probabilities computed by NHST actually refer to the likelihood of data conditional on a hypothesis being true, and the difficulty of interpreting null effects. Posterior odds are computed using sums of squares values from the standard analysis of variance (ANOVA) and are readily converted to conditional probabilities (probability of the model being correct, given the obtained data). We designate the conditional probability for a model as p_{BIC}, which quantifies the evidence in favor of one model over another. The conditional probabilities associated with two competing models are complementary in the sense that they sum to 1.0. Raftery (1995) provides verbal descriptions of the evidentiary strength associated with ranges of values that these probabilities may take on (.50−.75: weak; .75−.95: positive; .95−.99: strong; >.99: very strong). These categories are similar to those proposed by Jeffreys (1961).

The effects of interest in the experiments we report are the main effect of priming and the interaction between priming and orientation of the prime. The possible main effect of prime orientation is of only secondary interest because longer response times with a rotated prime would not be especially surprising. The combined requirements of attending to a briefly presented prime and executing a grasp response would be more demanding when the prime is rotated away from its canonical view than when it is presented in normal orientation. Previous studies have shown that under conditions of divided attention, object identification is more difficult when the target is rotated rather than upright even with repeated exposures (e.g., Murray, 1995). Therefore, the models we test using the Bayesian analysis refer only to the main effect of priming and its interaction with prime orientation.

The first model comparison we conducted for total response time in Experiment 1A contrasted a priming main effect model, in which equal priming across the two object orientations was assumed, with a null effect model. This analysis excluded variability associated with the prime orientation main effect and the interaction between prime orientation and priming, just as would be done when testing the main effect of priming in a standard ANOVA. The Bayesian analysis yield a posterior probability favoring the main effect model of $p_{\mathrm{BIC}} = .989$, which constitutes strong evidence for that model in Raftery's (1995) classification system. The second model comparison contrasted the main effect model with an interaction model in which the priming effect goes in opposite directions for the normal and rotated orientation conditions. This interaction model is the standard interaction contrast for a 2 × 2 design in ANOVA and captures the hypothesis that the action representation evoked by a handled object is determined by the object's canonical orientation, not by its depicted view. This comparison indicated that the data clearly supported the main effect model over the interaction model, $p_{\mathrm{BIC}} = .893$.

The means for the movement time measure are shown in the lower part of Figure 3. The pattern of means suggests only a very small effect of priming. The same two model comparisons were computed for these data as were applied to the total response time data. The evidence only weakly supported the main effect model over the null effect model, $p_{\mathrm{BIC}} = .689$. Similarly, there was weak support for the main effect model over the interaction model, $p_{\mathrm{BIC}} = .719$.

The results for Experiment 1B are shown in Figure 4. The total response time and movement time measures revealed a pattern similar to that seen in Experiment 1A. The Bayesian model comparisons used in Experiment 1A were also applied to these data. For the total response time measure, the priming main effect model was strongly supported over the null effect model, $p_{\mathrm{BIC}} = .986$, and it was also clearly supported over the interaction model, $p_{\mathrm{BIC}} = .931$. In the movement time data, the main effect model for priming was very strongly preferred over the null effect model, $p_{\mathrm{BIC}} = .998$, and it was also strongly preferred relative to the interaction model, $p_{\mathrm{BIC}} = .960$.

Discussion

Clear effects of prime congruency were obtained when the prime object was in its canonical orientation. A cued action that conformed to the affordance of the object was produced more rapidly than an action that was incongruent with that affordance. Interestingly, this congruency effect carried over into movement time, indicating that the transport phase of the reach and grasp response was affected by the prime. Of additional interest is the fact that when the prime was rotated 90° away from its canonical orientation, priming was determined by the affordance generated

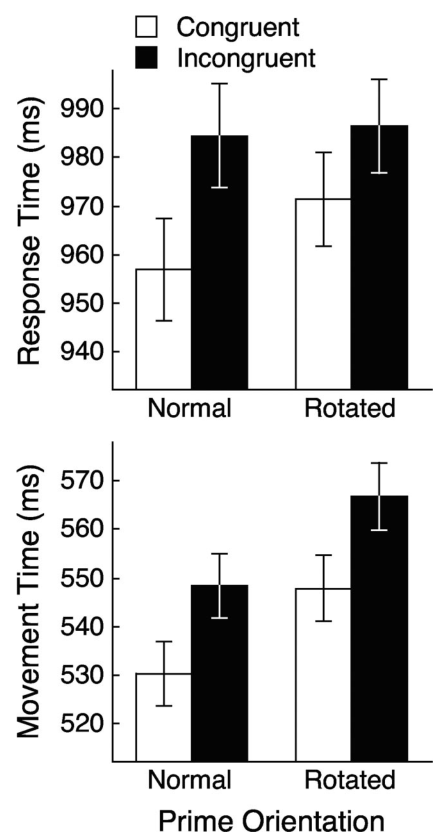

Figure 4. Mean response time in Experiment 1B as a function of prime congruency and prime orientation. The upper panel shows the means for the total response time measure and the lower panel shows the means for the movement time measure. Error Bars represent 95% within-subjects confidence intervals appropriate for evaluating the congruency effect within each orientation condition.

by the rotated form rather than the canonical form. A beer mug, for example, rotated by 90° affords a horizontal grasp if the evoked action representation is based on the literal view of the object. The priming effect for rotated objects shows that indeed the affordance yielded by such objects is determined by the depicted view, not by memory for the object's canonical orientation.

