Evidence for Motor Simulation in Imagined Locomotion

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A series of experiments examined the role of the motor system in imagined movement, finding a strong relationship between imagined walking performance and the biomechanical information available during actual walking. Experiments 1 through 4 established the finding that real and imagined locomotion differ in absolute walking time. We then tested whether executed actions could provide a basis for imagined walking rate using 2 approaches. Experiments 5 and 6 used a perceptual-motor recalibration paradigm, finding that after physically walking in a treadmill virtual reality environment, actors recalibrated the time to imagine walking to a previously viewed target. This finding mirrors previous perceptual-motor recalibration work measuring actual walking to previously viewed targets. Experiments 7 and 8 used a dual-task paradigm in which actions performed concurrently with imagined walking increased the similarity between real and imagined walking time, but only when they were biomechanically consistent with the act of walking. The striking influence of biomechanical information on imagined locomotion provides evidence for shared motor systems in imagined and executed movements and is also directly relevant to the mechanisms involved in egocentric spatial updating of environmental layout.

Keywords: motor imagery, locomotion, spatial updating, space perception

Imagining an action can serve a number of useful goals such as preparation for and prediction of the outcome of an action, memory of a previous event, or interpretation of others’ actions and intentions (Gallese & Lakoff, 2005; Jeannerod, 1994; Johnson-Frey, McCarty, & Keen, 2004). There is substantial research suggesting that imagined actions share similar underlying mechanisms and functional goals with physically executed actions, a claim often referred to as functional equivalence. Two dominant methodological approaches have supported this claim: response time data collected in behavioral experiments, and measures of neural activity through functional neuroimaging techniques. Neuroimaging research demonstrates similar, but not identical, brain activation in real and imagined movement tasks (Grezes & Decety, 2001; Michelon, Vettel, & Zacks, 2006). Response time measures generally indicate that the time required to physically move the body or a body part is highly correlated to the time required to imagine the movement, regardless of whether explicit instructions are given to imagine the movement (Decety, Jeannerod, & Prablanc, 1989; Decety & Michel, 1989; Jeannerod, 1994, 1995, 2001; Papaxanthis, Pozzo, Skoura, & Schieppati, 2002; Papaxanthis, Schieppati, Gentili, & Pozzo, 2002; Parsons, 1994). Despite the evidence that people can and do imagine actions, the extent to which actual computations for action known as motor simulation, versus memory and/or attentional processes are involved is not well established (Jeannerod, 1994; Michelon et al., 2006). Furthermore, claims about motor imagery and motor simulation have not been generalized across different types of actions.

The focus of the present work is on a task of imagined visually directed walking, which has received little investigation with respect to its motor mechanisms and could well involve different underlying processes compared to the imagined actions more typically studied involving arm and hand movements. Locomotion is particularly interesting and a unique example of imagined movement because it involves simulated full-body movement and the concurrent updating of environmental spatial information. Although claims have been made about the similarity of real and imagined walking in terms of response time, results about absolute timing are mixed and the extent of motor simulation remains unclear. Neuroimaging work has begun to make inferences about the similarity of real and imagined walking by finding brain activation in plausible spatial and motor regions (Jahn et al., 2004), but the methodology inherently prohibits real walking and limits any direct comparison—a limitation not faced in studies of simple discrete real and imagined actions such as hand movements. In addition, a distinct but related literature on memory for spatial layout suggests performance differences in spatial updating given real versus imagined movement (May, 2004; Rieser, 1989). The present work takes a behavioral approach to test more directly the role of motor simulation in imagined locomotion and spatial updating by manipulating the timing of imagined walking with the presence of biomechanical information. We find that providing biomechanical information associated with walking before or concurrent with imagined walking influences imagined walking performance, suggesting a direct link between real and simulated action in the context of full-body locomotion through space.

Studies of absolute distance perception to locations beyond arm’s reach frequently use an action-based measure of distance.
that involves walking to previously viewed targets without vision. The distance walked is used as an indicator of perceived absolute distance. It is generally believed that this blind-walking task relies on spatial updating of one’s position in space with movement and has been shown to be quite accurate for distances up to about 25 meters (Loomis, Da Silva, Fujita, & Fukusima, 1992; Rieser, Ashmead, Taylor, & Youngquist, 1990). Imagined walking may also serve as an indicator of spatial updating and consequently of distance perception as well. Several comparisons between physical and imagined blind walking have suggested functional equivalence through measures of response time. Decety et al. (1989) first demonstrated that imagined walking to target times were the same as blind walking to target times, at least for individuals with high-imagery ability. Plumert, Kearney, Cremer, and Recker (2005) compared time-to-walk to target estimates and blind walking to target and found accuracy in distance walked with equivalent performance in time-to-walk estimates (converted to distances by multiplying time estimates by participants’ eyes-open baseline walking speed). In two other experiments, Plumert et al. (2005) also found that time-to-walk estimates with eyes open or eyes closed did not differ from a baseline eyes-open walking speed for distances of 20 to 40 feet. Other studies have found equivalent mean walking times, though with increased variability in imagined walking times (Courtine, Papaxanthis, Gentili, & Pozzo, 2004; Papaxanthis, Pozzo et al., 2002).

Although the research described above suggests a clear systematic effect of increase in imagined walking time with increasing target distance, this is at most indirect evidence to support the claim that imagined locomotion is the covert simulation of actual walking, driven by the same motor system. It is possible that other high-level spatial cognitive processing could lead to the same results without direct motor simulation. Previous work on motor imagery has attempted to address this type of concern about other imagined tasks by demonstrating that both real and imagined actions conform to Fitts’ law (Bakker, De Lange, Stevens, Toni, & Bloem, 2007; Decety, 1993; Decety & Jeannerod, 1995; Decety & Michel, 1989; Stevens, 2005), face similar biomechanical constraints (Parsons, 1994), or are accompanied by analogous physiological responses (Decety, Jeannerod, Durozard, & Bavarel, 1993; Decety, Jeannerod, Germain, & Pastene, 1991). We sought to test the motor component of imagined locomotion by providing additional biomechanical information related to walking in two different ways: (a) perceptual-motor adaptation in a virtual environment prior to imagined walking, and (b) the addition of a secondary task performed concurrently with imagined walking.

One central difference between real and imagined locomotion is the absence of overt motor execution in imagined walking. Blind walking is accompanied by biomechanical feedback about movement speed via motor efferent copy, vestibular changes, and haptic feedback whereas imagined walking lacks all of these body-based indicators of movement. The biomechanical information lacking in imagined walking might provide critical information about rate of walking that must be mentally simulated to maintain and update memory for the spatial surroundings and spatial layout. Stevens (2005) demonstrated that biomechanical and cognitive interference affected imagined walking times, potentially by interfering with participants’ ability to mentally simulate walking. Results such as these may directly relate to results in the spatial updating domain, showing that real body movement facilitates pointing to targets compared to the same imagined movement transformation (e.g., May, 2004). We reasoned that if imagined locomotion does rely on similar processes as real walking, then manipulating biomechanical information associated with walking would influence imagined walking performance.

