

# Hand Path Priming in Manual Obstacle Avoidance: Evidence That the Dorsal Stream Does Not Only Control Visually Guided Actions in Real Time

Steven A. Jax and David A. Rosenbaum  
Pennsylvania State University

According to a prominent theory of human perception and performance (M. A. Goodale & A. D. Milner, 1992), the dorsal, action-related stream only controls visually guided actions in real time. Such a system would be predicted to show little or no action priming from previous experience. The 3 experiments reported here were designed to determine whether priming exists for visually guiding the hand to targets with obstacles sometimes in the way. In all 3 experiments, priming was observed in the curvature of hand paths. Hand paths when no obstacles were present were more curved if obstacles had recently appeared than if obstacles had not recently appeared. The results also show that hand path priming was not the result of active prediction, persisted for many trials, and generalized over the workspace. The times to initiate movements also reflected the use of a sophisticated visual search strategy that took obstacle likelihood into account.

*Keywords:* motor control, dorsal stream, reach, obstacle, movement plan

A significant contribution to the study of human perception and performance has been the identification of separate visual processing streams for action, on the one hand, and for recognition, on the other hand (the dorsal and ventral streams, respectively; Goodale & Milner, 1992). One critical difference between these two streams is the time span over which recent experience can prime later behavior. For example, object naming, a process that relies on the ventral stream (van Turennout, Bielarowicz, & Martin, 2003), can be primed over a 48-week delay (Cave, 1997). By contrast, dorsal stream processing is thought to occur with little or no influence from recent experience. Indeed, Cant, Westwood, Valyear, and Goodale (2005), in discussing the role of the dorsal stream, claimed that “visually guided actions are programmed and executed in real-time” and that such actions “appear to be programmed primarily—if not entirely—using visual information that is on the retina when the action is about to be executed” (p. 225).

If dorsal stream processing occurs in real time, one would predict that visually guided actions should not show evidence of

action priming (differential performance on an action task based on recent experience). Several examples of such priming have been reported, however. For example, grasping movements can be primed by a preceding stimulus whose orientation matches that of a to-be-grasped object (Craighero, Bello, Fadiga, & Rizzolatti, 2002; Craighero, Fadiga, Rizzolatti, & Umiltá, 1998; Craighero, Fadiga, Umiltá, & Rizzolatti, 1996; Vogt, Taylor, & Hopkins, 2003) or by the observation of another’s grasp (Castiello, Lusher, Mari, Edwards, & Humphreys, 2002; Edwards, Humphreys, & Castiello, 2003). However, other studies have failed to report action priming. Cant et al. (2005) extended the method of Craighero et al. (1996), which only used movements made to remembered targets, to include grasps made to visible targets. Cant et al. obtained evidence for priming of grasping movements made to remembered targets but not to seen targets. Similarly, Garofeanu, Kroliczak, Goodale, and Humphreys (2004) asked whether grasping or naming an object would be primed by previous experience with either type of response involving the same object. These authors found that naming latencies were reduced by both grasping and naming primes but that initiation times for grasping responses were not reduced by either type of prime (for similar results, see Experiment 3 of Cant et al., 2005).

Can the claim that the dorsal stream operates entirely in real time be reconciled with this evidence for action priming? One possibility, favored by Cant et al. (2005) and Garofeanu et al. (2004), relies on the observation that the dorsal stream is highly interconnected with other neural systems. Thus, some of the previously obtained evidence for action priming may stem from priming outside the dorsal stream. For example, recent evidence suggests that movements made to remembered targets rely on visual representations in the ventral stream (Hu & Goodale, 2000; Milner, Paulignan, Dijkerman, Michel, & Jeannerod, 1999; Westwood & Goodale, 2003). Therefore, action priming in the studies of Craighero and colleagues, which used remembered targets, may

---

Steven A. Jax and David A. Rosenbaum, Department of Psychology, Pennsylvania State University.

The work was supported by National Institutes of Health Grant F31 NS 047784-01 to Steven A. Jax and by National Science Foundation Grant SBR-94-96290, National Institute of Mental Health Grants KO2-MH0097701A1 and R15 NS41887-01, and grants from the Research and Graduate Studies Office of the College of Liberal Arts, Pennsylvania State University to David A. Rosenbaum. We thank Mike Blaguszewski, Teresa Carpenter, Andrew Campbell, Chris Hess, and Michelle Wickham for help with data collection.

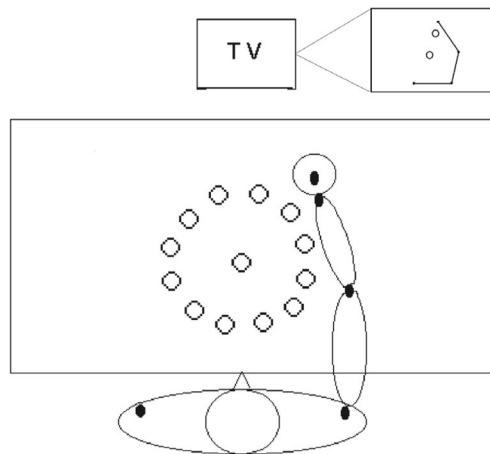
Correspondence concerning this article should be addressed to Steven A. Jax, who is now at the Moss Rehabilitation Research Institute, 213 Korman Building, 1200 West Tabor Road, Philadelphia, PA 19141, or to David A. Rosenbaum, Department of Psychology, Pennsylvania State University, University Park, PA 16802. E-mail: jaxs@einstein.edu or dar12@psu.edu

be explained by ventral stream priming. Similarly, the mirror-neuron system (Rizzolatti & Craighero, 2004), which occupies the ventral premotor and inferior parietal lobes (an area between the dorsal and ventral streams; Buxbaum, 2001; Glover, 2004), may underlie priming from action observation (Castiello et al., 2002; Edwards et al., 2003). Considering these possibilities, previous examples of action priming do not necessarily refute the claim that the dorsal stream operates entirely in real time.

One limitation of a motor system that relies only on real-time processing is that it potentially sacrifices computational efficiency when a sequence of similar movements is required. In this situation, a more efficient approach would be to maintain a plan in memory and edit those features that distinguish the just-used plan from the next-needed plan. In contrast to a real-time processing system, a system utilizing plan reuse should show action priming because the preceding movement plan would be used as a substrate for subsequent planning. Within the motor system, evidence for the reuse of plans has been observed in studies of speech and finger-tapping movements (Rosenbaum, Weber, Hazelett, & Hindorff, 1986) as well as in studies of where an object is grasped (Cohen & Rosenbaum, 2004). It is unclear, however, whether this evidence for action priming in the form of plan reuse did not also stem from priming outside the dorsal stream. For example, speech and finger-tapping movements may not rely on the dorsal stream due to their minimal use of visual guidance. Similarly, the selection of grasp locations may rely on nondorsal stream representations of previous interactions with that object. Consistent with this claim, Jeannerod, Decety, and Michel (1994) found that an optic ataxic patient, whose dorsal stream was damaged, was more accurate when grasping familiar objects than unfamiliar objects (e.g., lipstick container or similarly sized dowel).

In this study, we pursued the possibility that the dorsal stream controls movements by reusing properties from previous movement plans, a process that would produce action priming. In particular, we examined the ability of participants to reach around obstacles under visual guidance, which has been shown to be disrupted in patients with dorsal stream but not ventral stream damage (McIntosh, McClements, Dijkerman, Birchall, & Milner, 2004; Schindler et al., 2004). The use of visually guided obstacle avoidance also has the merit of allowing us to examine action priming without significant influence of priming from the ventral stream (as in the studies by Craighero et al., 1996, 1998, 2002) or from the mirror-neuron system (as in Castiello et al., 2002, and Edwards et al., 2003).

The question we asked was whether the curvature of recent hand paths would be reused on, and therefore prime, subsequent hand paths. To explore this possibility, we used a procedure in which participants moved the hand on a horizontal surface from a central circle to each of a number of peripheral target circles (see Figure 1). After the hand reached the peripheral target, it rested briefly and then moved back to the center. This out-and-back sequence constituted a trial. In some trials, an obstacle sat midway between the center circle and the peripheral target, but in other trials, no obstacle appeared. To test for hand path reuse, we analyzed hand paths in which successive trials either did or did not have an obstacle. The main question was whether hand paths in obstacle-absent trials would be more curved if preceded by obstacle-present trials than if preceded by obstacle-absent trials. The analogous question pertained to hand path straightness in obstacle-present



*Figure 1.* Overhead view of the setup used in all experiments. Participants made movements between a central starting circle and each of 12 peripheral target circles (open circles). Infrared light-emitting diodes (IREDS; filled ovals) were attached to the participant's right arm. The IREDS were used to display an image of the arm that the participants viewed on the TV monitor during performance (upper right corner of figure; shown in a view rotated from the vertical orientation of the TV monitor).

trials: Would hand paths in obstacle-present trials be straighter if preceded by obstacle-absent trials than if preceded by obstacle-present trials?

The present experiments also were designed to address five subsidiary questions. First, does hand path reuse only depend on the immediately preceding trial? If hand path reuse reflects the continued buildup of response strengths, there should be long-term as well as short-term hand path priming effects. Second, does hand path reuse depend on the angular separation of successively tested targets? The lower the functional level at which hand path reuse operates (e.g., at the muscle-command level), the smaller the angular separation over which priming should generalize. Third, does hand path reuse affect the time to complete a movement as well as the curvature of the path? For example, if longer hand paths lead to longer movement times (MTs), the priming effect from previous obstacle-present movements should increase the time it takes participants to complete obstacle-absent movements. Fourth, does hand path reuse depend on participants' expectancies? If hand path reuse is an aftereffect rather than a reflection of participants' predictions, it should be equally strong regardless of whether obstacles are predictable or unpredictable. Finally, does the reaction time (RT) to begin moving to a target depend on the presence or absence of an obstacle and on whether the preceding trial or trials did or did not have an obstacle? If participants form expectancies concerning obstacles and if the presence or absence of obstacles affects RTs, RTs should depend on the likelihood that obstacles will appear.

## Experiment 1

### Method

#### Participants

Fifty-one right-handed Pennsylvania State University undergraduates participated in Experiment 1 for course credit. All par-

ticipants were treated in accordance with the Institutional Review Board's approval of this and the other studies described here.

### *Materials, Design, and Procedure*

The participant sat at a table in front of a TV set and made arm movements that, through the use of a motion tracking system, caused a stick figure corresponding to the arm to move on the TV screen (see Figure 1). There was no perceptible delay between the participant's movements and the visual feedback. The stick figure moved as the participant did, to and from targets and around obstacles that also were displayed on the TV screen. The reason for using virtual targets and obstacles was to control the timing of the appearance of the targets and obstacles more precisely, inconspicuously, and safely than would have been possible with physical objects. A stick figure representation of the whole arm was used so that the obstacle had to be avoided with the entire upper extremity, as in real-life manual obstacle avoidance.

Before the experiment began, infrared light-emitting diodes (IREDs) were attached to the participant's left and right shoulders, right elbow, right wrist, and the top of a vertically oriented wooden dowel (3 cm in diameter, 9 cm high), which was mounted on a round base (15 cm in diameter, 0.75 cm thick), the underside of which was covered with felt to allow the manipulandum to slide with very little friction over the smooth table top. Participants wore a spandex-Lycra shirt to which the IREDs were attached. This shirt allowed the IRED positions to faithfully reflect the anatomical landmarks beneath them while also permitting free movement. The IRED locations were recorded by an OPTOTRAK 3020 motion tracking system (Northern Digital, Inc., Waterloo, Ontario, Canada) sampling at 100 Hz. The  $x$ - $y$  IRED positions from the OPTOTRAK were input to a program used to display the instantaneous positions of the arm along with relevant targets and obstacles on the TV monitor.