The evidence we have obtained for a congruency effect in Experiment 1 indicates that the prime evokes action representations that are not simply based on the identity of the object without regard to its displayed orientation. Because sensitivity of motor representations to object orientation is a hallmark of the dorsal stream, we take this initial result as encouraging evidence for the possibility that dorsal stream mechanisms play a role in the priming effects we have observed. The fact that the movement phase of the reach and grasp was affected by congruency offers a further indication that the representation responsible for priming influences on-line processing of action. Exactly how the movement is modulated by the prime would require a detailed kinematic analysis, a topic for future investigation. Nevertheless, the present results appear consistent with the possibility that the priming effects we have established are at least partly determined by dorsal stream mechanisms responsible for the programming and execution of a reach and grasp response.

Attending to the orientation of the prime in Experiment 1B did not substantially alter the pattern of results established in Experiment 1A. Congruency effects were robust when the object was presented in its canonical orientation and when the object was rotated 90°. These results indicate that the evoked action representation depended on the literal view of the prime. A vertically oriented handle invites a vertical grasp, whereas a horizontal handle dictates a horizontally oriented grasp. Therefore, higher level influences based, for example, on the proper function of the object (Millikan, 1984), seem to play no role in the priming of reach and grasp responses. We will present evidence that challenges this possible inference at a later point by examining the influence of commensurability on the evocation of a motor affordance. For now, however, we turn to the question of the durability of the priming effect seen in Experiment 1 and we show that this effect vanishes when a 1 s interval is placed between the prime and the cued action, consistent with the claim by Jax and Rosenbaum (2009) that dorsally driven priming effects endure for only a short time.

Experiment 2

A fundamental issue underlying the visuomotor priming effects demonstrated in Experiment 1 concerns the role of the dorsal as opposed to the ventral visual stream. One influential view is that the dorsal stream programs reach and grasp actions entirely on the basis of retinal input, without regard to higher level representations based on object identity. In addition, the dorsal system makes no reference to motor representations computed prior to the current action; the dorsal stream, to epitomize this view, has no memory (Milner & Goodale, 2008). Against this view is some recent evidence indicating that dorsally controlled actions can indeed be influenced by prior motor events, but only within a narrow time window of less than one second (Jax & Rosenbaum, 2009). If the priming effect of a handled object is driven by the dorsal pathway, then we should expect this effect to be similarly short-lived. We test this possibility in Experiment 2.

Method

A sample of 24 subjects was drawn from the same pool as in Experiment 1. The materials and procedure were identical to those of Experiment 1A, except that on each trial involving a reach and grasp response there was a blank interval of 1,000 ms between erasure of the object prime (which was visible for 300 ms) and onset of the hand cue that indicated which response was required.

Results

The mean error rates in making reach and grasp responses and in reporting the identity of the object prime were 0.3% and 0.2%, respectively. As in Experiment 1, no errors were observed for most subjects so we do not report inferential statistics for these data.

Reach and grasp response times were analyzed as in Experiment 1. Mean total response time and mean movement time are shown in Figure 5. The pattern of means indicates that no priming effect was found in either measure, regardless of prime orientation. A Bayesian comparison of a model that included a main effect of priming (averaged across prime orientation) and a null effect

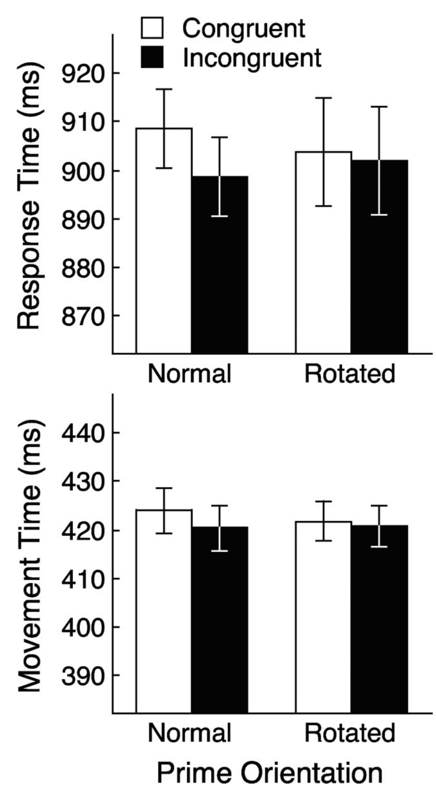

Figure 5. Mean response time in Experiment 2 as a function of prime congruency and prime orientation. The upper panel shows the means for the total response time measure and the lower panel shows the means for the movement time measure. Error Bars represent 95% within-subjects confidence intervals appropriate for evaluating the congruency effect within each orientation condition.

model indicated that for the total response time measure, the null effect model was preferred, $p_{BIC} = .739$. A similar outcome was obtained when these models were compared using the movement time data, whereby the null effect model was again preferred, $p_{BIC} = .735$. Because these model comparisons favored the null effect model over the main effect model, we did not conduct Bayesian contrasts of the main effect model and the interaction model. Although the results of the Bayesian analyses provided only weak support for the null effect model, we note that the means shown in Figure 5 indicate that whatever small differences were produced by the congruency manipulation went in the direction opposite to what was seen in Experiment 1.

To provide more convincing evidence for the impact of introducing the 1 s delay between the prime and action cue, we compared the size of the priming effect observed in Experiment 1 to the effect found in Experiment 2, collapsing across prime orientation. A Bayesian comparison of a model including an interaction between priming effect and experiment against a null effect model indicated that for the total response time measure, the interaction model was very strongly preferred, $p_{BIC} = .992$. Much the same result was found when the movement time measure was used for this comparison, $p_{BIC} = .987$. Thus, the priming effect found in Experiment 1 was clearly reduced or eliminated when a delay was inserted after the prime object.