Prior work on the calibration of real locomotion suggested that observers recalibrate their actions quite easily as a result of the changing relationship between perceptual and biomechanical information for self-motion. Rieser, Pick, Ashmead, and Garing (1995) demonstrated this effect by having participants walk on a treadmill while it was pulled by a tractor at a speed different than their walking. Blind walking to targets on the ground, which was initially accurate, recalibrated. Visual motion slower than the participant’s biomechanical speed of walking led to an overshoot of distances in a posttest blind-walking task and visual motion faster than the participant’s biomechanical speed of walking led to an undershoot in the posttest. Pick, Rieser, Wagner, and Garing (1999) extended this effect to rotational locomotion. Recently, similar recalibration of real locomotion has been established using a treadmill virtual environment (VE; Mohler, Thompson, Creem-Regehr, Willemsen, et al., 2007) and head-mounted display virtual environments (Mohler, Creem-Regehr, & Thompson, 2006; Waller & Richardson, 2008). Together, the results show that after only minutes of adapting to a given relationship between the act of walking and the perceptual information specifying walking, actors will change their subsequent walking behavior. If imagined locomotion relies on the same perceptual-motor mechanisms as real locomotion, we should find similar recalibration effects for the imagined walking task.

Before testing the role of manipulated biomechanical information associated with walking on imagined locomotion, we felt it important to establish the methodology and results of a visually directed imagined walking task. As stated above, a few studies have compared the timing of real and imagined walking and suggested equivalent absolute timing. Others, however, have found a temporal difference between the two tasks, finding faster imagined walking compared to real walking in a path-following task (Stevens, 2005). The aim of the first experiment presented here was to establish the methodology of imagined walking in our own laboratory, closely following the design of Decety et al.’s (1989) earlier experiment. Our results indicated highly related real and imagined walking times, with a systematic bias of faster imagined versus real walking. Experiments 2 through 4 compared the time to walk or imagine walking to previously viewed targets, manipulating motor preparation, visual input, or task type order, to demonstrate that this discrepancy between real and imagined walking time was replicable and not due to a number of specifics about our methodology. Following this, the final four experiments manipulated biomechanical information. Experiments 5 and 6 utilized the adaptation design in a treadmill VE established in Mohler, Thompson, Creem-Regehr, Willemsen, et al. (2007) to assess the influence of perceptual-motor adaptation on imagined walking. Experiments 7 and 8 returned to testing in the real-world but provided additional biomechanical information through a concurrent task related (stepping in place) or unrelated (hand movements) to the act of walking.

Experiment 1

The intent of the first experiment was to establish the methodology to compare real and imagined locomotion and to examine the behavioral similarity between the two tasks. More specifically,
we wanted to determine if the earlier claim of equivalence between real and imagined walking times to target held for a more general population than the “high imagers” tested by Decety et al. (1989). Our own pilot work as well as recent work in other labs (Stevens, 2005) suggested that imagined walking time would resemble real walking time, but that it would be systematically shorter (i.e., imagined walking rate would be faster than real walking rate). We closely followed the paradigm used by Decety et al. (1989) in which participants were cued to walk or imagine walking after viewing a target and lowering a blindfold, but we did not screen for imagery ability.

Method

Participants. Thirteen participants completed Experiment 1. Undergraduate participants were compensated with credit towards fulfilling a course requirement; participants from the university community were compensated with $10 for their participation. Each participant was run through the experiment individually over the course of approximately 1 hr. We followed a criterion that participants with real or imagined walking times three or more standard deviations from the mean times were excluded from further analysis. One participant in this experiment was excluded.

Materials. The experiment was conducted in a hallway approximately 3-m wide and approximately 24-m long between the participant starting point and the end of the hallway. The hallway was lined with a series of closed doors on both sides, electrical outlets, and some posters. The participant starting location and target placement locations were marked on the tiled floor at distances of 4, 6, and 8 m but were not visible to the participant.

Targets consisted of six flat objects constructed from foamboard approximately 1-cm thick and covered with colored posterboard. Three triangular targets varied in size and color, ranging from 20 cm to 29 cm along the triangular leg and three hexagonal targets varied in size and color, ranging from 19 cm to 29 cm along each side. Targets were randomly mixed with distance to avoid associations between certain target shapes or sizes and target distances. To discretely move targets out of the path of walking participants, a fishing line was attached to the target on each trial; the line was routed along the baseboard of the right wall and terminated behind the participant. A second experimenter pulled the line to silently move the target out of the path of the blindfolded, walking participant.

Noise-canceling headphones were used to reduce sound localization as a cue to position tracking and a wireless microphone was used to avoid acoustic localization of the experimenter. A blindfold was constructed from safety goggles blacked out with black acrylic paint and black felt. Distances walked during the blindwalking task were measured using a Sonin Combo Pro ultrasonic distance measuring device (Sonin model 10300, Charlotte, NC). Time to walk or imagine walking to target was recorded from the handheld stopwatch held by the participant.

Procedure. After providing informed consent, participants were tested for visual acuity. Participants unable to read an eye chart at 20/30 or better or who demonstrated lack of stereo fusion were excluded from analysis. After reading written instructions for the task, participants were outfitted with noise-canceling headphones and a blindfold and were informed as to the general nature of the task to be completed. Participants then practiced blind walking in a hallway, first being led by an experimenter by the shoulders and then walking independently with an experimenter following behind and providing verbal indications of when to turn and stop. After approximately 5 min of blind walking, or until the participant demonstrated and professed comfort with blind walking, the experimenter verbally described and demonstrated the experimental task. Participants informally practiced the tasks to be completed during the experiment proper (without performance feedback), reinforcing the written and verbal instructions for the participant and allowing the experimenter to ensure proper understanding of the task.

Participants were instructed to view a target on the floor in a hallway and to attempt to form a “mental image” of the hallway and target, so that when they closed their eyes, they could visualize the hallway scene described above. Participants were instructed to spatially update their position in the hallway as they walked or imagined walking to the target and to avoid using alternative strategies to direct their action or imagined action toward the target (i.e., counting steps, seconds, or using any metric). They were told to visualize their position in the hallway and in relation to the target as they walked or imagined walking towards the target and to stop walking or imagining walking when they reached the target and were standing directly on top of the target. To avoid providing tactile feedback about the target’s location, a second experimenter moved the target out of the participants’ paths while they walked. On real blind-walking trials, the blindfolded participants were guided by the experimenter back to the starting location. Participants were also instructed to start a handheld stopwatch simultaneously with their first step or imagined step in the walk towards the target and to stop the stopwatch simultaneously with their last step or imagined step onto the target’s location. On real blind-walking trials, the distance walked was recorded for each trial; for both real and imagined walking trials, the time to walk or imagine walking to target was recorded from the handheld stopwatch. After instruction and training, participants completed two practice trials without feedback (one real and one imagined walking) followed by 18 trials. These trials were randomly mixed between real and imagined walking trials and among distances and targets, with each of the three target distances (4, 6, or 8 m) repeated three times for both real and imagined walking.