At the beginning of each block of trials, a circle appeared at the center of the TV monitor. The participant moved his or her "hand" (i.e., the stick figure's end-effector dot) into this circle, whereupon its color changed from blue to green. After the end-effector dot stayed within the start circle for 250 ms, 1 of 12 peripheral target circles appeared, at which time the participant was supposed to move the hand as quickly as possible into the target circle while avoiding an obstacle if one was present. When the end-effector dot entered the target circle, the target turned from blue to green. After the end-effector dot stayed in the target for 250 ms, the target circle disappeared, signaling the participant to move as quickly as possible back to the start circle while avoiding an obstacle if one was present. The center and peripheral target circles were all 2.4 cm in diameter (as measured on the table top), their centers were all 16 cm from the center of the start circle, and they were spaced around the center circle at 30° intervals. The angular positions of the targets were rotated 15° counterclockwise from the cardinal directions (0° being the straight-ahead angle) to allow all targets to be reached in the obstacle condition.

Within each block of trials, each target position was presented equally often in an order that was random except for the constraint that the same target location not appear in successive trials. Each participant performed 10 blocks of 48 trials. The first 2 blocks were considered practice and were not analyzed.

There were three groups of 17 participants, distinguished by the frequency with which obstacles appeared between the start and target circles. For participants in one group, the obstacle always appeared; for a second group, the obstacle sometimes appeared (with  $p = .50$ ); and for a third group, the obstacle never appeared. Given these three groups, four trial types were possible: (a) trials in which an obstacle appeared when obstacles always appeared (hereafter referred to as *A trials*), (b) trials in which an obstacle appeared when obstacles sometimes appeared (hereafter referred to as *+ trials*), (c) trials in which an obstacle did not appear though obstacles sometimes appeared (hereafter referred to as *- trials*), and (d) trials in which an obstacle did not appear when obstacles never appeared (hereafter referred to as *N trials*). The *+* and *-* trials were the trials of primary interest, whereas the *A* and *N* trials were the comparison, or control, trials.<sup>1</sup>

Whenever an obstacle appeared, it sat midway between the start circle and a target circle. Each obstacle was a filled red circle whose size was the same as the start and target circles. The obstacle was presented at the same time as the target circle and remained on the screen until the participant returned to the center circle. Participants were instructed to avoid hitting the obstacle with any portion of the stick figure arm, which turned red when a collision occurred. To encourage participants to move quickly throughout the entire block and avoid obstacle collisions, we showed them a score,  $S = T(1 + C)$ , at the end of each block, where  $T$  was the total time (in ms) to complete the block and  $C$  was the number of collisions. Participants were urged to strive for ever lower end-of-block scores.

### *Results*

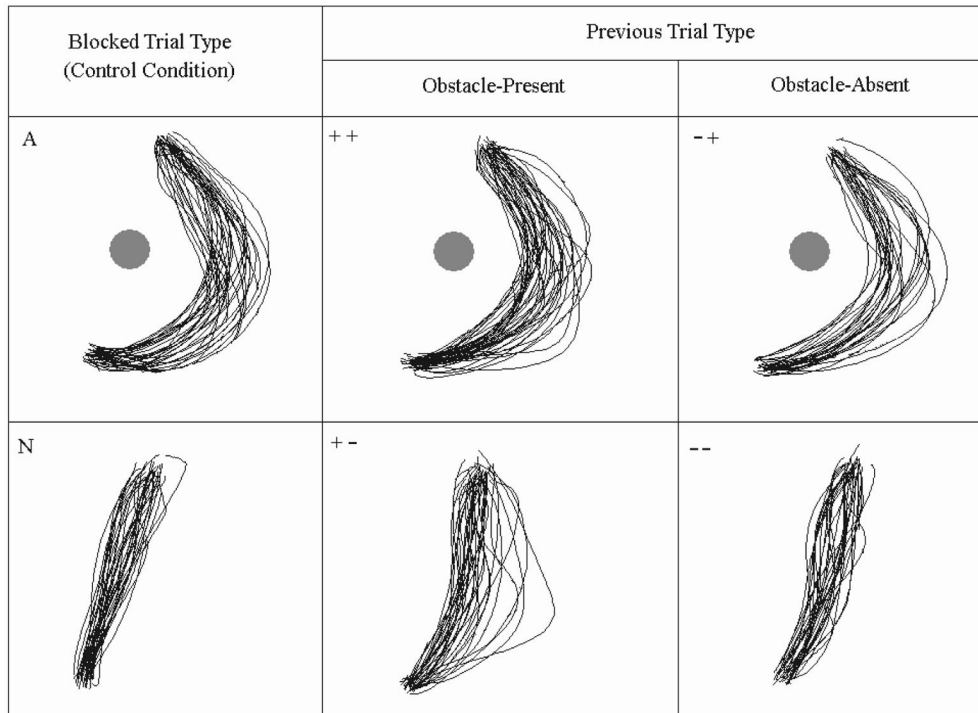
Onsets and offsets of individual movements were identified using a 30 mm/s hand velocity criterion. Trials in which any of the IREDs were not in view of the OPTOTRAK (approximately 3% of trials) were removed from analysis, as were trials in which a collision occurred (approximately 1.5% of trials). The frequency of collisions was approximately the same across conditions.

For all analyses to be reported, we used two sets of inferential statistics. The first was an analysis of variance (ANOVA) to compare data within the mixed-trial blocks. The second used independent-samples  $t$  tests with Bonferroni correction for multiple comparison (overall  $\alpha$  of .05) to compare data in the mixed-trial blocks with their respective blocked-trial control conditions (e.g., comparing the *+* and *A* conditions).

### *Outward Movements*

*Hand path curvature.* Sample hand paths for outward movement are shown in Figure 2. As expected, the hand paths were curved when an obstacle was always present (*A*) and were straight when an obstacle was never present (*N*). In those trials in which it was possible that an obstacle might appear and did (*++* and *-+*),

<sup>1</sup> Because all participants completed the same number of blocks, there were twice as many trials included in each participant's mean in the *A* and *N* conditions (384 trials each) than in the *+* and *-* conditions (192 trials each). The same number of blocks was used to equalize the total number of movements performed by each participant, thereby allowing us to control for fatigue or practice effects.



*Figure 2.* Examples of hand paths to one target from the start position (lower left circle in each panel). Hand paths are shown for trials in which an obstacle appeared (top) or did not appear (bottom). Left: Hand paths in the control conditions in which an obstacle always appeared (A) or never appeared (N). Middle and right: Hand paths in the experimental conditions in which an obstacle could either appear or not. The middle and right panels are from trials in which an obstacle appeared in the preceding trial and an obstacle appeared in the shown trial (+ +), an obstacle appeared in the preceding trial and no obstacle appeared in the shown trial (+ -), an obstacle did not appear in the preceding trial and an obstacle appeared in the shown trial (- +), or no obstacle appeared in the preceding trial and no obstacle appeared in the shown trial (- -).

the hand paths were curved, as needed to circumvent the obstacle. In those trials in which it was possible that an obstacle might appear but did not in either the shown trial or in the preceding trial (- -), the hand paths were a bit more curved than when no obstacle could ever appear (N). The most important result concerned the + - condition, in which it was possible that an obstacle might appear but did not and an obstacle appeared in the preceding trial. As seen in the + - panel of Figure 2, some hand paths were much more curved in this condition than in any other condition in which no obstacle appeared.

To quantify hand path curvature, we calculated two measures for each movement path. The first, *initial angular offset*, characterized the hand path's curvature at the start of the movement, whereas the second, *curvature index*, characterized the hand path as a whole. Initial angular offset was defined as the absolute value of the angular deviation between the position of the hand 150 ms after movement initiation and the direct path to the target. We used a time of 150 ms because movement properties up to this time were likely to be preprogrammed, whereas movement properties after this time were more likely to have been altered on the basis of feedback (Elliot, Helsen, & Chua, 2001). The curvature index was defined as the maximum perpendicular distance of the hand from a straight line connecting the starting and end points of the

movement, divided by that straight line distance and multiplied by 100.<sup>2</sup>

Mean values of the initial angular offsets for the outward movements are shown in Figure 3. These values were evaluated in mixed-trial blocks with a 2 (trial type: + or -) × 2 (previous trial type: + or -) ANOVA. As seen in Figure 3, there was a main effect of trial type, in which initial angular offsets were higher in the obstacle-present than obstacle-absent trials,  $F(1, 16) = 116.62$ ,  $p < .001$ . There was also a main effect of previous trial type, with initial angular offsets being larger for movements preceded by an obstacle-present than an obstacle-absent trial,  $F(1, 16) = 75.89$ ,

<sup>2</sup> Another possible measure is the side of the obstacle around which the hand moved. We chose not to report this measure, however, because most movements circumvented the obstacle on the same side for any given target location. This similarity within and across participants was due to the constraint that the arm not collide with the obstacle. The location of many of the targets afforded only a single side on which the arm could avoid the obstacle. For example, the obstacles for targets located near the 12 o'clock and 6 o'clock positions only could be avoided by selecting a path to the right of the obstacle. The lack of variability both within and across participants made this variable uninformative.

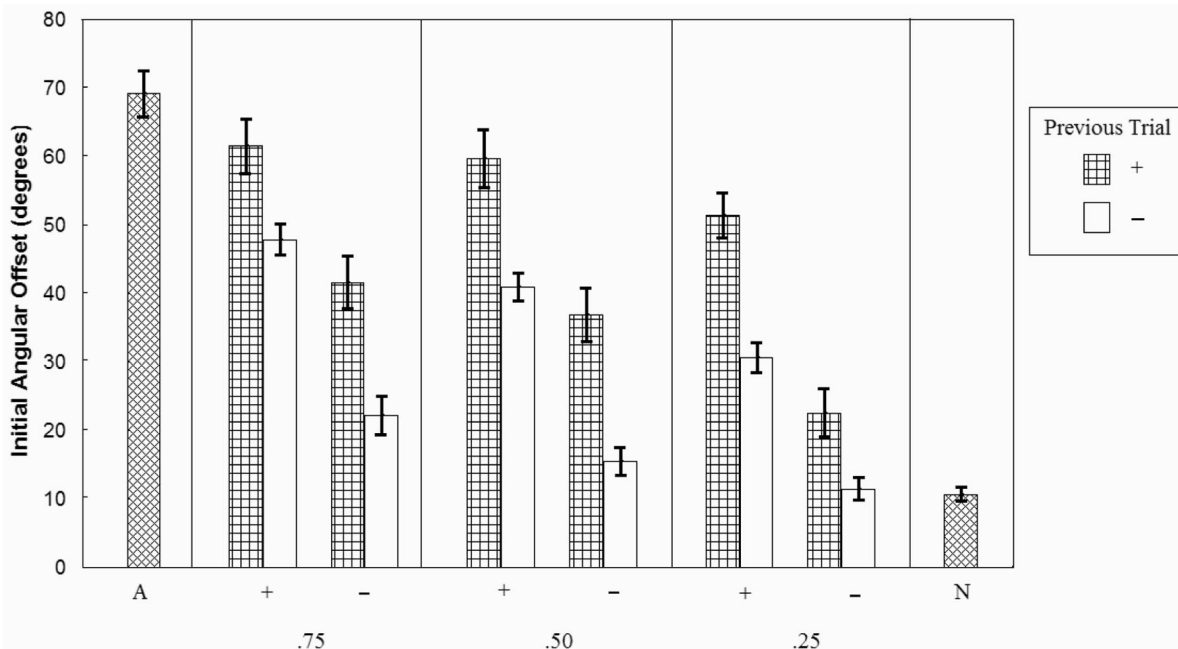


Figure 3. Mean initial angular offsets ( $\pm 1$  SE, denoted by the error bars) for outward movements in Experiment 1 (.50 condition) and in Experiment 3 (.75 and .25 conditions) when an obstacle always appeared (A), when an obstacle could sometimes appear and did (+), when an obstacle could sometimes appear and did not (-), and when an obstacle never appeared (N). The values of .50, .75, and .25 refer to the probabilities of obstacles in the mixed-trial blocks of the two experiments.

$p < .001$ . Trial type and previous trial type did not interact,  $F(1, 16) < 1$ .

Initial angular offsets also displayed a global context effect of the possibility of obstacle presence or absence. As seen in Figure 3, both obstacle-present conditions of the mixed-trial blocks (-+ and ++ had lower initial angular offsets than were seen in the A condition, and both obstacle-absent conditions of the mixed-trial blocks (-- and -+) had higher initial angular offsets than were seen in the N condition ( $p < .05$  for all four comparisons).