Discussion

The priming effects on a reach and grasp action documented in Experiment 1 are extremely short-lived. This evidence could explain previous failures to demonstrate visuomotor priming of visually driven grasp actions (Cant, Westwood, Valyear, & Goodale, 2005; Garofeanu, Króliczak, Goodale, & Humphrey, 2004). In other words, it is entirely possible that visuomotor priming driven by the dorsal stream does occur, but that the influence of the prime object endures for less than one second. If this assumption is correct, then it follows that previous claims of dorsally driven actions as encapsulated (insulated from previous events or knowledge) are incorrect. We infer that the priming effects we have established here are the result of the short-lived influence of an evoked motor representation on the programming and execution of a reach and grasp response. We will consider the implications of this claim in more detail after further examining the kind of knowledge that underlies the priming effects we have reported.

Experiment 3

We have seen that a handled object like a beer mug rotated 90° counterclockwise from the canonical orientation evokes the affordance of a closed grasp with the palm facing downward. At face value, this result might be taken to imply that it is the pure physical affordance of the handle (Symes et al., 2007) that is responsible for priming. That is, the representation of the grasp posture evoked by the object is based only on the shape and orientation of the handle. We have suggested that this assumption is questionable, however, given convincing evidence that actions are habitually represented in terms of anticipated outcomes, and that such action-outcome associations may have the same influence on performance as elementary stimulus-response mapping rules known to play a fundamental role in mental set (Kühn, Seurinck, Fias, & Waszak, 2010; Massen & Prinz, 2007).

The fact that intended actions—and presumably, also the motor affordances automatically associated with an object—include a perceptual representation of the expected outcome, leads us to take into account the properties of the whole object in considering the effects of changes in orientation. A right-handed grasp directed to the handle of an object like a beer mug on its side will have a different outcome, depending on whether the open end of the mug is facing left or right. If the opening is facing left, a right handed grasp is F-commensurate, because the outcome of the grasp is the object in its canonical upright orientation after a simple clockwise wrist rotation. A right-facing beer mug on its side entails that the same grasp applied to the handle is F-incommensurate, because the outcome would be an inverted beer mug, unless the wrist and shoulder are rotated in an awkward counterclockwise direction to ensure the mug ends in a position commensurate with its proper function (with the opening of the barrel facing up). Actions are planned to take into account the "end-state comfort" of the limb (Rosenbaum et al., 1990). We assume that end-state comfort plays a similar role in the evocation of a motor affordance just as it does in the planning of an intended action. A grasp applied to a handled object in certain orientations would be F-incommensurate because the outcome of that grasp would require an awkward and uncomfortable position of the limb to use the object.

In the final experiment, we examine whether F-commensurability plays a role in the affordance evoked by a handled object. Evidence that commensurability matters implies that the action representation is not simply determined by the physical affordance of the handle. Rather, motor affordances depend also on the outcome of an action in relation to the known functional properties of the object.

Method

Twenty-four subjects drawn from the same population as in the earlier experiments were tested. The materials and procedure were the same as in Experiment 1A, with one exception. Images of rotated prime objects were created by rotating each object 90° from its canonical view so that the resulting orientation presented to the dominant hand a grip that is F-incommensurate. For example, the image of the beer mug was mirror reflected, then rotated 90° clockwise for right-handed subjects (see Figure 6). When rotated in this way, application of a horizontal closed grasp using

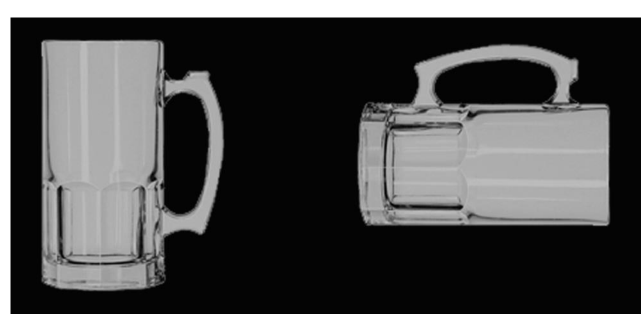

Figure 6. An example prime object from Experiment 3 shown in normal and rotated orientation, where rotation was to an F-incommensurate position for a right-handed subject.

the right hand would conform to the handle's orientation, but if actually applied to the object in the viewed orientation it would result in a grip that would not allow the object to be used normally (i.e., the grip would result in holding the beer mug upside down after a normal wrist rotation).

Results

The mean error rates in making reach and grasp responses and in reporting the prime object at the end of each trial were 0.4% and 0.3%, respectively. No inferential tests of these measures are reported because of floor effects.

Reach and grasp response times were analyzed as in the earlier experiments and the means for total response time and for movement time are shown in Figure 7. Unlike the pattern of means in Experiment 1, here in the total response time measure there is a strong indication the priming was found only with normally oriented objects, but not with objects rotated to an incommensurate view. Our primary interest in this experiment was to test a model in which priming would be obtained only for normally oriented objects as opposed to a model that assumed priming would be equal across both prime orientations. Therefore, we computed a Bayesian contrast between a main effect model equivalent to that tested in the earlier experiments and an interaction model in which it was assumed that no priming effect would occur for rotated primes. This model is a special case of a two-way interaction in which it is assumed that three of the four conditions (here, congruent and incongruent rotated primes along with incongruent normal primes) would generate equal performance, and that the fourth condition (congruent normal primes) would yield shorter response times than the other three conditions combined. When these models were fit to the total response time data, the Bayesian analysis indicated that the interaction model was strongly preferred, $p_{\mathrm{BIC}} = .939$. The comparison of these models based on movement time data provided very weak evidence in favor of the interaction model, $p_{\mathrm{BIC}} = .568$, because only a relatively small priming effect with normally oriented primes was found in movement time.