On each trial, after viewing the scene for as long as necessary to form a mental image of the hallway and target, participants lowered a blindfold and were then verbally cued by the experimenter to either “walk” to the target or “imagine” walking to the target. On receiving the verbal cue, participants were instructed to immediately begin the cued task. At the completion of the trial, the experimenter read the time from the participant-held stopwatch and recorded the time, as well as the distance walked on real-walking trials. No feedback as to performance was provided until after the completion of the experimental session.

Results and Discussion

For each participant, the time to walk (in seconds) was averaged over three trials for each of three target distances for real walking and imagined walking. A 2 (task type) × 3 (distance) repeated-measures analysis of variance (ANOVA) revealed that imagined walking time ($M = 4.47$) was shorter than real walking time ($M = 5.70$), $F(1, 11) = 58.94$, $p < .001$, $\eta^2_p = 0.84$. Time to target
increased with distance, as indicated by a significant main effect of distance, $F(2, 22) = 55.91, p < .001, \eta^2_g = 0.92$; and planned linear contrast ($p < .001$; see Figure 1). There were no significant interactions between task type and target distance. A repeated-measures ANOVA conducted on variable error, a measure of within-subject variability calculated as the standard deviation of the means by distance for each participant, revealed no significant effects or interactions, although the effect of target distance approached significance.

These results suggest a discrepancy between absolute real and imagined walking time, unlike the Decety et al. (1989) results. Consistent with Decety et al., however, time to imagine walk and time to physically walk both increased systematically with increasing target distance. It is important to note as well that blind walking to targets was overall accurate, consistent with previous studies of blind walking (see Table 1). Although the similar linear increase in response time is suggestive of similar processes underlying real and imagined locomotion in this task, two questions are in need of further investigation. First, is the difference in absolute timing a function of the specific methodology used in the present task, or does it generalize to other variations of the task? This question was addressed in Experiments 2 through 4. Second, can more direct evidence for shared motor representations in real and imagined walking be found beyond simple comparisons between the timing of the real and imagined task? This second question was addressed in Experiments 5 through 8.

Experiment 2

Experiment 1 demonstrated a significant difference between the time to imagine walking to previously viewed targets and to physically walk to previously viewed targets. Because this result differed from a number of previous studies, we conducted several experiments that addressed several potential explanations. Experiment 2 was designed to test the hypothesis that preparation for imagined walking might be different than preparation for real walking. Such preparation might include attention to different aspects of the visual environment, some degree of preplanning of action or advanced recall of biomechanical walking rate. Unlike Experiment 1, participants in Experiment 2 were cued to the nature of the task (real or imagined) before they closed their eyes.

Method

Participants. Thirteen participants completed Experiment 2. Compensation and participation details were the same as in Experiment 1.

Materials. The same hallway, targets, and noise canceling headphones previously described in Experiment 1 were employed in Experiment 2.

Procedure. Experiment 2 mirrored that of Experiment 1 in all respects except that participants in Experiment 2 were provided with task knowledge in advance of closing their eyes to prepare for the two tasks. The experimenter gave participants a verbal cue to the type of task to be performed (“walk” or “imagine”) while they remained viewing the target and hallway. After the verbal cue, participants continued to view the hallway for as long as necessary before lowering the blindfold and beginning the cued task. This differed from the procedure of our first experiment in that Experiment 1 required participants to lower the blindfold before receiving the task cue to imagine or physically walk. As in Experiment 1, no performance feedback was provided.

Figure 1. Mean absolute time to target for real blind walking and imagined walking for Experiments 1 through 4. The gray and black lines for Experiment 4 represent the two task order conditions.
Table 1
Quantitative Results of Blind-Walking Task From Experiments 1 Through 4 and 7 and 8, Based on a Linear Fit Through the Mean Values for Each Target Distance

<table>
<thead>
<tr>
<th>Experiment</th>
<th>Slope</th>
<th>Intercept</th>
<th>R²</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.876</td>
<td>0.374</td>
<td>0.999</td>
</tr>
<tr>
<td>2</td>
<td>1.043</td>
<td>−0.532</td>
<td>0.999</td>
</tr>
<tr>
<td>3</td>
<td>0.994</td>
<td>−0.152</td>
<td>0.999</td>
</tr>
<tr>
<td>4</td>
<td>1.038</td>
<td>−0.186</td>
<td>0.999</td>
</tr>
<tr>
<td>7</td>
<td>0.871</td>
<td>0.107</td>
<td>0.999</td>
</tr>
<tr>
<td>8</td>
<td>1.001</td>
<td>−0.338</td>
<td>0.992</td>
</tr>
</tbody>
</table>

Results and Discussion

As in Experiment 1, imagined walking times (M = 4.72) were significantly shorter than real walking times to target (M = 5.60). A 2 (task type) × 3 (target distance) repeated measures ANOVA yielded significant differences between real and imagined times to target: F(1, 12) = 9.88, p = .008, η² = 0.45. There was also a main effect of task distance, F(2, 24) = 142.29, p < .001, η² = 0.92; planned linear contrasts suggest that time-to-target increased linearly with target distance for both tasks (p < .001; see Figure 1). There were no significant interactions. A repeated-measures ANOVA conducted on variable error as defined in Experiment 1 revealed no significant effects or interaction.

As in Experiment 1, it is also apparent that mean distance walked for the blind-walking task was accurate at all target distances (see Table 1). These results are consistent with a general finding of accuracy in blind walking that has been replicated in numerous studies (Loomis et al., 1992; Rieser et al., 1990), though there was an average tendency to undershoot target distances slightly. In conclusion, Experiment 2 suggests that biases in imagined walking are no due solely to different task preparation process for real and imagined walking. We continued to address potential causes for biased imagined walking performance in Experiment 3.

Experiment 3

Experiment 3 tested the role of vision during the imagined walking task. In Experiments 1 and 2, participants performed eyes-closed imagined walking, which intuitively might be predicted to facilitate imagined walking performance by reducing the visual conflict between one’s real and imagined position in the environment. However, it might also be that the additional processing required in remembering the visual environment with eyes closed added to the already cognitively taxing imagined walking task, and contributed to the discrepancy in response times. Eyes-open walking would reduce the need for visual memory of the environment and might lead to more similar absolute timing of real and imagined walking.

Method

Participants. Sixteen participants from the university community completed Experiment 3. Compensation and participation mirrored that described in Experiments 1 and 2.

Materials. The same hallway environment, stimuli, and other materials previously described were utilized in Experiment 3.

Procedure. Experiment 3 closely resembled Experiments 1 and 2 in design and materials used except that imagined walking trials were performed with eyes open. Initial measures and training and trial arrangement were identical to Experiments 1 and 2, but during practice and experimental trials participants were instructed to leave their eyes open during imagined walking trials. In addition, participants were instructed not to view the handheld stopwatch during eyes-open imagined walking trials.