Complementary conclusions were reached using the curvature index measure, as shown in Figure 4. The curvature index ANOVA showed a main effect of trial type,  $F(1, 16) = 464.32$ ,  $p < .001$ , a main effect of previous trial type,  $F(1, 16) = 46.18$ ,  $p < .001$ , and an interaction between the two variables,  $F(1, 16) = 40.29$ ,  $p < .001$ . In this interaction, overall curvature on obstacle-absent trials was higher when an obstacle appeared in the previous trial (+-) than when an obstacle did not appear in the previous trial (--). This outcome replicated what was found with the initial angular offset measure. However, in contrast to what was found for initial angular offsets, the curvature index was not statistically different when obstacle-present trials were preceded by obstacle-absent trials (-+) and when obstacle-present trials were preceded by obstacle-present trials (++). The mean curvatures in both of these conditions were statistically indistinguishable from curvatures in the A condition (both  $ps > .50$ ).

*Effect of obstacle recency.* We next analyzed the effect of obstacle recency, which was defined as the number of trials since an obstacle appeared. The data are shown in Figure 5. For trials in mixed-trial blocks (the + and - conditions), initial angular offsets

decreased with fewer preceding obstacle-present trials (comparing recency of 3 with recency of 1) and also decreased with more preceding obstacle-absent trials (comparing recency of -1 with recency of -3). The effects of obstacle recency on initial angular offset were evaluated with two 2 (previous trial type: + or -)  $\times$  3 (obstacle recency) ANOVAs, performed separately for the obstacle-present and obstacle-absent conditions of the mixed-trial blocks. The obstacle recency factor had three levels: most prior obstacle exposure (recency of 3 and -1), medium prior obstacle exposure (recency of 2 and -2), or least prior obstacle exposure (recency of 1 and -3). For movements in the obstacle-present condition, there was a main effect of previous trial type,  $F(1, 16) = 63.75$ ,  $p < .001$ , a main effect of obstacle recency,  $F(2, 32) = 5.67$ ,  $p = .008$ , but no significant interaction between the two variables,  $F(2, 32) < 1$ . The same pattern of results was observed for movements in the obstacle-absent condition. There was a main effect of the previous trial type,  $F(1, 16) = 76.72$ ,  $p < .001$ , a main effect of prior obstacle recency,  $F(2, 32) = 3.32$ ,  $p = .049$ , but no interaction between the two variables,  $F(2, 32) < 1$ .

With more repetitions of a given trial type, initial angular offsets in the mixed-trial blocks became more similar to, but still statistically different from, their corresponding blocked controls. Thus, initial angular offsets for obstacle-absent trials in the mixed-trial blocks became more similar to, but never statistically equivalent to ( $p < .05$ ), initial angular offsets of N trials. Similarly, initial angular offsets for obstacle-present trials in the mixed-trial blocks became more similar to, but never statistically equivalent to ( $p < .05$ ), initial angular offsets for A trials.

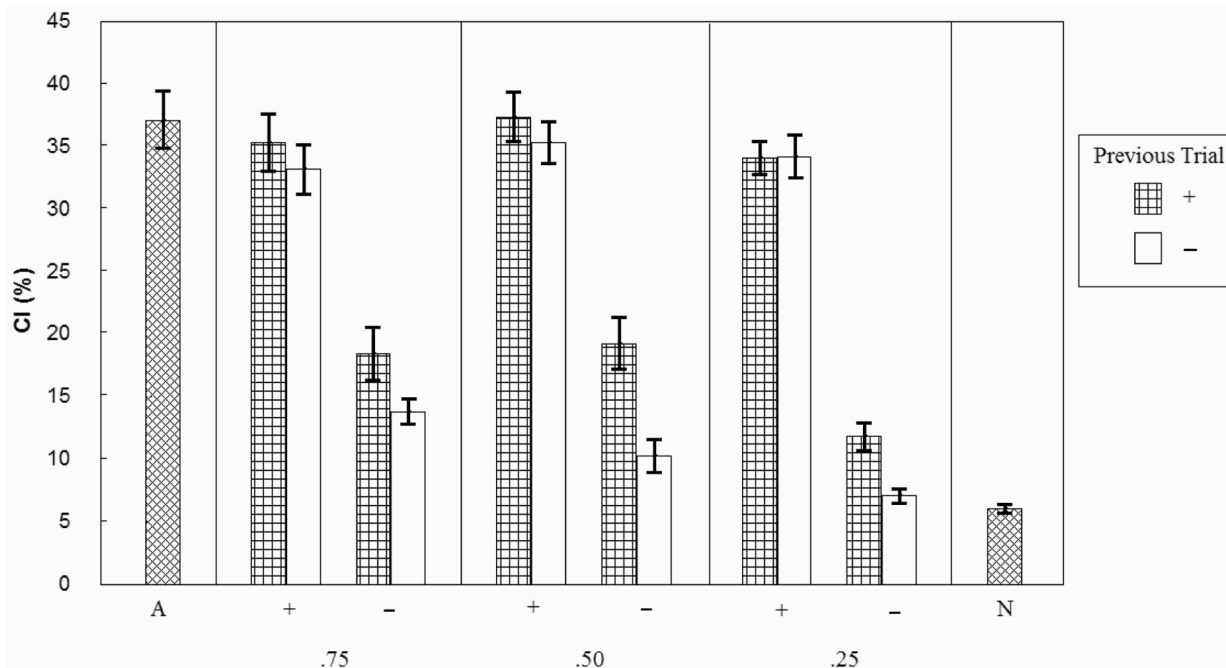


Figure 4. Mean curvature index (CI) value ( $\pm 1$  SE, denoted by the error bars) for outward movements in Experiment 1 (.50 condition) and in Experiment 3 (.75 and .25 conditions) when an obstacle always appeared (A), when an obstacle could sometimes appear and did appear (+), when an obstacle could sometimes appear and did not appear (-), and when an obstacle never appeared (N). The values of .50, .75, and .25 refer to the probabilities of obstacles in the mixed-trial blocks of the two experiments.

Analogous effects of obstacle recency on curvature index were obtained for the obstacle-absent but not obstacle-present trials, which showed no effect of either previous trial type or obstacle recency. For more details, see Jax (2005).

*Angular separation between targets in successive trials.* The next analyses were concerned with hand path priming over the workspace. We studied how hand path priming depended on the angular separation between targets in successive trials. These effects are shown in Figure 6. We focus on the conditions in which a trial type switch occurred and analyzed the relevant data with a single-factor ANOVA examining the effect of the angular separation factor. When an obstacle-present trial was preceded by an obstacle-absent trial (- +), the priming effect was not affected by the angular separation between the two targets,  $F(5, 80) = 0.78$ . However, when an obstacle-absent trial was preceded by an obstacle-present trial (+ -), initial angular offsets were greatest when the target separation was near  $30^\circ$  or near  $180^\circ$  and decreased for intermediate values, a trend that was best fit with a quadratic contrast,  $F(1, 16) = 23.78$ ,  $p < .001$ . Analogous effects of angular separation on curvature index were obtained. For more details, see Jax (2005).

### Inward Movements

All of the analyses presented so far concerned outward movements from the central circle to the peripheral circles. We focused on these movements because only in outward movements was obstacle status uncertain. Nonetheless, we wanted to know whether the priming observed in the outward movements carried

over to the inward movements. The initial angular offsets for the inward movements are shown in Figure 7 and were again evaluated with a 2 (trial type: + or -)  $\times$  2 (previous trial type: + or -) ANOVA. The ANOVA showed a main effect of trial type,  $F(1, 16) = 1,222.20$ ,  $p < .001$ , a main effect of previous trial type,  $F(1, 16) = 17.40$ ,  $p < .001$ , and an interaction between the two,  $F(1, 16) = 6.86$ ,  $p = .012$ . Post hoc analyses of this interaction showed that the pattern of priming observed for the outward portion of trials also occurred during the inward portion of obstacle-absent trials ( $p < .05$ ) but not obstacle-present trials ( $p > .05$ ). Thus, the priming effects from a preceding obstacle-present trial affected both the subsequent outward movements and the immediately following inward movements. The curvature index data were analogous. For more details, see Jax (2005).

### RT

The analyses described above concerned participants' hand paths. We also analyzed participants' RTs to see whether those times also showed priming effects. RTs were defined as the time between target presentation and the time of movement onset (when the hand's speed exceeded 30 mm/s).

As shown in Figure 8, RTs depended on the previous trial type more so than on the current trial type. RTs were longer in - + and - - trials (i.e., when an obstacle was possible and an obstacle did not appear in the previous trial) than in any other type of trial. This conclusion was confirmed with a 2 (trial type: + or -)  $\times$  2 (previous trial type: + or -) ANOVA. The ANOVA yielded no main effect of trial type,  $F(1, 16) < 1$ , a main effect of previous

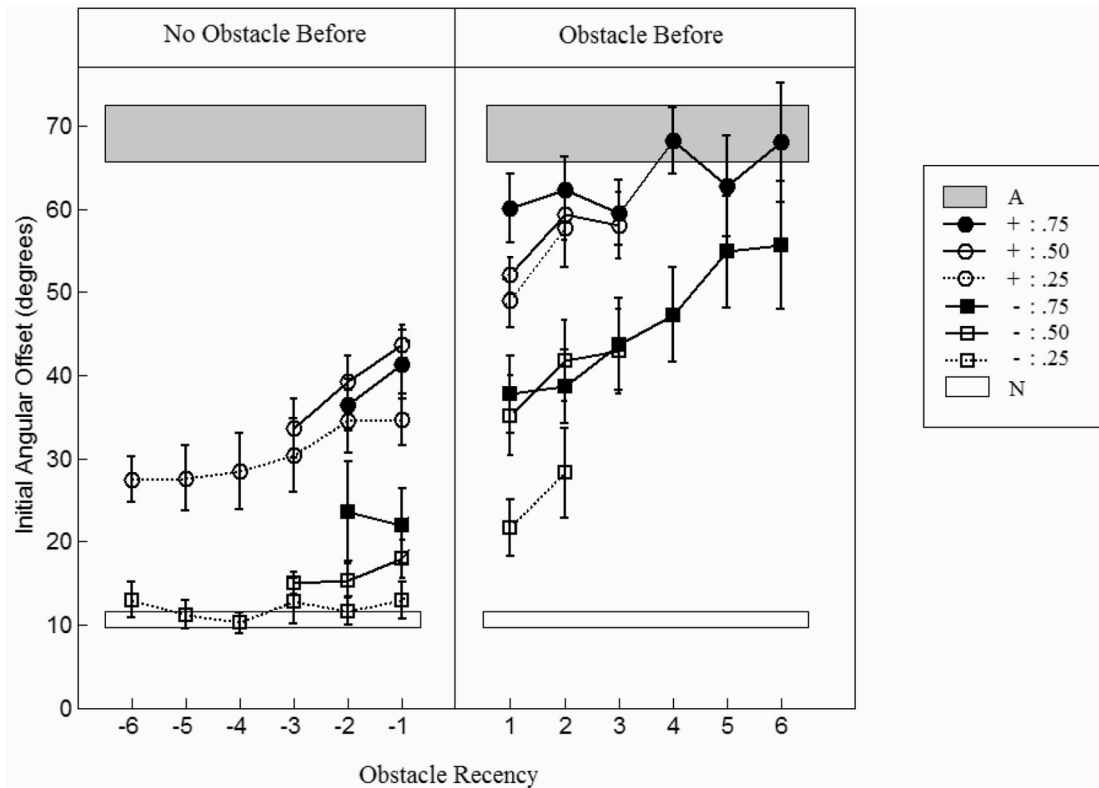


Figure 5. Mean initial angular offsets ( $\pm 1$  SE, denoted by the error bars) for outward movements in Experiment 1 (.50 condition) and in Experiment 3 (.75 and .25 conditions) when an obstacle appeared (A; circles) and an obstacle did not appear (N; squares), plotted as a function of how recently an obstacle appeared or did not appear in the preceding trials. Positive values refer to number of preceding trials with an obstacle. Negative values refer to number of preceding trials without an obstacle. For the A and N conditions, obstacle recency is not a meaningful variable, but mean initial angular offsets and  $\pm 1$  SE values from the A condition (gray bar) and N condition (white bar) are included for comparison purposes. The values of .50, .75, and .25 refer to the probabilities of obstacles in the mixed-trial blocks of the two experiments.

trial type,  $F(1, 16) = 38.32$ ,  $p < .001$ , and no significant interaction between the two variables,  $F(1, 16) < 1$ . Comparisons of the obstacle-present and obstacle-absent trials of the mixed blocks with their respective blocked controls showed no difference in RT for trials preceded by an obstacle-present trial ( $p > .60$ ) but reliably longer RTs for trials preceded by an obstacle-absent trial ( $p < .05$ ).