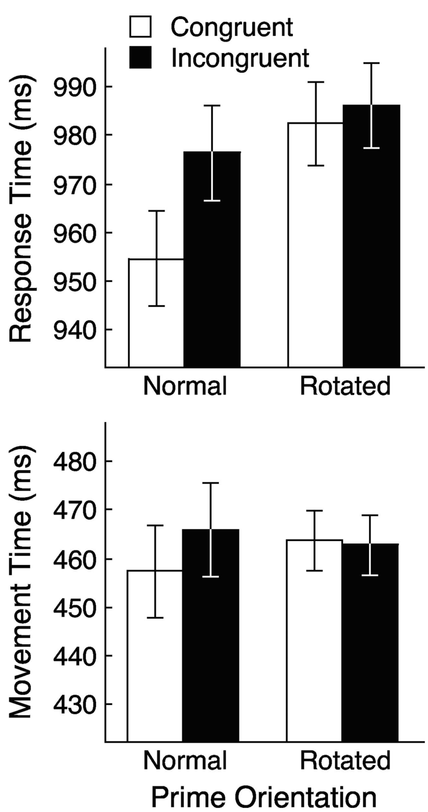

Figure 7. Mean response time in Experiment 3 as a function of prime congruency and prime orientation. The upper panel shows the means for the total response time measure and the lower panel shows the means for the movement time measure. Error Bars represent 95% within-subjects confidence intervals appropriate for evaluating the congruency effect within each orientation condition.

Discussion

We found striking evidence that the motor representation automatically evoked by the image of a handled object is not based solely on the orientation of the handle, but includes higher-level information concerning the end-state of the object in relation to the actor. A beer mug on its side in an F-incommensurate orientation yields no corresponding affordance, whereas the same rotated object in an F-commensurate orientation evokes a robust priming effect. This outcome converges with an experiment by Creem and Proffitt (2001) showing that subjects pick up a handled object presented in a non-canonical orientation using a grip that is commensurate with its function, even though the starting point of the hand action requires an awkward posture. We infer that objects like a beer mug are inherently perceived in terms of their use unless additional context dictates an alternative grasp possibility. For example, if the goal is to place a beer mug on a drying rack, then the final state of the object should be inverted and the grasp posture should reflect this goal. We note that an alternative explanation for the sensitivity to commensurability is that subjects simply prefer the canonical view of an object as the more familiar orientation. An action applied to a rotated object may then be influenced not by the function but by prior experience based on typical views of an object. Against this explanation, is the fact that in Experiment 1, congruency effects were equivalent for upright and rotated objects. If the affordance of a handled object is partly dependent on the canonical view, then we should expect a stronger congruency effect for objects in the upright orientation. The results of Experiment 1 speak clearly against this expectation. Instead, the affordance is determined by the depicted view in relation to the functional outcome of the action applied to the object.

Our results further clarify the nature of affordances automatically evoked by an object by showing that although action representations include information about object orientation, an additional constraint on the evocation of an affordance is the projected end-state of the object, given the intended hand posture (see also Rosenbaum et al., 2006). The failure to obtain priming for objects in certain orientations establishes that the conventional function of an object serves as a tacit context supplied by the actor. The projected end-state contributes to automatic priming in the sense that priming effects are modulated by the function of the object, and a grasp posture that is incommensurate with the function is apparently not automatically evoked.

The mechanism by which F-commensurability influences the evocation of an affordance is of great interest. A number of possibilities can be conjectured in the light of previous theoretical work. According to the notion of competing affordances (Cisek, 2007), an object initially evokes multiple action representations and context serves to drive the activation of the relevant affordance to threshold, while the activation strength of irrelevant affordances diminishes. On this account, an F-incommensurate grasp might be briefly evoked and quickly fade away, given the modulating influence of context tacitly applied by the actor. An alternative possibility is that the F-incommensurate grasp is actively prevented by a suppression mechanism analogous to the kind of suppression observed in spatial correspondence effects induced by objects, like an arrow, that orient the observer to one or the other side of space (Eimer & Schlaghecken, 1998). A careful examination of the temporal dynamics of the priming effects we have reported may yield insight into the nature of the process that eliminates priming by objects in an F-incommensurate orientation.

General Discussion

Handled objects automatically evoke action representations under certain task conditions, a phenomenon documented both in behavioral studies and in a substantial number of neuroimaging reports. We inquired into the nature of these representations, noting that definite limitations apply to a widely used methodology based on the differences in speeded key-press responses to handled objects oriented in such a way as to favor a left- or right-handed affordance (e.g., Phillips & Ward, 2002; Tucker & Ellis, 1998; Vainio et al., 2007). These studies show only that responses are faster when an effector (a hand, a foot, or a finger) is aligned with the handle, and so do not yield information on the central component of the evoked affordance, namely, the reach and grasp action associated with the object.

On one view, the reach and grasp component of an action representation is based on the affordance of the object in its current orientation. A frying pan with its handle oriented vertically invites a closed grasp with the wrist oriented vertically and the thumb pointing up. The notion of a perceived affordance (Norman, 1999), however, includes contributions from the prior history of an object as well as its current visible properties. Thus, our interest was on the combined influence of these two sources of information when a handled object, acting as a prime, alters a cued reach and grasp response. In Experiments 1 and 2, we established congruency effects demonstrating that an object in its canonical orientation evokes a reach and grasp action consistent with its affordance. We also wished to determine how congruency effects vary given a 90° rotation of an object. If the handle alone is responsible for evoking the reach and grasp affordance, then rotating the object should yield a corresponding rotation of the wrist so that the orientation of the hand now matches the object's orientation. An object like a frying pan, rotated so that its handle points downward now affords a vertically oriented closed grasp response. If the visible form of the object alone, rather than the canonical form, evokes the hand action representation, then we should expect the congruency effect to be determined by the action that fits the literal view.