Results and Discussion

As in Experiments 1 and 2, imagined walking times (M = 4.13) were significantly shorter than real blind-walking times (M = 5.25). A 2 (task type) × 3 (target distance) repeated measures ANOVA yielded significant differences between real and imagined times to target, F(1, 15) = 32.53, p < .001, η² = 0.68. In addition to a main effect of target distance, F(2, 30) = 268.71, p < .001, η² = 0.95 (p < .001 for planned linear contrasts; see Figure 1); there was also a significant interaction between target distance and task type, F(2, 30) = 11.53, p < .001, η² = 0.44. A repeated-measures ANOVA conducted on variable error as defined in Experiment 1 revealed no significant main effects or interactions. Consistent with Experiments 1 and 2 and prior work, mean distance walked for the blind-walking task was accurate at all target distances (see Table 1).

The results of Experiment 3 fail to demonstrate equivalent performance in the timing of real blind-walking and eyes-open imagined walking. The robust finding of faster imagined walking performance (as demonstrated by shorter imagined walking times) is not eliminated by providing supplementary visual information during imagined walking. In Experiment 4 we assessed whether shorter imagined walking times are due to order or practice effects.

Experiment 4

Experiment 4 assessed whether experience with one task would influence performance on the second task. To examine order and practice effects, we had participants complete a block of real blind walking to target trials followed by a block of imagined blind walking to target trials, or vice versa.

Method

Participants. Twenty-five participants completed Experiment 4 (12 in each of two groups after one was excluded as an outlier, per the criterion described in Experiment 1). Compensation and participation requirements were identical to Experiments 1 through 3.

Materials. The same hallway environment, stimuli, and other materials previously described in Experiments 1 through 3 were utilized in Experiment 4.

Procedure. Experiment 4 closely resembled Experiments 1 through 3 in design and materials used. Unlike Experiments 1 through 3, blind-walking and imagined walking trials were presented in blocks, with order counterbalanced across participants. Participants performed a block of 11 trials (2 initial practice trials) of blind walking followed by 11 trials (2 initial practice trials) of...
eyes-closed imagined walking. A second group of participants completed the counterbalanced condition, first performing the block of imagined walking trials followed by the block of real blind-walking trials. Within each block, participants walked or imagined walking to targets at randomized distances of 4, 6, or 8 m (as in Experiments 1 through 3).

Results and Discussion

A 2 (task type) × 3 (target distance) × 2 (task order) repeated-measures ANOVA with task order as a between-subject factor demonstrated no significant difference between performance as a function of the order of the task blocks. Here, as in Experiments 1, 2, and 3, imagined walking times \( (M = 4.84) \) were significantly shorter than real walking times \( (M = 5.69) \), \( F(1, 22) = 27.48, p < .001, \eta_p^2 = 0.56 \). As in the previously described experiments, there was also a main effect of target distance, \( F(2, 44) = 352.63, p < .001, \eta_p^2 = 0.94 \). Planned linear contrasts suggest that time-to-target increased linearly with target distance for both tasks \( (p < .001; \text{see Figure 1}) \). There were no significant interactions nor was there a main effect of task order.

A repeated-measures ANOVA conducted on variable error as defined in Experiment 1 revealed a significant effect of target distance, \( F(2, 44) = 6.38, p = .004 \). Planned linear contrasts suggested that the variable error increased with target distance \( (p = .012) \). Finally, as in the previously described experiments, mean distance walked for the blind-walking task was accurate at all target distances (see Table 1).

Between-Experiment Results for Experiments 1 Through 4

We found similar results between Experiments 1 through 4 in that imagined walking times were consistently shorter than real blind-walking times and followed-up this finding with a between-experiment analysis. Because each experiment included real and imagined walking as a within-subject factor, we calculated difference scores for each experiment between the mean real and imagined walking times for each participant at each distance and analyzed the difference scores using a 4 (experiment) × 3 (target distance) ANOVA, with experiment as a between-subject factor. Notably, there was no significant main effect of experiment \( (p = .48) \). There was a significant main effect of target distance, \( F(2, 122) = 8.03, p = .001, \eta_p^2 = 0.12 \) (for planned linear contrast); and an interaction between target distance and experiment, \( F(6, 122) = 2.48, p = .027, \eta_p^2 = 0.11 \). Repeated contrasts suggested the main effect of target distance resulted from an increase of the difference at 6 m and 8 m \( (p < .001 \text{ and } p = .024, \text{respectively}) \). Repeated measures ANOVAs on the difference scores conducted individually for each experiment revealed a significant effect of target distance only for Experiment 3, \( F(2, 30) = 11.53, p < .001, \eta_p^2 = 0.44 \); suggesting that a difference between times at distances of 6 m and 8 m in Experiment 3 contributed to the significant interaction.

We also compared sighted, blind, and imagined walking from additional data acquired from participants before Experiments 3 and 4. Participants in Experiments 3 and 4 performed three sighted-walking to target trials before the experiment session to test the hypothesis that the discrepancy between imagined and real blind-walking time was a result of a tendency for participants to walk more slowly with their eyes closed. It is possible that imagined walking speed would resemble the speed of eyes-open walking more than eyes-closed walking. This also allowed for a comparison that more closely followed the methodology of Plumert et al. (2005) who included a baseline eyes-open walking measure as well as a comparison between eyes-open and eyes-closed time-to-walk judgments. To test sighted walking, participants were led to an adjacent hallway and were asked to walk with vision to a target at each of three distances \( (5, 7, \text{and } 9 \text{ m}) \) before the start of the experiment. Participants self-timed their walks with the handheld stopwatch and they were instructed not to look at the stopwatch during or after each trial.

For each of the three types of walking, we divided the mean time to target (for each of the target distances used) by the actual target distance. A repeated measures ANOVA conducted on this ratio of time/distance collapsed across the two experiments yielded a main effect of walking type, \( F(2, 78) = 27.83, p < .001, \eta_p^2 = 0.42 \). Planned contrasts indicated that sighted walking \( (M = 0.831 \text{ sec/m}) \) was faster than blind walking \( (M = 0.927 \text{ sec/m}) \), \( F(1, 39) = 19.85, p < .001, \eta_p^2 = 0.34 \). However, imagined walking \( (M = 0.756 \text{ sec/m}) \) was even faster than sighted walking, \( F(1, 39) = 8.35, p = .006, \eta_p^2 = 0.18 \). These results differ from those of Plumert et al. (2005), who suggested that baseline sighted-walking speed and imagined walking time to target differed only at longer distances (beyond those tested here). In sum, the present results suggest that imagined walking speed may be more similar to sighted walking than to blind walking, but the absolute time to imagine walking remained shorter than either of the real-walking conditions.

These results suggest that the difference in temporal characteristics of real and imagined locomotion as seen in Experiment 1 are replicable and unlikely due to differences in preparation for real and imagined actions, differential cognitive load in real and imagined walking or order/practice effects of real and imagined walking. Varying these factors did not reduce the discrepancy in absolute time between the real and imagined tasks. The bias in imagined walking performance seen here contributes to a growing body of evidence that absolute imagined walking performance is not identical to real blind walking or sighted walking (e.g. Stevens, 2005). In the experiments described below, we further investigate the discrepancy between absolute real and imagined walking performance and suggest that the unique properties of locomotion as an action task may contribute to the bias in imagined locomotion.