### MT

Finally, we examined whether priming of hand path curvature also affected the time participants took to complete their movements. MTs were highly correlated with overall hand path curvature, as shown in Figure 9. This relationship was strongest in the mixed-trial blocks, in which the correlation between mean curvature index and mean MT was .993 ( $p = .007$ ), and was slightly weakened when the blocked-trial control conditions were also included ( $r = .921$ ,  $p = .009$ ). The strong correlation between hand path curvature and MT showed that the priming effects from a preceding obstacle-present trial affected both the curvature of hand paths and the time to complete those movements.

### Discussion

Experiment 1 was designed to test for priming effects in manual obstacle avoidance, a task that relies on the dorsal, action-related stream. In contrast to the claim that the dorsal stream computes action entirely in real time (Cant et al., 2005), we obtained clear evidence for priming from previous trials. When obstacles were present, initial angular offsets (a measure of hand path curvature at the start of a movement) were larger when previous trials had obstacles than when previous trials did not have obstacles. Similarly, and perhaps most surprisingly, when obstacles were absent, initial angular offsets also were larger when previous trials had obstacles than when previous trials did not have obstacles. These effects depended on the number of previous trials with or without an obstacle. The larger the number of previous trials with an obstacle, the larger the initial angular offset. Similarly, the larger the number of previous trials without an obstacle, the smaller the initial angular offset. These results show that a hand path's curvature was primed by experience on recent trials.

Priming also generalized across the workspace but in an unexpected way. In trials in which an obstacle did not appear but an

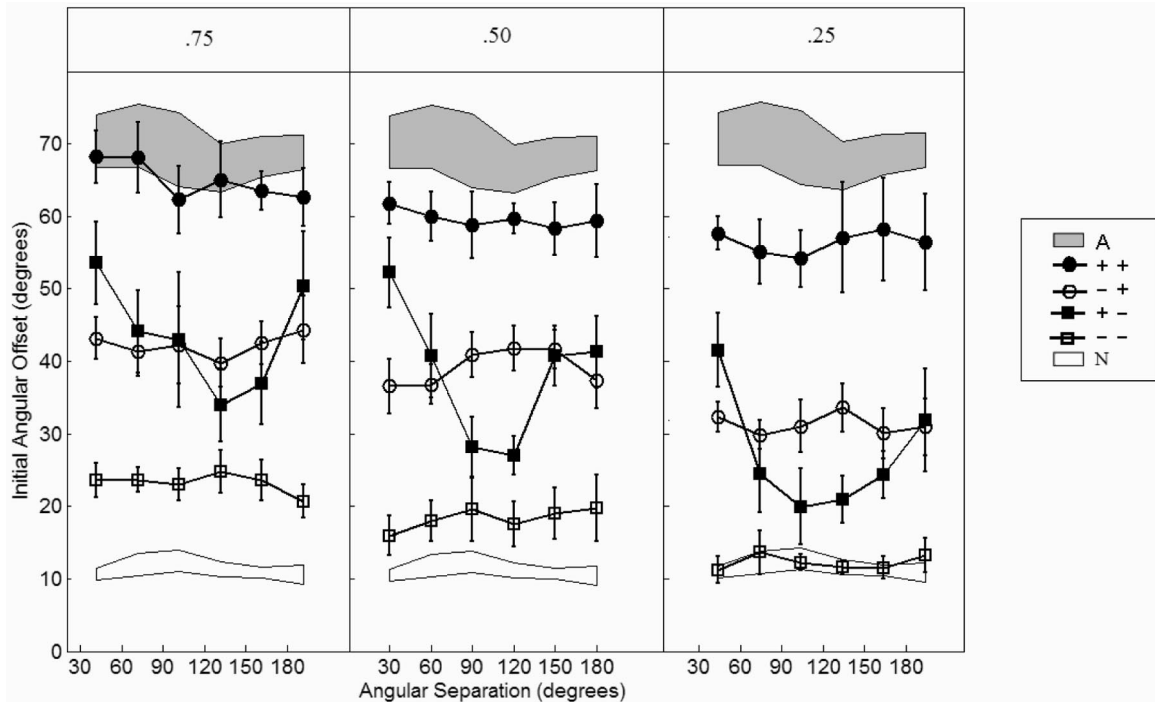


Figure 6. Mean initial angular offset values ( $\pm 1$  SE, denoted by the error bars) for outward movements in Experiment 1 (.50 condition) and in Experiment 3 (.75 and .25 conditions), plotted as a function of angular separation between targets in successive trials. The values of .50, .75, and .25 refer to the probabilities of obstacles in the mixed-trial blocks of the two experiments.

obstacle appeared in the preceding trial, initial angular offsets varied nonmonotonically with angular separation, reaching a minimum in the range of  $90^{\circ}$ – $120^{\circ}$  (see Figure 6). One interpretation of this result is that when successive targets were close together, participants were primed to generate hand paths with initial angular offsets similar to what they had generated before for outward movements. When successive targets were farther apart and approached  $180^{\circ}$ , participants were primed to generate hand paths with initial angular offsets similar to what they had generated for just-completed inward movements. The basis for the latter hypothesis is that inward movements from one target to the center shared direction with outward movements from the center to another target  $180^{\circ}$  away.

Whereas initial angular offsets reflected the starting direction of participants' hand paths, the curvature index reflected the maximal deviation of the hand from the straight line connecting the beginning and end of the movement. As such, the curvature index reflected properties of the movement as a whole. Consistent with the view that the starting direction foreshadowed properties of the entire coming movement, the curvature index followed the same patterns as the initial angular offset, with only one exception, namely that when an obstacle was present, the curvature index was no different if an obstacle had appeared or had not appeared in the previous trial. This outcome presumably reflected the fact that when an obstacle was present, participants sought some minimal acceptable clearance around it. Such a tendency would have attenuated possible priming effects (including the effects of previous trial type, obstacle recency, and angular separation between trials

in successive trials) for overall path curvature in the obstacle-present trials.

Of greater interest was the fact that in obstacle-absent trials, the curvature index, like the initial angular offset measure, was markedly affected by whether an obstacle appeared in the preceding trials. Given the nature of this effect, a possible inference is that the preceding obstacle-avoiding movement plans were reused and incompletely modified on the subsequent obstacle-absent trials, even though this resulted in movements that were needlessly circuitous and took more time to complete than straighter movements. A possible reason for participants' lack of care about needlessly circuitous movements is that such movements probably were not that biomechanically costly in the present experiment. The biomechanical advantage of moving along the shortest path apparently was outweighed by the computational cost of changing from a curved to a straight hand path. Consistent with this view, inward movements also were curved for obstacle-absent trials when those trials occurred after obstacle-present trials. Furthermore, hand path curvature, like initial angular offset, changed in a graded fashion with the number of preceding obstacle-absent or obstacle-present trials, as if participants allowed the overall curvature of their hand paths, including the initial directions of those hand paths, to swell or shrink depending on the overall likelihood of obstacles in the preceding trials. We will expand on this proposal in the General Discussion section.

The RT data also fit with the view that participants probably were not very concerned about generating straight hand paths when obstacles were possible but did not appear, for RTs were no



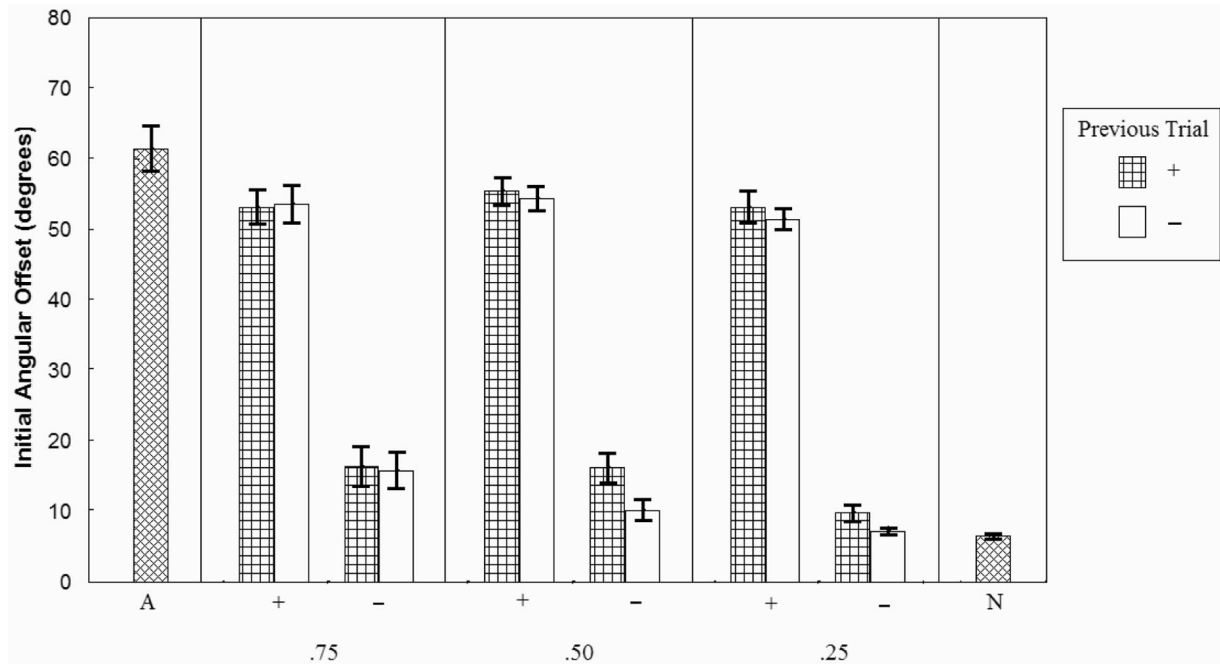


Figure 7. Mean initial angular offset values ( $\pm 1$  SE, denoted by the error bars) for inward movements in Experiment 1 (.50 condition) and in Experiment 3 (.75 and .25 conditions) when an obstacle always appeared (A), when an obstacle could sometimes appear and did appear (+), when an obstacle could sometimes appear and did not appear (-), and when an obstacle never appeared (N). The values of .50, .75, and .25 refer to the probabilities of obstacles in the mixed-trial blocks of the two experiments.