The logic of this argument, however, does not take into account the functional properties of the object nor how these properties are altered once the object is rotated from its normal upright position. We argue that affordances automatically evoked by an object are not defined merely in relation to the hand action consistent with the current viewpoint of the object, but include information about the outcome of the action in relation to the object's conventional function. Consider, for example, an upright beer mug with its handle facing to the right. Now imagine the object is rotated 90° counterclockwise (see Figure 2). A right-handed action directed toward the handle will result in the object being grasped in such a way as to be ultimately commensurate with its conventional function because the hand, after grasping the object, can easily rotate to restore the object to its canonical orientation. This is not the case if the beer mug has been rotated as shown in Figure 6. Now a right-handed action directed toward the handle will not result in a grasp that readily enables the object's function. We denoted a reach and grasp action on a rotated object as F-commensurate if that action, once carried out, restores the object's typical orientation (consistent with its proper function) after a simple wrist rotation. An F-incommensurate action applied to the handle will result in an orientation that violates the object's function (i.e., holding the beer mug upside down).

If the affordance evoked by an object includes not only information about the orientation of its handle, but also the commensurability of the grasp action, then only particular rotations of the object from its normal position (those yielding F-commensurate grasps) should automatically evoke an action representation. We found striking evidence consistent with this argument in our experiments. For objects oriented to afford F-commensurate grasps, congruency effects indicated that the action representation afforded by the object matched the perceived orientation of the handle rather than the canonical form (Experiment 1). For objects affording grasps that were F-incommensurate, no congruency effect was found (Experiment 3).

These results converge with neuropsychological evidence. For example, in a case of "anarchic hand" syndrome, the patient experiences involuntary actions directed toward objects. Riddoch, Edwards, Humphreys, West, and Heafield (1998) instructed a patient to pick up a coffee cup positioned left or right of center, and the location of the object cued which hand to use in responding (e.g., left hand when the cup was left of center). The handle of the cup was aligned or misaligned with the response hand. Involuntary reach and grasp responses to the handle interfered with the cued action. For example, a cup positioned on the left with its handle oriented to the right yielded intrusion errors from the right hand. Moreover, intrusion errors were greater for upright cups (which were F-commensurate) than for inverted cups (F-incommensurate). Additional evidence (Riddoch, Humphreys, Edwards, Baker, & Willson, 2003) comes from cases of spatial neglect in which pairs of objects configured in F-commensurate relationships (e.g., a corkscrew poised over the top of a wine bottle) were more likely to be reported together than the same object pairs positioned in an F-incommensurate relationship (e.g., a corkscrew positioned below a wine bottle). This neuropsychological evidence, combined with our priming results, indicates that action representations automatically evoked by handled objects are not simply based on the orientation of the handle, but include higher level information about the function of the object in relation to the action being carried out.

It is of interest to consider in more detail how F-commensurability modulates the evocation of motor affordances, given one or both hands as possible response options. Massen and Prinz (2007) and Herwig and Massen (2009) provided evidence that tool-use actions are represented not in terms of an abstract internal model of the possible behaviors of a tool (Johnson-Frey, 2003), but in terms of particular target-to-movement mappings that capture the relationship between a targeted physical outcome (e.g. touching a particular object with a lever) and a specific movement of the limb applied to the tool. Selecting a target-movement mapping for a tool or utensil depends on the goal state of the actor, the orientation of the object and the effector chosen to carry out the movement. If both hands are potentially available to grasp a handled object, we can think of F-commensurability as being a determining factor in the resolution of competition between the two hands. A frying pan with the handle oriented to the left is F-incommensurate with a right-handed inverted closed grasp, but F-commensurate with the same grasp applied by the left hand. If both hands are initially recruited during the evocation of the grasp representation associated with a frying pan (Bub & Masson, 2010), F-commensurability may play a crucial role in favoring the activation of one hand (in this case, the left) over the other. Assuming that we are routinely faced with such competition between effectors in our daily interactions with handled objects, the speed and effortlessness with which an F-commensurate grasp is selected—the typical outcome of an action applied to a handled object (Creem & Proffitt, 2001)—suggest a powerful control mechanism that is sensitive to the effect of a left or right-handed grasp posture.

In the case of only one hand as the possible choice for grasping (and therefore no response competition between hands), might the nonparticipating hand nonetheless be recruited to yield a covert F-commensurate grasp representation when the action generated by the responding hand is F-incommensurate? For example, in our priming task, would a frying pan with the handle oriented towards the left, evoke a left-handed grasp representation even when the task is always to respond to the cue with the right hand? We view this as an unlikely possibility, given evidence from single-cell recording in monkeys on the simultaneous planning of multiple potential actions (Cisek & Kalaska, 2002). Neural activity associated with several different affordances is seen only if these alternatives are simultaneously available as potential responses; the neural activation for the irrelevant movement quickly dissipates as soon as the response can be rejected as an option.

We turn now to consider whether the priming effects we have documented are informative about the functional division between the ventral and dorsal visual pathways in goal-directed reach and grasp responses. According to Goodale and Milner (2004), the spatial coordinates and motor program for grasping an object are determined by the dorsal stream immediately before the movement is initiated, and are not stored in memory. A strong prediction derived from this claim is that dorsally-driven reach and grasp actions should not be influenced by the prior evocation of motor representations, and therefore should not be susceptible to visuomotor priming (Goodale, Cant, & Króliczak, 2006).