Experiment 5

Experiments 1 through 4 consistently demonstrated that imagined walking to targets was significantly faster than blind walking to targets. Although these experiments did not show equivalence in terms of absolute real and imagined time to walk, the two tasks appear fundamentally similar in relative time as a function of distance. There are at least two possible accounts of these results. It may be that the highly correlated response times imply similar underlying mechanisms of real and imagined locomotion and that both tasks are informed by similar motor processes. This would be consistent with previous explanations of motor imagery supporting functional equivalence between executed and imagined actions. In contrast, instead of motor simulation, observers might have been
using a cognitive strategy to judge steps or time that would lead to
the systematic, but biased response time effects. To test these
alternatives, we used an approach novel to the measurement of
imagined actions that involved manipulating perceptual-motor
information during walking prior to the imagined walking task. We
examined imagined locomotion by using an adaptation paradigm
used previously to test the calibration of real locomotion.

Perceptual-motor recalibration has been studied in the context of
spatial updating tasks such as blind walking and has proven to be
a robust phenomenon in both real and virtual environments
(Mohler, Thompson, Creem-Regehr, Willemsen, et al., 2007;
Rieser et al., 1995). A mismatch between visual information about
self-movement and biomechanical information about self-
movement can affect subsequent spatial updating, by “recalibrating” the rate at which one visualizes or imagines the world moving
by while walking without vision. The effect of this recalibrated
perceptual-motor relationship yields systematic effects on blind-
walking performance. Whereas blind-walking performance under
normal circumstances is generally accurate, blind walking after
adaptation to a rate of visual flow that is faster than the biome-
chanical rate of walking is underestimated. After adaptation to a
rate of visual flow slower than the rate of walking, blind-walking performance reflects an overshoot of targets. These findings are
unlikely to reflect a change in the perception of distances (but see
Proffitt, Stefanacci, Banton, & Epstein, 2003), but instead suggest
that the rate at which a moving observer dynamically updates his
or her representation of position in space is malleable. The recal-
ibration effect has been investigated in several contexts, but the
results generally converge on the finding that distance walked in a
spatial updating task is subject to the relationship between the
perception of self-motion from vision (or nonvisual information,
see Durgin & Pelah, 1999; Durgin et al., 2005) and the perception
of walking rate as indicated by biomechanical indicators of self-
motion. If imagined walking is similarly affected by perceptual-
motor adaptation, such results would support the notion of similar
perceptual-motor mechanisms underlying real and imagined loco-
motion.

Method

Participants. Twenty-one undergraduate psychology students
participated in Experiment 5 in partial fulfillment of a course
requirement. Participants were randomly assigned to either a
visually faster condition (n = 10) or a visually slower condition
(n = 11).

Materials and design. A pre/posttest design with two inter-
vening conditions (visually faster and visually slower) was
used. After the pretest phase, participants underwent an adap-
tation phase in which they walked for 10 min on a custom-built
treadmill virtual environment, the Sarcos Treadport (Mohler,
Thompson, Creem-Regehr, Willemsen, et al., 2007). Three 8'
by 8' rear-projection screens surround the front side of the
Treadport, providing an approximately 180° horizontal field of
view. Participants walked at a constant speed of 1.3 m/s while
viewing a computer-generated “endless” hallway visually sim-
ilar to the pretest hallway moving by at a rate that differed from
the treadmill belt speed. The 1.3 m/s walking speed was deter-
mined by prior work in our laboratory to be a “comfortable”
walking speed (Mohler, Thompson, Creem-Regehr, Pick, &
Warren, 2007). Participants in a visually slower condition
viewed a rate of visual flow through the virtual hallway half as
fast as their walking speed (.65 m/s) whereas participants in a
visually faster condition viewed a rate of visual flow twice their
walking speed (2.6 meters/second).

Procedure. Participants were screened for normal vision, fa-
miliarized with blind walking as previously described, and trained
in imagined walking. Following this training, participants com-
pleted two practice and nine pretest trials of imagined walking to
targets at randomized distances of 6, 8, and 10 m (each distance
repeated three times) in a hallway similar in dimension and aesthet-
tics to the hallway used in Experiments 1 through 4.

As in the previously described experiments, participants self-
timed their imagined walks to targets. Participants were explicitly
instructed to begin the stopwatch simultaneously with their first
imagined step forward and stop the watch on imagining placing
both feet in the perceived location of the target. This imagined
walking task was practiced in the context of real walking to targets
to promote consistency between real walking and imagined walk-
ing.

Immediately following the last imagined walking trial of the
pretest, participants were led into an adjacent lab and onto the
Treadport. After 10 min of adaptation (see Materials and design
section above), participants were blindfolded and led to the adja-
cent hallway. During the posttest participants again performed two
practice and nine imagined walking to target trials.

Results and Discussion

The results from this experiment show that imagined actions are
recalibrated similarly to real locomotion. The posttest imagined
walking time to target increased in the visually slower condition by
14.99% compared to pretest. Imagined walking time in the visually
faster condition decreased by 13.69% in posttest compared to
pretest. These changes in time to target mirror the changes in
distance walked in previous recalibration of real walking experi-
ments (Mohler, Thompson, Creem-Regehr, Willemsen, et al.,
2007; see Figure 2). A t test for independent means conducted on
this percentage change (posttest time – pretest time/pretest time)
confirmed that the percentage change in imagined walking times
differed significantly as a function of the perceptual-motor recal-
ibration condition, t(19) = 3.1, p = .006 (two-tailed), Cohen’s d =
1.42. Consistent with Experiments 1 through 4, imagined walking

![Figure 2](image-url)
times increased linearly with target distance supporting the claim that participants did imagine walking to targets. One-way ANOVAs performed on pretest and posttest times as a function of distance confirmed a linear increase in time to target for both visually faster and visually slower conditions ($p < .001$ for all contrasts).

Our results are qualitatively similar to those from previous experiments demonstrating perceptual-motor recalibration (Mohler, Thompson, Creem-Regehr, Willemsen, et al., 2007; Rieser et al., 1995). In previous work with blind walking, distances walked during a blind-walking task changed as a function of the recalibrated relationship between visual indications of self-motion and biomechanical indications of self-motion. Participants who experienced a rate of visual motion faster than their walking speed tended to undershoot targets in posttest compared to pretest whereas participants who experienced a rate of visual motion slower than their walking speed tended to overshoot targets in posttest. In terms of the rate of spatial updating, these changes are intuitive; the recalibrated relationship between visual motion and biomechanical motion informed the rate of spatial updating while blind walking in posttest.

Our present finding supports the claim that the motor mechanisms underlying real and imagined locomotion are similar, at least in terms of the perceptual-motor relationships that inform both. Together with Experiments 1 through 4, the results suggest that although absolute timing may be different, both real and imagined tasks are influenced by perceptual-motor calibration. As previously mentioned, spatial updating during both real and imagined actions requires imagined updating of the spatial relationships that change concurrently with movement. Imagined movement, however, also requires a mental simulation of biomechanical action that corresponds to the rate of imagined spatial updating. This missing biomechanical input may be difficult to imagine or retrieve; indeed, many participants reported difficulty imagining how fast they were walking in Experiments 1 through 4. After extensive adaptation to a specific mapping of biomechanical walking and visual flow as in Experiment 5, participants changed their rate of imagined walking as a function of the learned relationship between visual and biomechanical information specifying perception of self-motion. The significant difference in imagined walking time in the visually faster versus visually slower conditions provides further support for the claim that observers simulate walking and corresponding spatial updating during the imagined walking task.