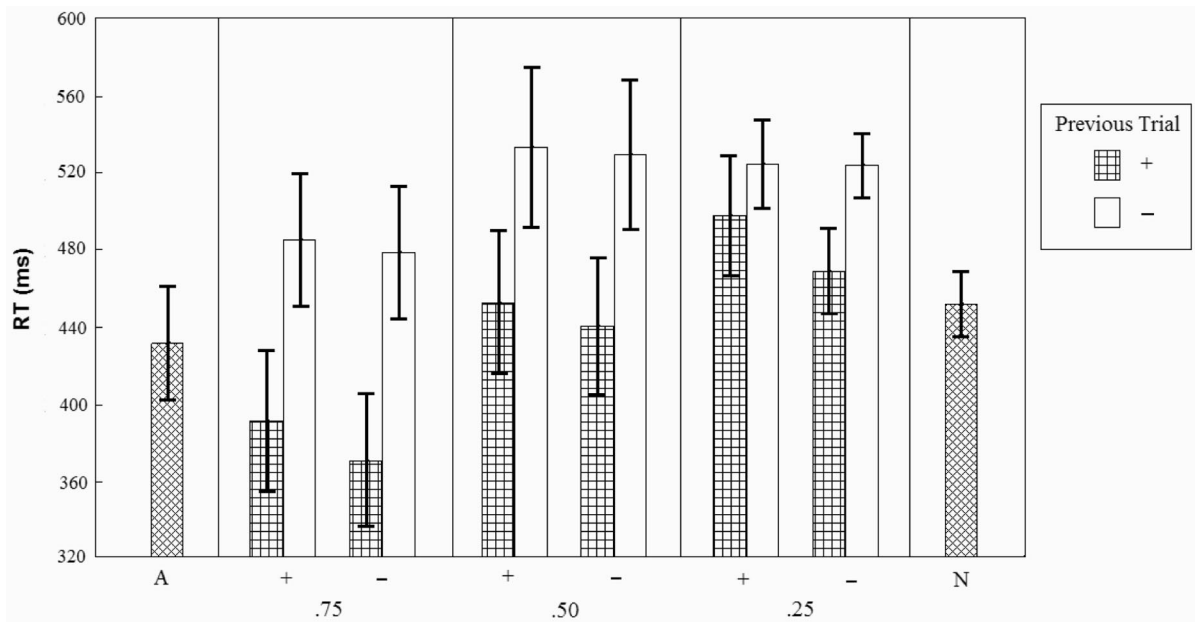


Figure 8. Mean reaction times (RTs;  $\pm 1$  SE, denoted by the error bars) for outward movements of Experiment 1 (.50 condition) and Experiment 3 (.75 and .25 conditions) when an obstacle always appeared (A), when an obstacle could sometimes appear and did appear (+), when an obstacle could sometimes appear and did not appear (-), and when an obstacle never appeared (N). The values of .50, .75, and .25 refer to the probabilities of obstacles in the mixed-trial blocks of the two experiments.

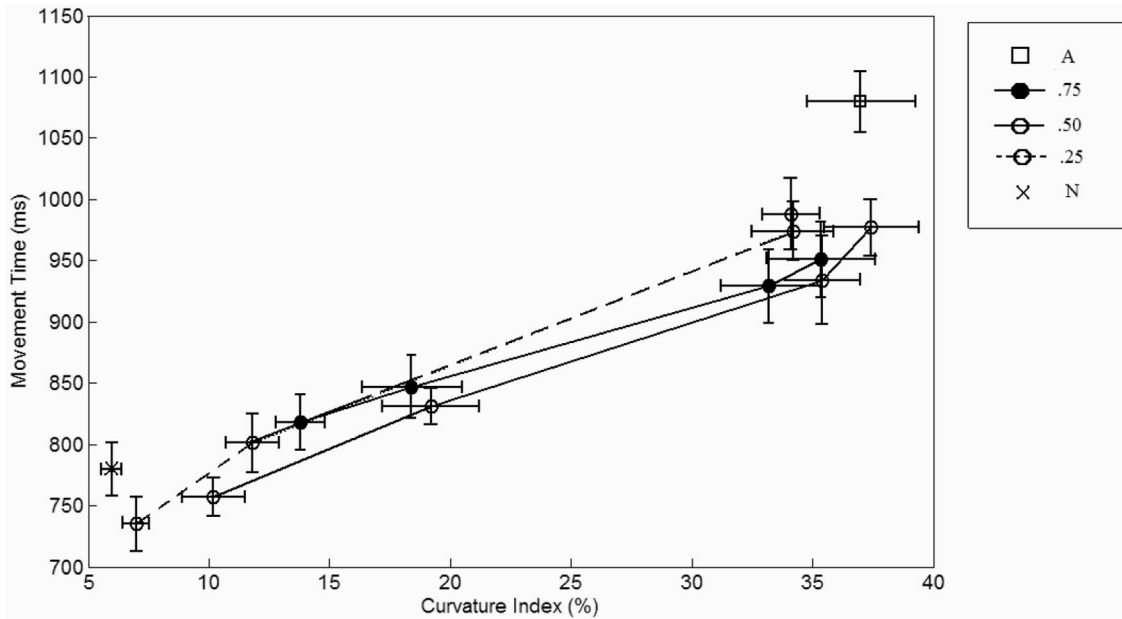


Figure 9. Relation between mean movement time ( $\pm 1 SE$ , denoted by the error bars) and mean curvature index ( $\pm 1 SE$ , denoted by the error bars) in Experiment 1 (.50 condition) and in Experiment 3 (.75 and .25 conditions) when an obstacle always appeared (A), when an obstacle could sometimes appear (.75, .50, and .25 conditions), and when an obstacle never appeared (N). The values of .50, .75, and .25 refer to the probabilities of obstacles in the mixed-trial blocks of the two experiments. For the mixed-trial blocks, lines connect the four conditions factorially crossing trial type (obstacle present or obstacle absent) and previous trial type (obstacle present or obstacle absent).

longer in the + - condition than in the other conditions. One would have expected RTs to be longer in the + - condition than in other conditions if participants cared a lot about changing plans from curved to straight movements. The one significant effect in the RTs—namely that RTs were longer following obstacle-absent trials in the mixed conditions than in any other condition—may have reflected a feature of perceptual processing or attention rather than motor preparation per se. We will return to this point in the *Discussion* section of the next experiment.

## Experiment 2

We interpreted the results of Experiment 1 as evidence that hand path curvature was primed by previous trials because the perceptual-motor system reused and modified previous movement plans (the reuse hypothesis). An alternative interpretation (the expectancy hypothesis) is that the random nature of trial type switches led participants to actively develop expectations about the presence or absence of an obstacle on the upcoming trial. For example, if participants expected trial type switches, they may have anticipated an obstacle-present trial if the previous trial had been an obstacle-absent trial (and vice versa). Such expectations could have led to the observed sequential effects.

To distinguish between these alternatives, we eliminated uncertainty about the upcoming trial types in Experiment 2 by using a predictable sequence of obstacle-present and obstacle-absent trials. The expectancy hypothesis predicted that the effects of previous trial type would be weakened or eliminated when trial types were

predictable. The reuse hypothesis predicted no change in sequential effects, all else being equal.

## Method

The method was the same as in Experiment 1 except that the order of obstacle-present and obstacle-absent trials followed a predictable AABBA pattern. There were two groups of participants. Those in the *informed* group were told what the pattern would be. Those in the *uninformed* group were not. The rationale for having the two groups was to provide a further test of the expectancy hypothesis. If participants formed expectancies and used those expectancies to affect their motor preparation, one would expect participants given no instructions about perfectly predictable sequences to pick up on that predictability. On the other hand, if participants did not form expectancies or failed to use expectancies during motor preparation, one would expect participants given no instructions about perfectly predictable sequences to behave like participants exposed to random sequences.

Thirty-four participants completed Experiment 2, half in the informed group and half in the uninformed group. None of the participants in Experiment 2 had been in Experiment 1. Half of the participants in each group began with obstacle-present trials, whereas the other half of the participants began with obstacle-absent trials.

## Results

Trials in which any of the IREDs was out of view of the OPTOTRAK (approximately 2.8% of trials) were removed from

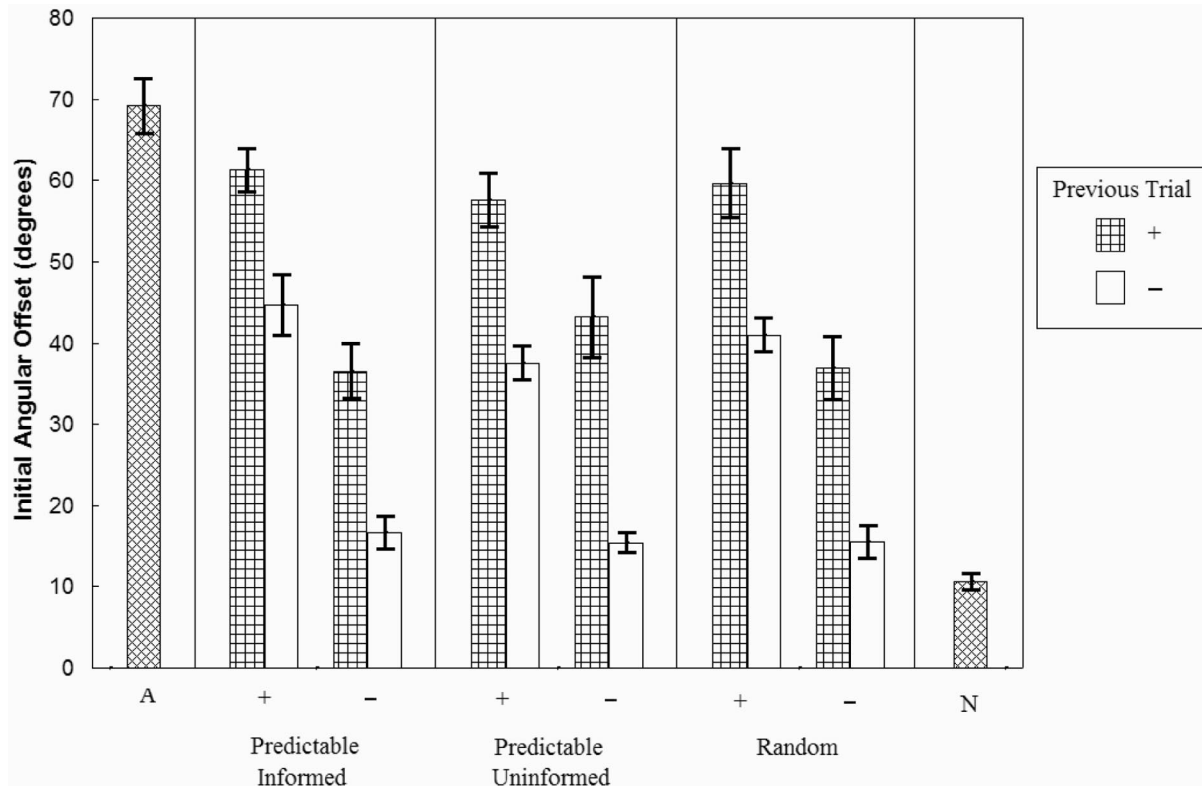


Figure 10. Mean initial angular offset values ( $\pm 1$  SE, denoted by the error bars) for outward movements in Experiment 2 when an obstacle always appeared (A), when an obstacle could sometimes appear and did appear (+), when an obstacle could sometimes appear and did not appear (-), and when an obstacle never appeared (N) for the group given instructions about sequence predictability (second panel) and for the group given no instructions about sequence predictability (third panel), along with data from Experiment 1 (all other panels).

analysis, as were trials in which there was a collision (approximately 0.7% of trials).

### Outward Movements

*Initial angular offsets and hand path curvature.* Mean initial angular offsets for the outward movements of Experiment 2 are shown in Figure 10. The most striking feature of the data from both groups was how similar they were to the data of the participants in Experiment 1. This impression was confirmed with a 3 (group: random, predictable informed, predictable uninformed)  $\times$  2 (trial type: + or -)  $\times$  2 (previous trial type: + or -) ANOVA. There was no main effect of group,  $F(2, 48) = 0.11, p = .88$ , and none of the interactions between group and other factor(s) were reliable (all  $F_s < 1$ ). The only significant effects, replicating the results of Experiment 1, were a main effect of trial type,  $F(1, 48) = 248.97, p < .001$ , and a main effect of previous trial type,  $F(1, 48) = 168.57, p < .001$ . Analogous effects of trial type and previous trial type on curvature index were obtained for the obstacle-absent but not for the obstacle-present trials, which showed no effect of previous trial type. For details, see Jax (2005).

*Effect of obstacle recency.* The effects of obstacle recency for outward movements were also similar to what they were in Experiment 1. Again, no differences were observed among the two groups of Experiment 2 and the participants of Experiment 1. This

impression was confirmed with two 3 (group: random, predictable informed, predictable uninformed)  $\times$  2 (obstacle recency: -1 and 2 for obstacle-present trials; -2 and 1 for obstacle-absent trials<sup>3</sup>) ANOVAs, performed separately for both trial types. For obstacle-present trials, there was no main effect of group,  $F(2, 48) < 1$ , a main effect of obstacle recency,  $F(1, 48) = 119.91, p < .001$ , and no interaction between the two variables,  $F(2, 48) = 2.62, p = .10$ . For obstacle-absent trials, there was no main effect of group,  $F(2, 48) < 1$ , a main effect of obstacle recency,  $F(1, 48) = 112.81, p < .001$ , and no interaction between the two variables,  $F(2, 48) < 1$ . Analogous effects of obstacle recency on curvature index were obtained for the obstacle-absent but not for the obstacle-present trials, which showed no effect of either previous trial type or obstacle recency. For details, see Jax (2005).