Evidence consistent with this view of the dorsal system has been put forward by Cant et al. (2005) and Garofeanu et al. (2004). They demonstrated that neither object orientation, nor shape, nor identity, acting as priming events, have any influence on a visually guided reach and grasp response. These experiments however, can be called into question given the relatively long delays they all introduced between prime and target (this ranges from over a second to minutes). The visuomotor priming effects we have documented in Experiment 1 are surprisingly short-lived, given that they are no longer seen when the interval between the prime and the target is increased from 300 ms to 1,000 ms (Experiment 2). Interestingly, the brief duration of the motor representations evoked by the prime is quite consistent with a report by Jax and Rosenbaum (2009) showing that a visually guided manual obstacle avoidance task is susceptible to the presence or absence of an obstacle on the previous trial but only if the intertrial interval is sufficiently brief. Their hand-path priming effect was virtually eliminated if 1,000 ms was interposed between trials. Jax and Rosenbaum speculated that the brevity of the dorsal system's capacity to retain information is related to the statistical properties of movement: The shorter the delay between successive movements, the more likely the movements will have features in common.

There is good reason to assume that the methodology we have developed to yield priming effects induced by a handled object on a visually guided reach and grasp action must include the contribution of both ventral and dorsal visual pathways. The task of viewing and naming manipulable man-made objects is known to activate the dorsal stream, including the left posterior parietal cortex (Chao & Martin, 2000; Martin & Chao, 2001; see Creem-Regehr, 2009, for a review). Recognition and imitation of a visually depicted hand action also activates parietal regions (Buccino et al., 2004; Shmuelof & Zohary, 2005). In order for dorsally-driven priming to occur, of course, it must be the case that the visually guided action (in the present context, the cued reach and grasp action applied to one of two response elements) can be influenced by a previously evoked motor representation (in this case, the motor representation evoked by the handled object). It cannot be, we infer, that the dorsal stream has no memory for prior actions, as Goodale and colleagues would argue. Indeed, in a recent study, Króliczak, McAdam, Quinlan, and Culham, (2008) found that the dorsal pathway (including the bilateral anterior intraparietal sulcus, the intraparietal sulcus, the left supramarginal gyrus, and the right mid superior parietal lobe) showed clear adaptation to a repeated grasp of the same type applied to different objects. These authors suggest, on the basis of their results, that the claim that dorsally-driven visuomotor priming does not occur should be revisited. Our results can be taken as behavioral evidence confirming the idea that visually guided reach and grasp actions are susceptible to the influence of previously evoked motor representations under the right task conditions.

Finally, we consider the potent influence of F-commensurability on the perceived affordance of a handled object in the light of the different computational roles attributed to the dorsal and ventral pathways in the programming and execution of a grasp action. Neuropsychological evidence indicates that the dorsal system on its own, without the proper input from the ventral stream, cannot make use of higher-level constraints on the programming of an action, including such constraints as the end-state comfort of a grasp (Dijkerman, McIntosh, Schindler, Nijboer, & Milner, 2009) and most likely, its F-commensurability. The recent discovery of strong direct neural connections between the ventral and the dorsal pathways (see

Grafton, 2010, for a review), however, raises questions about the possible dynamic interplay between dorsal and ventral streams when normal subjects engage in reach and grasp actions. In a recent study, Cohen, Cross, Tunik, Grafton, and Culham (2009) concluded that ventral-stream representations affect the execution of a grasp only when movement is delayed and the object is no longer in view, so that the action itself is based on memory rather than an immediate percept. Cohen et al. applied transcranial magnetic stimulation (TMS) to either the lateral occipital cortex (LO; ventral stream) or to the anterior-inferior parietal sulcus (aIPS; dorsal stream), time-locked to the onset of hand movement. TMS affected the kinematics of the reach and grasp responses when applied to both the aIPS or the LO regions, but only in the delayed movement condition. By contrast, TMS to LO had no effect on movement kinematics in the immediate percept condition, although it did, of course, have an influence when applied to aIPS. Cohen et al. inferred that the ventral stream has no influence on the execution of reach and grasp actions when movements are guided by the visual percept of the object.

Our motor task is not based on memory; subjects viewed the target response element continuously as they executed a cued reach and grasp action. Nevertheless, we show clearly that this dorsally driven response is influenced not only by a depicted view of a handled object, but also by an understanding of the commensurability of the cued action with the function of the object. Of interest, this effect influenced the transport phase of the movement after lift-off, implying that the object primed more than just the planning of the action, but also its execution. Furthermore, the fact that the priming effects were limited to a very short temporal window (Experiment 2) lends additional support to claim that these effects are due to the dynamic interaction of a dorsal stream modulated by input from the ventral stream.

We have clear evidence, then, that a visually guided action can be influenced by higher level object properties. It is already known that one type of higher level information, object identity, does not influence the dorsal stream. For example, Valyear, Culham, Sharif, Westwood, and Goodale (2006) used an fMRI adaptation procedure to show that a region in the dorsal stream is sensitive to changes in object orientation but not to changes in object identity. The reverse was found in the ventral stream: sensitivity to change in object identity but no sensitivity to change in orientation. Our results show a more subtle influence of the properties of an object on the planning and execution of a visually guided reach and grasp action. The motor representation automatically afforded by a handled object is determined not just by the orientation of the handle, but ultimately by the perceived outcome of the action in relation to the object's function. It is not possible to confirm the modulation of dorsal stream activity by F-commensurability using fMRI at this stage. A change in orientation will always induce dorsal stream activity even for an F-incommensurate position. We are not saying that no actions are evoked by an object in such a position, only that a particular grasp action afforded by the commensurate view will not be evoked by the same object presented in the incommensurate view, and that such a modulation of afforded actions depends on an understanding of object function.

A more promising direction would be to examine how the kinematics of a reach and grasp action are altered by TMS applied to ventral and dorsal regions during the execution of an action that is F-commensurate or F-incommensurate. We note that even when the instruction is to pick up and move an object to a new location, subjects grasp a handled object using an F-commensurate posture (Creem & Proffitt, 2001). If the subject is instead required by instruction to employ an F-incommensurate grasp, then we conjecture that the commensurate grasp will continue to be evoked. Competition between the two grasps should be manifest in the temporal dynamics of the required action. We propose that the kinematics of a target grasp (e.g., a horizontal closed grasp) made to a handled object will differ depending on whether the object is in an F-commensurate or an F-incommensurate orientation, with respect to the grasp. TMS applied to the ventral stream should disrupt the higher level representations on which the effects of commensurability depend, thereby abolishing the modulation of the reach and grasp kinematics.