We reasoned that if it was the overt walking on the treadmill that provided a basis for the spatial updating rate during imagined walking, then adaptation to visual motion alone would not be likely to influence subsequent imagined walking. Alternatively, the faster or slower rate of visual motion could, on its own, be used in the dynamic updating of the environment with real or imagined self-movement, without requiring the input of overt walking. To test these alternatives, we conducted Experiment 6 in which two additional studies used the same design and procedure except that participants remained stationary while standing on a nonmoving treadmill belt during the 10-min adaptation phase. In addition, two groups of participants were tested; one group performed real blind walking during the pretest and posttest while the other group performed imagined blind walking.

### Experiment 6

We hypothesized that adaptation in Experiment 5 influenced imagined walking times because spatial updating during imagined walking relies on motor simulation concurrent with an imagined rate of visual motion (just as in recalibration of blind walking). If adaptation to visual motion alone, without the corresponding biomechanical information for self-motion, also induced changes in performance, we might interpret the results as visual effects not reliant on overt motor execution. Experiment 6 consisted of two between-subject groups in which participants either blind walked or imagined walking to targets before and after an adaptation phase. During this adaptation phase, in contrast to Experiment 5, participants passively viewed visual motion at a rate either faster or slower than the typical walking speed.

#### Method

**Participants.** A total of 37 participants from the University of Utah psychology undergraduate pool and paid participants from the surrounding community participated in the two experiments. Twenty participants were assigned to a real blind-walking condition. Of these, 10 participants were randomly assigned to the visually faster condition and 10 were assigned to the visually slower condition. A total of 17 participants were randomly assigned to an imagined walking condition, with 9 participants in the visually faster condition and 8 in the visually slower condition.

**Materials and design.** The same materials, hallway environment, and treadmill virtual environment used in Experiment 5 were employed in Experiment 6.

**Procedure.** The procedure in Experiment 6 mirrored that of Experiment 5 except that participants stood stationary on the treadmill belt during the 10-min adaptation phase and observed a rate of visual flow either twice the comfortable walking speed (2.6 m/s) in the visually faster condition or half the comfortable walking speed (0.65 m/s) in the visually slower condition.

Participants in the real blind-walking condition performed a blindfolded walk to previously viewed targets in pretest and posttest, as in Mohler, Thompson, Creem-Regehr, Willemsen, et al. (2007). Distance walked was recorded. Participants in the imagined walking condition performed imagined walking to targets in the pretest and posttest, as in Experiment 5, yielding imagined walking time-to-target for each trial.

#### Results and Discussion

Overall, there was no effect of visual-motion adaptation on subsequent real or imagined walking. To determine whether visual motion adaptation produced any significant effect on spatial updating in a real blind-walking task, we examined changes in distance walked in the real blind-walking condition, as in Mohler, Thompson, Creem-Regehr, Willemsen, et al. (2007). As expected, a 2 (visual flow condition) × 2 (pretest vs. posttest) × 3 (target distance) repeated measures ANOVA revealed a significant main effect of target distance, $F(2, 36) = 707.74$, $p < .001$; suggesting that participants walked farther for greater target distances ($p < .05$ for planned linear contrasts). There were no other significant main effects or interactions. Participants in the visually faster condition undershot targets on average by 1.63% in the posttest
compared to pretest and participants in the visually slower condition also undershot targets on average by about 3.57%. These small undershoots in both conditions were not significantly different, as revealed by a t test for independent means, t(18) = −0.59, p = .56, Cohen’s d = .28, implying that the adaptation to either visually faster or visually slower visual motion had no effect on distance walked. This lack of a recalibration effect is consistent with recent findings of Waller and Richardson (2008) who demonstrated that walking did not recalibrate within a head-mounted-display virtual environment after the manipulation of visual information alone.

For participants in the imagined walking condition, we compared imagined walking time to target, as in Experiment 5 using a 2 (visual flow condition) × 2 (pretest vs. posttest) × 3 (target distance) repeated-measures ANOVA. As in the blind-walking condition described above, there was only a significant main effect of target distance, F(2, 30) = 99.48, p < .001; suggesting that participants took longer to imagine walking longer distances than for shorter target distances (p < .05 for planned linear contrasts). Participants in both conditions tended to take slightly longer to imagine reaching the targets: In the visually faster condition, participants took an average 1.87% longer in their imagined walks to targets in the posttest compared to pretest and participants in the visually slower condition averaged a 7.2% increase in the posttest. These small increases in imagined walking times were not significantly different across visual-motion condition, as revealed by a t test for independent means, t(15) = 0.59, p = .57, Cohen’s d = .30. As in the blind-walking condition, it appears that the adaptation to either visually faster or visually slower visual motion had little effect on imagined time to target.

Taken together, the results from the blind-walking and imagined walking conditions of Experiment 6 converge on a conclusion that there is little effect of visual motion adaptation alone on real or imagined spatial updating. When viewed in light of the results of Mohler, Thompson, Creem-Regehr, Willemesen, et al. (2007) and Experiment 5, we suggest that perceptual-motor recalibration has analogous effects on both real and imagined walking that cannot be explained as simply adaptation to visual motion alone.

**Experiment 7**

Together, the results from Experiment 5 and 6 suggest an important role for the biomechanical information provided by physical walking in influencing the rate of spatial updating during imagined walking. Providing motor information corresponding to the visual flow during adaptation on the treadmill led to a change in subsequent imagined time-to-walk to targets, in support of the claim that imagined walking relies on motor simulation of walking. If the imagined walking task relied on nonmotor cognitive assessments of time or step counts, we would not expect a recalibration effect as a result of the manipulated relationship between visual and biomechanical information. In our final set of experiments, we tested the idea that motor information provided during the imagined walking task would also influence performance. A similar approach has been taken with the classic mental imagery task of mental rotation (Wexler, Kosslyn, & Berthoz, 1998; Wohlschlagler & Wohlschlager, 1998). For example, Wexler et al. demonstrated a motor component to the task of mental rotation by showing that a concurrent manual movement of a joystick at a given speed and direction, influenced time to mentally rotate objects. To further test this idea with locomotion, we asked participants to perform actions, concurrently with the imagined walking task, that were either biomechanically consistent or inconsistent with the act of walking. Participants were instructed to imagine walking to the target while either stepping in place (Experiment 7) or moving their arms in a circular motion (Experiment 8). All participants also performed real walking to the targets without vision. We predicted that action, but only that relevant to walking, would reduce the behavioral discrepancy between real and imagined walking to target times by providing additional biomechanical information to inform the imagined walking rate, influencing the spatial updating process.