<sup>3</sup> The number of previously repeated trial types was limited in Experiment 2 because of the nature of the predictable obstacle sequence. Obstacle-absent trials could only be preceded by one obstacle-absent trial (recency of -1) or two obstacle-present trials (recency of 2). Similarly, obstacle-present trials could only be preceded by two obstacle-absent trials (recency of -2) or one obstacle-present trial (recency of 1). Analyses therefore were limited to the cases that could be compared across experiments.

*Angular separation between targets in successive trials.* The effects of angular separation between targets in successive trials for outward movements were, as expected from the results described above, the same for the two groups in Experiment 2 and for the participants of Experiment 1. As in the previous analyses, no differences were observed among the three groups, as confirmed with two ANOVAs performed separately for obstacle-present trials preceded by obstacle-absent trials ( $- +$  trials) and for obstacle-absent trials preceded by obstacle-present trials ( $+ -$  trials). Both ANOVAs used a 3 (group: random, predictable informed, predictable uninformed)  $\times$  6 (angular separation) design. For the  $- +$  trials, there was no main effect of group,  $F(2, 48) = 0.21$ , no main effect of angular separation,  $F(5, 240) = 2.07$ ,  $p = .07$ , and no interaction between the two variables,  $F(10, 240) < 1$ . For  $+ -$  trials, there was no main effect of group,  $F(2, 48) < 1$ , a main effect of angular separation that was best fit with a quadratic contrast,  $F(1, 48) = 4.48$ ,  $p = .04$ , and no interaction between the two variables,  $F(10, 240) < 1$ . Analogous effects of angular separation on the curvature index were obtained. For details, see Jax (2005).

### Inward Movements

The initial angular offset results for inward movements in Experiment 2 were similar to those of Experiment 1. As confirmed with a 3 (group: random, predictable uninformed, predictable

informed)  $\times$  2 (trial type:  $+$  or  $-$ )  $\times$  2 (previous trial type:  $+$  or  $-$ ) ANOVA, no differences were observed among the three groups,  $F(2, 48) = 0.05$ ,  $p = .95$ . None of the interactions between group and the other factor(s) were reliable (all  $F$ s  $< 1$ ). The only significant effects, replicating the results of Experiment 1, were the main effect of trial type,  $F(1, 48) = 1,302.35$ ,  $p < .001$ , the main effect of previous trial type,  $F(1, 48) = 46.32$ ,  $p < .001$ , and the interaction between these two variables,  $F(1, 48) = 24.55$ ,  $p < .001$ . Analogous results were obtained for the inward movements' curvature index. For details, see Jax (2005).

### RT

Whereas the hand path data were virtually indistinguishable for the two groups tested in Experiment 2 and the group tested in Experiment 1, the same finding was not observed for RTs. The results are shown in Figure 11 and were analyzed with a 3 (group: random, predictable informed, predictable uninformed)  $\times$  2 (trial type:  $+$  or  $-$ )  $\times$  2 (previous trial type:  $+$  or  $-$ ) ANOVA. As shown in Figure 11, there was a main effect of group,  $F(2, 48) = 4.41$ ,  $p = .017$ , with the RTs in the informed group of Experiment 2 being shorter than the RTs in the uninformed group of Experiment 2 ( $p = .04$ ) as well as the participants in Experiment 1 ( $p = .02$ ). The latter two groups did not differ ( $p = .78$ ). Also replicating the results of Experiment 1, there was a main effect of previous trial

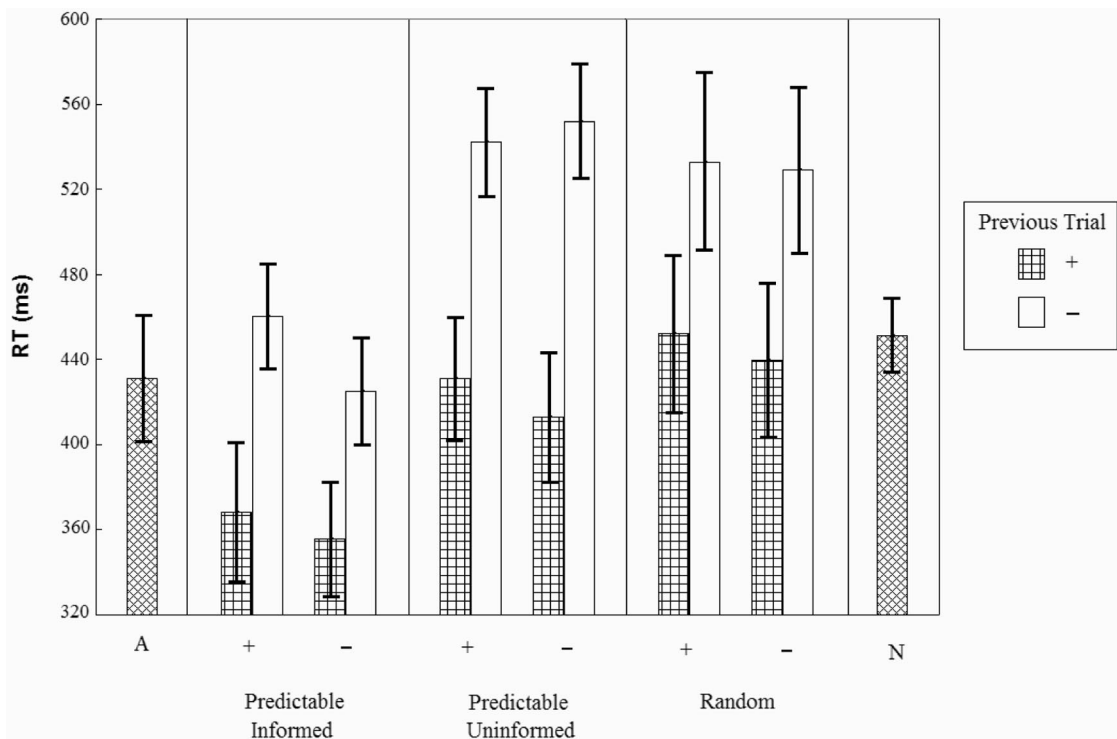


Figure 11. Mean reaction times (RTs;  $\pm 1$  SE, denoted by the error bars) for outward movements in Experiment 2 when an obstacle always appeared (A), when an obstacle could sometimes appear and did appear (+), when an obstacle could sometimes appear and did not appear ( $-$ ), and when an obstacle never appeared (N) for the group given instructions about sequence predictability (second panel) and for the group given no instructions about sequence predictability (third panel), along with data from Experiment 1 (all other panels).

type,  $F(1, 48) = 98.82, p < .001$ , with RTs being longer following trials without obstacles than following trials with obstacles.

### MT

As in Experiment 1, a strong correlation between mean curvature index and mean MT was observed for both groups of Experiment 2. For the informed group, the correlation was .99 ( $p = .01$ ), and for the uninformed group, the correlation was .98 ( $p = .02$ ). No differences in MT were observed among the three groups,  $F(2, 48) = 0.03, p = .96$ , as confirmed with a 3 (group: random, predictable uninformed, predictable informed)  $\times$  2 (trial type: + or -)  $\times$  2 (previous trial type: + or -) ANOVA. All interactions between group and the other variables were unreliable (all  $F$ s  $< 1$ ).

### Discussion

The goal of Experiment 2 was to determine whether the hand path priming effects observed in Experiment 1 were caused by expectations about the upcoming trial or by the reuse of previous movement plans. To distinguish between these two accounts, we used a predictable trial sequence in Experiment 2 and compared the results with those of Experiment 1, in which obstacle presence or obstacle absence was random in the mixed condition. On the basis of the expectancy hypothesis, we predicted that the priming effects when obstacle presence was predictable would be smaller than when obstacle presence was unpredictable, but on the basis of the reuse hypothesis, we predicted that the priming effects would not depend on obstacle predictability. The results support the reuse hypothesis. There were no significant differences in hand paths for the predictable sequences of Experiment 2 and the unpredictable sequences of Experiment 1.

We further distinguished between the expectancy hypothesis and the reuse hypothesis by telling or not telling participants about the predictable sequence order in Experiment 2. We found no differences between the hand paths of the two groups. On the one hand, this outcome is consistent with the view that participants were so tuned in to the sequential properties of the trials that telling them about it was unnecessary. On the other hand, because neither group's hand paths differed from the hand paths of the participants tested in Experiment 1, in which the sequence was random, another interpretation of the findings is preferable. According to this alternative interpretation, giving participants advance information about sequence order was simply unimportant to them. Expressing this idea another way, and in a way that repeats the main conclusion of Experiment 1, it was not especially costly for participants to make needlessly curved movements, whereas it was costly for participants to engage in the computational processes associated with straightening forthcoming hand paths. This interpretation is consistent with the reuse hypothesis rather than the expectancy hypothesis.

There is, however, yet another interpretation of the lack of difference between the informed and uninformed participants of Experiment 2 that must be considered, though it can be easily dismissed. According to this other interpretation, the informed participants simply did not listen to the instructions. The RT results argue against this interpretation, for RTs were shorter for the informed group in Experiment 2 than for both the uninformed group in Experiment 2 and for the participants of Experiment 1

(see Figure 11). This outcome shows that the instructions made a difference.

A final noteworthy feature of the results of Experiment 2 pertains to the fact that even though the RTs were shorter for the informed participants of Experiment 2 than for the other groups, the time it took for them to start moving from the center circle toward the next tested target was longer following trials without obstacles than following trials with obstacles. This pattern held for both groups in Experiment 2 and replicates what was found in Experiment 1. The consistency of the effect calls for an explanation. The third and final experiment was designed to provide one.

### Experiment 3

Why were RTs longer following trials without obstacles than following trials with obstacles? One possibility is related to the fact that obstacle locations were correlated with target locations. If participants picked up on this correlation, they may have narrowed the focus of their visual attention toward the center of the workspace if recent trials favored the likelihood of obstacle appearance, and they may have expanded the focus of their visual attention out toward the periphery if recent trials favored the likelihood of obstacle absence. Assuming that visual search is more efficient at smaller than larger eccentricities (Carrasco, Evert, Chang, & Katz, 1995; Wolfe, O'Neill, & Bennett, 1998), RTs would have been shorter when obstacles were likely than when obstacles were unlikely. To turn this post hoc account of the previous RT results into a prediction about new RT results, we ran another replication of Experiment 1 but with the probability of obstacles in mixed trials being .75 for one group of participants and .25 for another group of participants. The attention model outlined above predicted that RTs would shorten as the likelihood of an obstacle increased.

Using obstacle probabilities of .75 and .25 also allowed us to probe the limits of the hand path priming effects obtained in Experiments 1 and 2. In Experiment 1, hand path priming effects were still evident after three repetitions of an obstacle-present or obstacle-absent trial. However, because the probability of an obstacle was .50, the number of successive trials in which obstacles consistently appeared or did not appear was too small to determine when the priming effects would disappear. Using obstacle probabilities of .75 and .25 allowed us to extend the range of trials over which evidence for priming could be obtained.

### Method

The method was the same as in the mixed conditions of Experiment 1, except for the probabilities of obstacles. For one group of participants, the probability of obstacle-present trials was .25, whereas for another group of participants, the probability of obstacle-present trials was .75. Otherwise, as in Experiment 1, obstacle-present trials occurred randomly within each block. Each group included 17 participants. None of the participants in Experiment 3 had been in Experiment 1 or 2.

### Results

Trials in which any IRED was out of view of the OPTOTRAK (approximately 2.6% of trials) were removed from analysis, as

were trials in which there was a collision with an obstacle (approximately 1.7% of trials). The frequency of collisions was similar across the two probability conditions. Data from Experiment 1 ( $p = .50$ ) are included in the analyses and in the figures described below to facilitate evaluation of the effect of obstacle probability.