References

Bub, D. N., & Masson, M. E. J. (2010). Grasping beer mugs: On the dynamics of alignment effects induced by handled objects. *Journal of Experimental Psychology: Human Perception and Performance, 36,* 341–358.

Buccino, G., Vogt, S., Ritzl, A., Fink, G. R., Zilles, K., Freund, H.-J., & Rizzolatti, G. (2004). Neural circuits underlying imitation learning of hand actions: An event-related fMRI study. *Neuron, 42,* 323–334.

Cant, J. S., Westwood, D. A., Valyear, K. F., & Goodale, M. A. (2005). No evidence for visuomotor priming in a visually guided action task. *Neuropsychologia, 43,* 216–226.

Chao, L. L., & Martin, A. (2000). Representation of manipulable man-made objects in the dorsal stream. *Neuroimage, 12,* 478–484.

Cho, D. (T.), & Proctor, R. W. (in press). The object-based Simon effect: Grasping affordance or relative location of the graspable part? *Journal of Experimental Psychology: Human Perception and Performance.*

Cisek, P. (2007). Cortical mechanisms of action selection: The affordance competition hypothesis. *Philosophical Transactions of the Royal Society B, 362,* 1585–1599.

Cisek, P., Crammond, D. J., & Kalaska, J. F. (2003). Neural activity in primary motor and dorsal premotor cortex in reaching tasks with the contralateral versus ipsilateral arm. *Journal of Neurophysiology, 89,* 922–942.

Cisek, P., & Kalaska, J. F. (2002). Simultaneous encoding of multiple potential reach directions in dorsal premotor cortex. *Journal of Neurophysiology, 87,* 1149–1154.

Cohen, N. R., Cross, E. S., Tunik, E., Grafton, S. T., & Culham, J. C. (2009). Ventral and dorsal stream contributions to the online control of immediate and delayed grasping: A TMS approach. *Neuropsychologia, 47,* 1553–1562.

Creem, S. H., & Proffitt, D. R. (2001). Grasping objects by their handles: A necessary interaction between cognition and action. *Journal of Experimental Psychology: Human Perception and Performance, 27,* 218–228.

Creem-Regehr, S. H. (2009). Sensory-motor and cognitive functions of the human posterior parietal cortex involved in manual actions. *Neurobiology of Learning and Memory, 91,* 166–171.

Dijkerman, H. C., McIntosh, R. D., Schindler, I., Nijboer, T. C. W., & Milner, A. D. (2009). Choosing between alternative wrist postures: Action planning needs perception. *Neuropsychologia, 47,* 1476–1482.

Eimer, M., & Schlaghecken, F. (1998). Effects of masked stimuli on motor activation: Behavioral and electrophysiological evidence. *Journal of Experimental Psychology: Human Perception and Performance, 24,* 1737–1747.

Ellis, R., Tucker, M., Symes, E., & Vainio, L. (2007). Does selecting one visual object from several require inhibition of the actions associated with nonselected objects? *Journal of Experimental Psychology: Human Perception and Performance, 33,* 670–691.

Garofeanu, C., Króliczak, G., Goodale, M. A., & Humphrey, G. K. (2004). Naming and grasping common objects: A priming study. *Experimental Brain Research, 159,* 55–64.

Gibson, J. J. (1986). *The ecological approach to visual perception.* Hillsdale, NJ: Erlbaum.

Girardi, G., Lindemann, O., & Bekkering, H. (2010). Context effects on the processing of action-relevant object features. *Journal of Experimental Psychology: Human Perception and Performance, 36,* 330–340.

Goodale, M. A., Cant, J. S., & Króliczak, G. (2006). Grasping the past and present: When does visuomotor priming occur? In H. Ögmen & B. G. Breitmeyer (Eds.), *The first half second: The microgenesis and temporal dynamics of unconscious and conscious visual processes.* Cambridge, MA: MIT Press.

Goodale, M. A., & Milner, A. D. (1992). Separate visual pathways for perception and action. *Trends in Neuroscience, 15,* 20–25.

Goodale, M. A., & Milner, A. D. (2004). *Sight unseen: An exploration of conscious and unconscious vision.* New York: Oxford University Press.

Grafton, S. T. (2010). The cognitive neuroscience of prehension: Recent developments. *Experimental Brain Research, 204,* 475–491.

Handy, T. C., Grafton, S. T., Shroff, N. M., Ketay, S., & Gazzaniga, M. S. (2003). Graspable objects grab attention when the potential for action is recognized. *Nature Neuroscience, 6,* 421–427.

Herwig, A., & Massen, C. (2009). Action planning with two-handed tools. *Psychological Research, 73,* 727–740.

Hommel, B. (1993). Inverting the Simon effect by intention. *Psychological Research, 55,* 270–279.

Jax, S. A., & Rosenbaum, D. A. (2009). Hand path priming in manual obstacle avoidance: Rapid decay of dorsal stream information. *Neuropsychologia, 47,* 1573–1577.

Jeffreys, H. (1961). *Theory of probability.* Oxford: Oxford University Press.

Johnson-Frey, S. H. (2003). Cortical representations of human tool use. In S. H. Johnson-Frey (Ed.), *Taking action: Cognitive neuroscience perspectives on intentional acts* (pp. 185–217). Cambridge, MA: MIT Press.

Kellenbach, M. L., Brett, M., & Patterson, K. (2003). Actions speak louder than functions: The importance of manipulability and action in tool representation. *Journal of Cognitive Neuroscience, 15,* 30–46.