**Method**

**Participants.** Thirteen participants from the university community completed Experiment 7; 2 participants’ data were excluded as outliers based on the criterion described previously. Compensation and participation mirrored that of Experiments 1 through 4.

**Materials.** The same hallway, targets, noise-canceling equipment, and other materials used in Experiments 1 through 4 were used.

**Procedure.** The methodology of Experiment 7 followed that used in Experiments 1 through 4 except that during imagined walking trials, participants walked in place while imagining walking to targets with eyes closed. Participants were instructed to begin a handheld stopwatch simultaneously with their first step (for real or imagined walking) and to stop the watch when they perceived that they had reached the target location and had placed both feet on top of the target location.

**Results and Discussion**

There was no significant difference between absolute time to walk (M = 5.36) and time to imagine walking (M = 5.17) when participants stepped in place during the imagined task, confirmed by a 2 (task type) × 3 (target distance) repeated-measures ANOVA, F(1, 10) = 1.16, p = .306, ηp² = 0.10. Time to target increased with distance, shown by a significant effect of distance, F(2, 20) = 204.18, p < .001, ηp² = 0.95; and planned linear contrast (p < .001). Distance walked was close to accurate, as seen in previous experiments. Although Experiments 1 through 4 demonstrated clear differences between imagined walking time to target and real walking time to target, the results of the present experiment suggest that stepping in place during imagined walking reduced this discrepancy in absolute time (Figure 3). The similarity between real and imagined walking found in this experiment may be due to the biomechanical information inherent in the concurrent stepping action during imagined walking task. This action may have provided information about the imagined walking pace or rhythm that was absent in our previous experiments. Alternatively, the action may have simply provided a distraction as a secondary task that diverted attention away from spatial updating during imagined walking and added time to the walking judgment. Or it could be that any action, even that unrelated to the biomechanics of walking, could serve to set a normal walking pace during imagined action or to influence the initiation and cessation of self-timing. We examined these possibilities in Experiment 8.
Experiment 8

Experiment 7 demonstrated no significant difference between absolute time to walk to targets or to imagine walking to targets. To assess whether this similarity between real and imagined walking was linked to the biomechanical action of walking rather than simply to an accompanying action during imagined walking, we conducted a final experiment, similar to Experiment 7 using a concurrent overt action inconsistent with the act of walking. A difference between blind-walking times and imagined walking while performing a concurrent action irrelevant to walking would suggest that only those actions specifically compatible with walking facilitate imagined walking.

Method

Participants. Thirteen participants from the University of Utah community completed Experiment 8. Participants were compensated as previously described.

Materials. The same environment, blindfold, targets, and noise-cancelling equipment employed in all previous experiments were used in Experiment 8.

Procedure. Experiment 8 mirrored the procedure of Experiment 7 except that, during imagined walking trials, participants rotated their arms in a circular motion in front of themselves while standing still with eyes closed. More specifically, participants were instructed to begin a handheld stopwatch simultaneously with their first step or the initiation of the circular arm movement (during imagined walking trials) and to stop the watch when they perceived that they had reached the target location and had either placed both feet on top of the target location (real blind walking), or had reached the target location and stopped moving their arms in a circular motion (imagined trials).

Results and Discussion

As in Experiments 1 through 4, but in contrast to Experiment 7, a 2 (task type) × 3 (target distance) repeated-measures ANOVA indicated that imagined walking times (M = 5.38) were significantly shorter than real walking times (M = 6.27) despite the concurrent biomechanical activity unrelated to walking (see Figure 3), F(1, 12) = 10.33, p = .007, ηp² = 0.46. As in all previous experiments, there was a significant main effect of target distance, F(2, 24) = 75.89, p < .001, ηp² = 0.86; and times increased linearly with target distance (p < .001). As seen in Experiment 4, an ANOVA conducted on variable error revealed a main effect of target distance, F(2, 24) = 6.07, p = .007; showing a linear increase with target distance (p = .005). Blind-walking accuracy was accurate, as in previous experiments (see Table 1).

In sum, the inclusion of circular arm motion, a body movement unrelated to walking did not influence the difference between real and imagined walking times. Instead, imagined walking times were again significantly faster than real walking times at all target distances, replicating our earlier findings. Our results suggest that the increase in response time for imagined walking while stepping in place found in Experiment 7 likely cannot be attributed to the distraction of a secondary task, the rhythm of movement of any body part during imagined walking, or reliance on motor cues to initiate and cease stopwatch self-timing. The specificity of the stepping-in-place effect argues further for the role of biomechanical information on imagined locomotion in a spatial updating task.

Between-Experiment Results for Experiments 7 and 8

We found a difference between real and imagined walking performance in Experiment 8, as in Experiments 1 through 4 but not in Experiment 7. As with the comparison between Experiments 1 through 4, we analyzed difference scores between real and imagined walking times using a 2 (experiment) × 3 (target distance) ANOVA, with experiment as a between-subject factor and distance as a within-subject factor. The effect of experiment approached significance, F(1, 22) = 3.88, p = .062, ηp² = 0.15; and there was no effect of target distance.

General Discussion

We conducted an extensive study of imagined walking to previously viewed targets to examine the role of motor processing in this task. The act of imagined walking is especially interesting and critical to a broad understanding of motor imagery because it extends beyond body-part movement, requiring the representation and updating of environmental space. Thus, the study of imagined walking not only informs us about motor imagery processes, but also about the importance of biomechanical information in the updating of scenes. We found first, that imagined walking time systematically increases with target distance, as found in real blind walking to previously viewed targets, although it is consistently shorter than real blind-walking time. These results indirectly support a claim of motor simulation in imagined locomotion, but also
necessitate further direct evidence of motor processing in imagined locomotion. We hypothesized that this difference in absolute timing might reflect the role of the absent motor execution system in providing absolute information about rate of walking and corresponding updating of the environment. This would explain the discrepancy in absolute timing and would support the claim that observers do attempt to mentally simulate walking while imagining walking to previously viewed targets. We introduced two variations of the initial experiments to test this idea that relied on the presence of additional biomechanical information either prior to or concurrent with the imagined task. First, perceptual-motor recalibration of imagined walking was found to mirror previous results of real walking. Second, the addition of a relevant biomechanical task during imagined walking eliminated the difference in absolute timing between the real and imagined walking tasks. The finding that both manipulations affected imagined walking time suggests that (a) imagined locomotion relies on an internal motor representation, and (b) the biomechanical information for walking may be critical to an accurate spatial updating process.

The results found in Experiment 1 and replicated in Experiments 2 through 4 and 8 stand in contrast to the results of a number of studies that have shown equivalent performance in real and imagined walking (Curtine et al., 2004; Decety et al., 1989; Papaxanthis, Pozzo, et al., 2002; Plumert et al., 2005) and warrant some discussion. Each of the previous studies discussed differed from the present experiments in terms of methodology, participant populations, and/or instructions given to participants. These differences may be significant to recovering the chronometry of imagined walking. Decety et al., for example, screened for participants considered to be “high imagers.” Plumert et al. used a broader participant population, but provided instructions that were fairly ambiguous as to the strategy to be used to imagine walking to a target. In addition, Plumert et al. compared imagined and real walking with an approach different than in the present studies. They directly compared imagined walking time with blind-walked distances by transforming imagined walking times to imagined distances walked. They used an initially measured sighted-walking speed to scale time and distances. Finally, Curtine and colleagues used only one walked distance (though with different degrees of ground-plane incline), thereby potentially reducing the utility of a spatial updating strategy. It remains an open question as to how different instructions, training, or updating strategies might contribute to the similarity or differences seen across these previous experiments and our own. We showed that factors such as task preparation, order/practice effects, or greater cognitive load involved in imagined walking are likely not the causes of the difference between absolute timing of real and imagined locomotion.