### *Outward Movements*

*Initial angular offsets and hand path curvature.* Figure 3 shows the initial angular offsets for the outward movements. Overall, the less likely an obstacle was, the more directly toward the target the hand initially moved. Nonetheless, there was evidence for hand path priming in all three obstacle probability conditions. Initial angular offsets were evaluated with a 3 (obstacle probability: .75, .50, or .25)  $\times$  2 (trial type: + or -)  $\times$  2 (previous trial type: + or -) ANOVA. In this analysis, all main effects were significant ( $p < .001$  for each), as was the three-way interaction,  $F(2, 48) = 6.12, p = .004$ , in which the effect of previous trial type was smaller in the obstacle-absent trials of the .25 condition than in the obstacle-absent trials of the .50 or .75 conditions, a difference that was not observed across probabilities for obstacle-present trials.

All obstacle-present conditions of the mixed blocks had initial angular offset values that were lower than those in the A condition ( $p < .05$ ). Initial angular offsets on all obstacle-absent trials of the mixed-trial blocks were higher than those in the N condition ( $p < .05$ , Bonferroni corrected) except for obstacle-absent trials of the .25 probability condition preceded by other obstacle-absent trials. Analogous effects of obstacle probability, trial type, and previous trial type on curvature index were obtained for the obstacle-absent but not for the obstacle-present trials, which showed no effect of obstacle probability or previous trial type (see Figure 4). For more details, see Jax (2005).

*Effect of obstacle recency.* The effects of obstacle recency on initial angular offsets for outward movements are shown in Figure 5 and were evaluated using single-factor ANOVAs (including all values of recency for a given probability) performed separately for obstacle-present and obstacle-absent trials. Significant effects of obstacle recency were observed for obstacle-present trials and obstacle-absent trials of all probabilities ( $p < .001$  for each) such that movements became less curved with fewer preceding obstacle-present trials or with more preceding obstacle-absent trials. With more repetitions of a given trial type (either obstacle present or obstacle absent), initial angular offsets became more similar to their corresponding blocked controls. Thus, on obstacle-absent trials of the .25 condition, initial angular offsets returned to levels comparable ( $p > .05$ ) with those observed in the N condition when preceded by two or more obstacle-absent trials. Likewise, on obstacle-present trials of the .75 condition, initial angular offsets returned to levels comparable ( $p > .05$ ) with those observed in the A condition when preceded by four or more other obstacle-present trials. Analogous effects of obstacle probability and obstacle recency on curvature index were obtained for the obstacle-absent but not for the obstacle-present trials, which showed no effects of either obstacle probability or obstacle recency. For more details, see Jax (2005).

*Angular separation between targets in successive trials.* Although there was an overall effect of obstacle probability on hand path curvature, with lower obstacle probabilities associated with

less curvature, the effects of angular separation between targets in successive trials were essentially the same across probabilities, as seen in Figure 6. This was confirmed with two 3 (obstacle probability)  $\times$  6 (angular separation) ANOVAs, performed separately for - + and + - trials. For the initial angular offset measure of - + trials, there was a main effect of obstacle probability,  $F(2, 48) = 5.57, p = .007$ , no main effect of angular separation,  $F(5, 240) < 1$ , and no interaction between obstacle probability and angular separation,  $F(10, 240) < 1$ . For the initial angular offsets of + - trials, there was a main effect of obstacle probability,  $F(2, 48) = 6.20, p = .004$ , a main effect of angular separation,  $F(5, 240) = 8.50, p < .001$ , and no interaction between obstacle probability and angular separation,  $F(10, 240) < 1$ .

Analogous effects of obstacle probability and angular separation on curvature index were obtained for the obstacle-absent but not for the obstacle-present trials, which showed no effects of obstacle probability or angular separation. For more details, see Jax (2005).

### *Inward Movements*

Initial angular offsets for the inward movements of Experiment 3 are plotted in Figure 7 and were analyzed using a 3 (obstacle probability: .75, .50, or .25)  $\times$  2 (trial type: + or -)  $\times$  2 (previous trial type: + or -) ANOVA. All main effects and interactions were reliable at the  $p < .05$  level, except the main effect of probability ( $p = .17$ ) and the three-way interaction ( $p = .09$ ). When the effect of previous trial type was analyzed separately for each probability, hand path priming from the outward movements only carried over to the inward movements for the obstacle-absent trials of the .25 and .50 conditions. That is, the inward portions of the obstacle-absent trials in the .25 and .50 probability conditions were more curved when the outward portion of the trial had been preceded by an obstacle-present trial than when the outward portion of the trial had been preceded by an obstacle-absent trial. An overall effect of mixing the two trial types was observed in the .75 condition, though, such that inward movements were reliably more curved than in the N condition ( $p < .05$ ). Analogous results were obtained with the hand path curvature index measure. For more details, see Jax (2005).

### *RT*

The mean RTs obtained in Experiment 3 are included in Figure 8 and were analyzed using a 3 (obstacle probability: .75, .50, or .25)  $\times$  2 (trial type: + or -)  $\times$  2 (previous trial type: + or -) ANOVA. All three main effects and interactions were statistically significant ( $p < .05$ ), except for the three-way interaction ( $p = .615$ ) and the interaction between obstacle probability and trial type ( $p = .881$ ). Overall, RTs increased as the likelihood of obstacles decreased. In addition, when the effect of previous trial type was analyzed for each probability, the magnitude of the difference between RTs after obstacle-absent and after obstacle-present trials decreased as obstacles became less likely.

### *MT*

As in Experiments 1 and 2, the relation between MT and overall hand path curvature was strong in Experiment 3, as shown in Figure 9. The correlation between mean curvature index and mean

MT was .998 ( $p = .002$ ) for the .75 condition and .996 ( $p = .004$ ) for the .25 condition. When the data from all three probabilities were pooled (all points in Figure 9), the correlation between mean curvature index and mean MT was .946 ( $p < .001$ ).

### *Discussion*

The third experiment replicated and extended the findings of Experiments 1 and 2. As in the first two experiments, initial angular offsets and hand path curvature were higher following obstacle-present trials than following obstacle-absent trials. Thus, hand path priming was observed even when obstacle-present trials and obstacle-absent trials were not equally likely. In addition, by increasing the number of possible trial type repetitions in Experiment 3, we were able to show that hand path priming was eliminated (i.e., mixed conditions approximated blocked conditions) after a sufficient number of repetitions of obstacle-present or obstacle-absent trials following a switch to that type of trial. For obstacle-absent trials, hand path priming was eliminated after approximately two repeated trials in the .25 obstacle probability condition, and for obstacle-present trials, hand path priming was eliminated after approximately four repeated trials in the .75 obstacle probability condition.

The final aspect of the results discussed in this section concerns the RTs. The attention model introduced in the opening section of this experiment predicted that RTs would not only be longer after obstacle-absent trials than after obstacle-present trials but would also increase as obstacle probabilities decreased. Both of these predictions were supported. Finding that RTs were longer after obstacle-absent trials than after obstacle-present trials replicates what was found in Experiments 1 and 2, and the finding that RTs increased as obstacle probabilities decreased confirmed the prediction of the attention model.

There was another feature of the RT results that can be accounted for with the attention model. This was the finding that the difference between RTs after obstacle-present and obstacle-absent trials decreased as obstacles became less likely. The attention model can account for this outcome by saying that when the focus of attention was wide (when obstacles were unlikely overall), there was not much effect on the time to localize targets that either were or were not accompanied by obstacles. By contrast, when the focus of attention was narrower (when obstacles were likely overall), it mattered more whether obstacles did or did not appear.

### *General Discussion*

According to a prominent theory of human perception and performance (Goodale & Milner, 1992), the dorsal, action-related stream controls visually guided actions in real time. Such a system would be predicted to show little or no priming from previous experience. In contrast to this claim, we proposed that the dorsal stream controls hand paths by reusing properties from previous plans, a process that should produce action priming. The three experiments reported here were designed to determine whether priming effects exist for visually guided hand movements to targets with obstacles sometimes in the way. We asked our participants to perform reaching movements in the presence of or in the absence of an intervening obstacle. In support of the plan reuse hypothesis, we found clear evidence for action priming: Move-

ments in obstacle-absent trials were more curved when preceded by obstacle-present trials than when preceded by obstacle-absent trials, and obstacle-present movements were less curved if preceded by obstacle-absent movements than if preceded by obstacle-present movements. Priming was not limited to effects of the immediately preceding trial but depended on the past several trials. Priming also generalized across the workspace. Experiment 2 showed that evidence for plan reuse could not be explained by active anticipation. Experiment 3 showed that the priming persisted for many trials. In all three experiments, RTs were longer following obstacle-absent trials than following obstacle-present trials. Experiment 3 showed that RTs decreased as obstacles became more likely.

In the remainder of this General Discussion, we take up three issues. The first issue is why action priming occurred in the present study but not in some previous studies. The second issue is the presentation of a control scheme for planning obstacle-avoiding movements that can account for the observed priming effects, followed by a discussion of how this control scheme relates to other theories of motor control. The third issue is how the attention model, developed to account for the RT data, fits with the conclusions we have reached about motor control.

### *Conflicting Evidence for Dorsal Stream Priming*

The first issue our results raise is why action priming occurred in the present study but not in other studies of dorsal stream processing (e.g., Cant et al., 2005; Garofeanu et al., 2004). The most likely explanation is that priming can occur for some movement properties but not for others. This was true in the present study; we observed priming in hand path properties and MTs but not in initiation times. Similarly, in studies of action priming in the mirror-neuron system, Castiello et al. (2002) and Edwards et al. (2003) reported that some, but not all, movement properties can be primed. Thus, by only measuring movement initiation times, Cant et al. (2005) and Garofeanu et al. (2004) may have failed to obtain evidence for priming of other movement properties. Replications of these studies with more detailed measurement of the produced movements would be needed to confirm this hypothesis.

### *Proposed Control Scheme for Obstacle Avoidance*

That we observed priming presumably within the dorsal stream led us to consider what forms of lingering representations the dorsal stream might be able to maintain if processing does not occur entirely in real time. Does evidence for hand path priming imply that the dorsal stream maintained a complex representation of the entire hand path between movements? Or could the maintenance of a single movement parameter account for the observed priming effects? From our results, we believe that our participants may have maintained in working memory an abstractly defined hand path that could be applied to a range of directions as well as to both the outward and return movements. The coordinate frame in which the hand path was defined appears to have had its origin at the center of the workspace (in the center circle) and to have been rotatable so its primary axis extended to whichever target was tested. The length and direction of the orthogonal axis of this coordinate frame may have been altered to adjust a hand path's curvature index and, by implication, the initial angular offset

(notwithstanding online correction). If such a control scheme was used (for potentially supporting evidence, see Flash & Sejnowski, 2001; Sosnik, Hauptmann, Karni, & Flash, 2004), our hand path priming data could be explained by a lingering representation of a single parameter: the length of the axis orthogonal to the direct movement path. Thus, the dorsal stream may have retained this orthogonal-axis length from previous plans to form a rough template for upcoming hand paths. Then, after target presentation, this template may have been completed in real time to produce the full hand path. Future research will be needed to verify this proposition and examine priming for other movement parameters.

Our proposed mechanism for plan reuse is consistent with the claim of many theories of motor control (Flash & Hogan, 1985; Harris & Wolpert, 1998; Morasso, 1981; Uno, Kawato, & Suzuki, 1989) and obstacle avoidance (Bullock, Bongers, Lankhorst, & Beek, 1999; Hamilton & Wolpert, 2002; Sabes & Jordan, 1997), which assert that planning of hand movements primarily is done with respect to extrinsic (spatial, workspace) coordinates. One aspect of our results provides a new source of evidence for this claim, namely that hand path priming generalized over the workspace. This outcome suggests that priming effects such as those observed here must be ascribed to a high-level spatial representation and cannot merely be ascribed to lower level joint or muscle-command representations.