Kiesel, A., & Hoffmann, J. (2004). Variable action effects: Response control by context-specific effect anticipations. *Psychological Research, 68,* 155–162.

Króliczak, G., McAdam, T. D., Quinlan, D. J., & Culham, J. C. (2008). The human dorsal stream adapts to real actions and 3D shape processing: A functional magnetic resonance imaging study. *Journal of Neurophysiology, 100,* 2627–2639.

Kühn, S., Seurinck, R., Fias, W., & Waszak, F. (2010). The internal anticipation of sensory action effects: When action induces FFA and PPA activity. *Frontiers in Human Neuroscience, 4,* 54. doi:10.3389/fnhum.2010.00054

Loftus, G. R., & Masson, M. E. J. (1994). Using confidence intervals in within-subject designs. *Psychonomic Bulletin & Review, 1,* 476–490.

Martin, A., & Chao, L. L. (2001). Semantic memory and the brain: Structure and processes. *Current Opinion in Neurobiology, 11,* 194–201.

Massen, C., & Prinz, W. (2007). Programming tool-use actions. *Journal of Experimental Psychology: Human Perception and Performance, 33,* 692–704.

Masson, M. E. J., & Loftus, G. R. (2003). Using confidence intervals for graphically based data interpretation. *Canadian Journal of Experimental Psychology, 57,* 203–220.

McGrenere, J., & Ho, W. (2000). Affordances: Clarifying and evolving a concept. *Proceedings of the Graphics Interface 2000 Conference,* 179–186.

Millikan, R. (1984). *Language and other abstract objects.* Cambridge, MA: MIT Press.

Milner, A. D., & Goodale, M. A. (2006). *The visual brain in action.* New York: Oxford University Press.

Milner, A. D., & Goodale, M. A. (2008). Two visual systems re-viewed. *Neuropsychologia, 46,* 774–785.

Murray, J. E. (1995). The role of attention in the shift from orientation-dependent to orientation-invariant identification of disoriented objects. *Memory & Cognition, 23,* 49–58.

Norman, D. A. (1999). Affordances, constraints, and conceptual models. *Interactions, 6,* 38–42.

Pellicano, A., Iani, C., Borghi, A. M., Rubichi, S., & Nicoletti, R. (in press). Simon-like and functional affordance effects with tools: The effects of object perceptual discrimination and object action state. *Quarterly Journal of Experimental Psychology.*

Phillips, J. C., & Ward, R. (2002). S-R correspondence effects of irrelevant visual affordance: Time course and specificity of response activation. *Visual Cognition, 9,* 540–558.

Raftery, A. E. (1995). Bayesian model selection in social research. *Sociological Methodology, 25,* 111–163.

Riddoch, M. J., Edwards, M. G., Humphreys, G. W., West, R., & Heafield, T. (1998). Visual affordances direct action: Neuropsychological evidence from manual interference. *Cognitive Neuropsychology, 15,* 645–683.

Riddoch, M. J., Humphreys, G. W., Edwards, S., Baker, T., & Willson, K. (2003). Seeing the action: Neuropsychological evidence for action-based effects on object selection. *Nature Neuroscience, 6,* 82–89.

Rosenbaum, D. A., Cohen, R. G., Meulenbroek, R. G., & Vaughn, J. (2006). Plans for grasping objects. In M. Latash & F. Lestienne (Eds.), *Motor control and learning over the lifespan* (pp. 9–25). New York: Springer.

Rosenbaum, D. A., Marchak, F., Barnes, H. J., Vaughan, J., Slotta, J., & Jorgensen, M. (1990). Constraints for action selection: Overhand versus underhand grips. In M. Jeannerod (Ed.), *Attention and performance XIII* (pp. 321–342). Hillsdale, NJ: Erlbaum.

Shen, L., & Alexander, G. E. (1997). Preferential representation of instructed target location versus limb trajectory in dorsal premotor area. *Journal of Neurophysiology, 77,* 1195–1212.

Shmuelof, L., & Zohary, E. (2005). Dissociation between ventral and dorsal fMRI activation during object and action recognition. *Neuron, 47,* 457–470.

Symes, E., Ellis, R., & Tucker, M. (2005). Dissociating object-based and space-based affordances. *Visual Cognition, 12,* 1337–1361.

Symes, E., Ellis, R., & Tucker, M. (2007). Visual object affordances: Object orientation. *Acta Psychologica, 124,* 238–255.

Tucker, M., & Ellis, R. (1998). On the relations between seen objects and components of potential actions. *Journal of Experimental Psychology: Human Perception and Performance, 24,* 830–846.

Tucker, M., & Ellis, R. (2001). The potentiation of grasp types during visual object categorization. *Visual Cognition, 8,* 769–800.

Turner, P. (2005). Affordance as context. *Interacting with Computers, 17,* 787–800.

Ulrich, R., & Miller, J. (1994). Effects of truncation on reaction time analysis. *Journal of Experimental Psychology: General, 123,* 34–80.

Vainio, L., Ellis, R., & Tucker, M. (2007). The role of visual attention in action priming. *Quarterly Journal of Experimental Psychology, 60,* 241–261.

Valyear, K. F., Culham, J. C., Sharif, N., Westwood, D., & Goodale, M. A. (2006). A double dissociation between sensitivity to changes in object identity and object orientation in the ventral and dorsal visual streams: A human fMRI study. *Neuropsychologia, 44,* 218–228.

Wagenmakers, E.-J. (2007). A practical solution to the pervasive problems of *p* values. *Psychonomic Bulletin & Review, 14,* 779–804.

Wise, S. P., & Murray, E. A. (2000). Arbitrary associations between antecedents and actions. *Trends in Neuroscience, 23,* 271–276.

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