Surprisingly, the theories of extrinsic motor planning alluded to above do not predict priming effects of the sort found here (but see Sosnik et al., 2004). We doubt that any of these theories would strongly deny the possibility of priming effects, but the only theory of motor planning that explicitly predicts priming is one that, ironically, has focused on joint-level planning. This theory is from our own laboratory (Jax, Rosenbaum, Vaughan, & Meulenbroek, 2003; Rosenbaum, Meulenbroek, Vaughan, & Jansen, 2001) and focuses on the importance of specifying goal postures (vectors of joint angles) for movement planning after spatially defined goal positions are chosen. The theory's claims about the lower level production system are not critical for present purposes, except that the theory assumes that recently adopted motor solutions become favored candidates for future tasks. Because the theory of motor planning advanced by Jax et al. (2003) and Rosenbaum et al. (2001) is restricted to postures and movements in joint space, it does not predict the kind of widespread spatial generalization of priming found here. The theory is mute on the possibility of such generalization. Considering what the Jax–Rosenbaum theory says vis-à-vis what the other theories, cited above, say about motor planning, it is clear that some new theory is needed that combines the possibility of learning and priming effects with planning in extrinsic as well as intrinsic coordinates.

Whatever hybrid theory is developed, one feature it will need is a way of reconciling the seemingly incommensurate units of biomechanical costs, on the one hand, and computational costs, on the other hand. Our participants were willing to tolerate biomechanical inefficiency (i.e., generating hand paths that were more curved than strictly necessary) when additional planning or motor reprogramming would have been required to further reduce biomechanical costs. Moving in a more curved path than needed generally consumes more energy and takes more time than moving in a straight line. However, mentally changing a motor program also takes time (Meyer & Gordon, 1985; Rosenbaum & Kornblum, 1982) and presumably also uses other cognitive or neural re-

sources. Somehow our participants decided how to balance the need for reducing biomechanical and computational costs. The way they did so—how they compared these “apples and oranges”—is an important question for future research.<sup>4</sup>

#### *Attentional Model for Target Selection*

The final issue to be addressed here is how the attention model, developed to account for the RT data, fits with the conclusions we reached about motor control in this series of experiments. One noteworthy feature of the model is that it only relies on ideas about visual attention to account for the RTs. Motor programming and reprogramming do not figure in the model because nothing in the RT data requires the inclusion of these processes. Thus, it was not the case that RTs were consistently longer for obstacle-present trials than for obstacle-absent trials, as might have been expected if participants needed extra time to prepare curved rather than straight hand paths. Similarly, RTs were not longer when obstacles failed to occur and obstacles were likely than when obstacles failed to occur and obstacles were unlikely. One might have expected such an outcome if participants had spent time reprogramming provisional hand paths when likely obstacles failed to appear. Given that motor reprogramming is known to be time consuming (Meyer & Gordon, 1985; Rosenbaum & Kornblum, 1982), the fact that there was no reliable difference in RTs for the two conditions mentioned above provides further, indirect support for the idea that participants did not engage in significant motor reprogramming in these experiments. Such motor reprogramming might occur under other circumstances, for example, if much larger obstacles were used or if considerable force were required to avoid obstacles—say if a spring were attached to the hand perpendicular to the direct path from the home to the target. These possibilities can be explored in the future.

Another useful question for the future is whether the nature of the previously described attention allocation strategy interacts with motor demands more so than was evident here. Visual attention is known to be sensitive to hand motions through the space in which visual attention is directed (Tipper, Lortie, & Baylis, 1992). Such an interaction between attention and motor demands may underlie two findings in the RT data that are not entirely consistent with our attention allocation model. First, although there was a trend toward RTs being longer when the obstacle never appeared than when the obstacle always appeared, this difference was not as large as the RT difference in the mixed-trial conditions between trials preceded by obstacle-present trials and those preceded by obstacle-absent trials. Our attention model would predict that these differences should be the same. Second, our attention model would predict long RTs for obstacle-absent trials preceded by obstacle-present trials because attention would have to be shifted from the inner circle of obstacle locations to the periphery. RTs were not longer on these trials than on other trials in which attention was focused on the outer circle of target locations. Whether and how such attentional strategies depend on the detailed properties of forthcoming as well ongoing movements is a worthwhile issue for future research.

<sup>4</sup> One way of dealing with this issue is to assume a constraint hierarchy in which different costs are rank ordered for the task to be completed. The best solution is the one that satisfies the most constraints from top to bottom (Jax et al., 2003; Rosenbaum et al., 2001).



Finally, is there a conflict between our suggestion that, on the one hand, the hand path priming effects observed here reflected passive aftereffects rather than active anticipation versus our suggestion, on the other hand, that the RTs reflected visual attention? We think not. Perceptual preparedness can change without conscious mediation just as movement tendencies can.

## References

- Bullock, D., Bongers, R. M., Lankhorst, M., & Beek, P. J. (1999). A vector-integration-to-endpoint model for performance of viapoint movements. *Neural Networks, 12*, 1–29.
- Buxbaum, L. J. (2001). Ideomotor apraxia: A call to action. *Neurocase, 7*, 445–458.
- 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.
- Carrasco, M., Evert, D. L., Chang, I., & Katz, S. M. (1995). The eccentricity effect: Target eccentricity affects performance on conjunction searches. *Perception & Psychophysics, 57*, 1241–1261.
- Castiello, U., Lusher, D., Mari, M., Edwards, M., & Humphreys, G. W. (2002). Observing a human or robotic hand grasping an object: Differential motor priming effects. In W. Prinz & B. Hommel (Eds.), *Common mechanisms in perception and action: Attention and performance XIX* (pp. 315–333). New York: Oxford University Press.
- Cave, B. C. (1997). Very long-lasting priming in picture naming. *Psychological Science, 8*, 322–325.
- Cohen, R. G., & Rosenbaum, D. A. (2004). Where objects are grasped reveals how grasps are planned: Generation and recall of motor plans. *Experimental Brain Research, 157*, 486–495.
- Craigheo, L., Bello, A., Fadiga, L., & Rizzolatti, G. (2002). Hand action preparation influences the responses to hand pictures. *Neuropsychologia, 40*, 492–502.
- Craigheo, L., Fadiga, L., Rizzolatti, G., & Umiltà, C. (1998). Visuomotor priming. *Visual Cognition, 5*, 109–125.
- Craigheo, L., Fadiga, L., Umiltà, C. A., & Rizzolatti, G. (1996). Evidence for visuomotor priming effect. *NeuroReport, 8*, 347–349.
- Edwards, M. G., Humphreys, G. W., & Castiello, U. (2003). Motor facilitation following action observation: A behavioural study in prehensile action. *Brain and Cognition, 53*, 495–502.
- Elliot, D., Helsen, W. F., & Chua, R. (2001). A century later: Woodworth's (1899) two component model of goal-directed aiming. *Psychological Bulletin, 127*, 342–357.
- Flash, T., & Hogan, N. (1985). The coordination of arm movements: An experimentally confirmed mathematical model. *Journal of Neuroscience, 5*, 1688–1703.
- Flash, T., & Sejnowski, T. J. (2001). Computational approaches to motor control. *Current Opinion in Neurobiology, 11*, 655–662.
- Garofeanu, C., Kroliczak, G., Goodale, M. A., & Humphreys, G. K. (2004). Naming and grasping common objects: A priming study. *Experimental Brain Research, 159*, 55–64.
- Glover, S. (2004). Separate visual representations in the planning and control of action. *Behavioural and Brain Sciences, 27*, 3–24.
- Goodale, M. A., & Milner, A. D. (1992). Separate visual pathways for perception and action. *Trends in Neuroscience, 15*, 20–25.
- Hamilton, H., & Wolpert, D. M. (2002). Controlling the statistics of action: Obstacle avoidance. *Journal of Neurophysiology, 87*, 2434–2440.
- Harris, C. M., & Wolpert, D. M. (1998, August 20). Signal-dependent noise determines motor planning. *Nature, 394*, 780–784.
- Hu, Y., & Goodale, M. A. (2000). Grasping after a delay shifts size-scaling from absolute to relative metrics. *Journal of Cognitive Neuroscience, 12*, 856–868.
- Jax, S. A. (2005). *Sequential effects in reaching around obstacles*. Unpublished doctoral dissertation, Pennsylvania State University University Park Campus. Retrieved February 1, 2005, from <http://etda.libraries.psu.edu>
- Jax, S. A., Rosenbaum, D. A., Vaughan, J., & Meulenbroek, R. G. J. (2003). Computational motor control and human variables: Modeling movements in real and possible environments. *Human Variables, 45*, 5–27.
- Jeannerod, M., Decety, J., & Michel, F. (1994). Impairment of grasping movements following a bilateral posterior parietal lesion. *Neuropsychologia, 32*, 369–380.
- McIntosh, R. D., McClements, K. I., Dijkerman, H. C., Birchall, D., & Milner, A. D. (2004). Preserved obstacle avoidance during reaching in patients with left visual neglect. *Neuropsychologia, 42*, 1107–1117.
- Meyer, D. E., & Gordon, P. C. (1985). Speech production: Motor programming of phonetic features. *Journal of Memory and Language, 24*, 3–26.
- Milner, A. D., Paulignan, Y., Dijkerman, H. C., Michel, F., & Jeannerod, M. (1999). A paradoxical improvement of misreaching in optic ataxia: New evidence for two separate neural systems for visual localization. *Proceedings of the Royal Society of London, Series B: Biological Sciences, 266*, 2225–2229.
- Morasso, P. (1981). Spatial control of arm movements. *Experimental Brain Research, 42*, 223–227.
- Rizzolatti, G., & Craighero, L. (2004). The mirror-neuron system. *Annual Review of Neuroscience, 27*, 169–192.
- Rosenbaum, D. A., & Kornblum, S. (1982). A priming method for investigating the selection of motor responses. *Acta Psychologica, 51*, 223–243.
- Rosenbaum, D. A., Meulenbroek, R. G. J., Vaughan, J., & Jansen, C. (2001). Posture-based motion planning: Applications to grasping. *Psychological Review, 108*, 709–734.
- Rosenbaum, D. A., Weber, R. J., Hazelett, W. M., & Hindorf, V. (1986). The parameter remapping effect in human performance: Evidence from tongue twisters and finger fumlbers. *Journal of Memory and Language, 25*, 710–725.
- Sabes, P. N., & Jordan, M. I. (1997). Obstacle avoidance and a perturbation sensitivity model for motor planning. *Journal of Neuroscience, 15*, 7119–7128.
- Schindler, I., Rice, N. J., McIntosh, R. D., Rossetti, Y., Vighetto, A., & Milner, A. D. (2004). Automatic avoidance of obstacles is a dorsal stream function: Evidence from optic ataxia. *Nature Neuroscience, 7*, 779–784.
- Sosnik, R., Hauptmann, B., Karni, A., & Flash, T. (2004). When practice leads to co-articulation: The evolution of geometrically defined movement primitives. *Experimental Brain Research, 156*, 422–438.
- Tipper, S. P., Lortie, C., & Baylis, G. C. (1992). Selective reaching: Evidence for action-centered attention. *Journal of Experimental Psychology: Human Perception and Performance, 18*, 891–905.
- Uno, Y., Kawato, M., & Suzuki, R. (1989). Formation and control of optimal trajectory in human multijoint arm movement: Minimum torque-change model. *Biological Cybernetics, 61*, 89–101.
- van Turennout, M., Bielaowicz, L., & Martin, A. (2003). Modulation of neural activity during object naming: Effects of time and practice. *Cerebral Cortex, 13*, 381–391.
- Vogt, S., Taylor, P., & Hopkins, B. (2003). Visuomotor priming by pictures of hand postures: Perspective matters. *Neuropsychologia, 41*, 941–951.
- Westwood, D. A., & Goodale, M. A. (2003). Perceptual illusions and the real-time control of actions. *Spatial Vision, 16*, 243–254.
- Wolfe, J. M., O'Neill, P., & Bennett, S. C. (1998). Why are there eccentricity effects in visual search? Visual and attentional hypotheses. *Perception & Psychophysics, 60*, 140–156.

Received September 26, 2005

Revision received May 30, 2006

Accepted June 3, 2006 ■