It is important to consider imagined walking as a task involving two components, motor simulation of action and egocentric spatial updating. Although there is a good amount of evidence from behavioral, neuroimaging, and neuropsychological paradigms that similar motor mechanisms underlie executed and imagined movements, there is also research supporting the importance of body movement in spatial updating processes. We consider the current findings in light of prior work on motor imagery and egocentric spatial updating, below.

**Equivalence of Imagined and Executed Actions**

In addition to the research detailed above on real and imagined locomotion, other behavioral tasks have led to similar conclusions of parallel motor mechanisms of imagined and executed movements. Chronometric data suggest that the timing of real and imagined reaching are similar (Papaxanthis, Schieppati, et al., 2002). Writing and imagined writing also appear to share the same sequences of movements and similar durations (Decety & Michel, 1989; Papaxanthis, Pozzo, et al., 2002). Real and imagined actions also have been shown to adhere to Fitts’ Law in pointing tasks (Maruff & Velakoulis, 2000), figure tracing (Decety, 1993; Decety & Michel, 1989) and locomotion (Decety & Jeannerod, 1995). Finally, imagined actions are accompanied by physiological activity analogous to that seen in comparable overt actions. Imagined treadmill walking yielded increased heart rate and respiration that changed with the imagined effort of treadmill walking (Decety et al., 1993, 1991). Although tasks such as reaching, writing, and walking are goal-directed actions that may be explicitly imagined, other motor imagery tasks may be considered more implicit in the way they recruit body representations. These types of tasks typically involve left–right decisions about visually presented body parts and find strong correlations between the time to make a handedness decision and the time to imagine or physically move the body part (Parsons, 1987, 1994). These decisions are also influenced by the biomechanical constraints of the body.

The behavioral work is further supported by functional neuroimaging approaches finding similar neural substrates underlying real and imagined actions. Jeannerod (1994, 1995, 2001) suggested that action execution, motor simulation, or imagination and observation of action are linked to similar neural patterns of activation. More recently, several studies have demonstrated that imagined actions are correlated with novel patterns of activation but share significant overlap with real actions, particularly in fronto-parietal pathways and cerebellum (Grezes & Decety, 2001; Hanakawa et al., 2003; Johnson et al., 2002). Although there is some contradictory evidence about the involvement of primary motor areas in imagined actions, a number of studies have demonstrated that imagined hand, foot, or tongue movements are correlated with activation in somatotopically appropriate areas of primary motor cortex, premotor, and supplementary motor areas (Ehrsson, Geyer, & Naito, 2003; Michelon et al., 2006; Stippich, Ochmann, & Sartor, 2002). Work with clinical populations largely concurs, suggesting that damage to parietal cortex impairs ability to predict outcomes of imagined actions (Sirigu et al., 1996).

Taken together, prior work suggested a functional equivalence between real and imagined actions. This equivalence is critical to many of the proposed functions of imagined actions or motor simulation. Imagined actions must be synonymous with physically realizable actions if they are to aid in the interpretation or prediction of another’s actions, in the planning or prediction of outcome of one’s own actions, in rehearsing and recalling completed actions, or in assessing the effort or risk involved in a potential action. Consistent with work on imagined movement in other domains, we found evidence for functional equivalence between real and imagined locomotion. Time to walk increased linearly with distance in all imagined walking conditions, and perceptual-motor recalibration of imagined walking was found. Notably, we also found a distinction between executed and imagined walking in...
absolute time-to-walk that was eliminated with the addition of stepping in place during imagination. We suggest that this distinction arises in imagined locomotion, unlike simulation of movement of body parts, because of the interdependent task requirement of spatial updating. Many of the tasks typically used to assess behavioral similarity and neural activation of real and imagined actions are simple, repetitive or intrinsically body-based motor movements. More complex sequences of movements or movements requiring awareness or attention to external stimuli often show inconsistency in timing between real and imagined actions (Guillot & Collet, 2005). In the present task, participants not only simulated their body movement, but also imagined the changing relationship between their body position and the environment. We discuss these ideas further in the next section.

The Role of Active Movement in Spatial Updating

Blind walking is one example of spatial updating, the process of keeping track of locations in space as we move or as objects move. Spatial updating is an important skill that allows humans to maintain a stable representation of the world. Although it is clear that human observers have the ability to update positions in space from imagined self-movement, the greater ease of spatial updating with physical self-movement is well documented (Farrell & Robertson, 1998; Loomis, Klatzky, Golledge, & Philbeck, 1999; May & Klatzky, 2000; Rieser, 1999). Findings from paradigms that require observers to ignore a given physical movement during an updating task (e.g., Farrell & Robertson, 1998; May & Klatzky, 2000) show decrements in updating performance compared to control conditions, suggesting an automatic updating of space tightly coupled to physical body movement. This process would involve path integration in which velocity- or acceleration-based self-motion information is used to update one’s spatial displacement.

A body of work comparing spatial updating by pointing during real versus imagined movement suggests a much more difficult process for imagined movements, requiring additional processing costs revealed through increased latency and errors (Amorim & Stucchi, 1997; Easton & Sholl, 1995; May, 2004; Presson & Montello, 1994; Rieser, 1989; Wraga, 2003). Some have found greater costs for updating during imagined rotation versus translation (Presson & Montello, 1994; Rieser, 1989), whereas others have found performance differences between real and imagined movement for both translation and rotation, when controlling for object direction disparity (May, 2004).

Relevant to our present findings is the idea of an interference/conflict theory to describe the mechanisms involved in the task of imagined spatial updating (May, 2004; Presson & Montello, 1994). In imagined updating, the observer is asked to act from a spatial position that is different from his or her physical position. This results in conflict between the representations of object locations from the body-based (physical) reference frame and the imagined perspective. Support for May’s (2004) interference account is also found in work that has varied the modality of response measure. The conflict between physical and imagined positions should be greatest when an observer is asked to indicate spatial positions in a way that is attached to his or her physical reference frame. Several studies have found that the decrement in updating during imagined rotation is eliminated or reversed when viewers respond with verbal responses, which are likely less tied to the viewer’s physical reference frame than a motor response such as pointing (Avraamides, Klatzky, Loomis, & Golledge, 2004; de Vega & Rodrigo, 2001; Wraga, 2003).

A distinct possibility for imagined walking is that biomechanical information from stepping in place assists in imagined spatial updating because it eliminates a perceptual-motor conflict inherent to imagined locomotion. In all of our other imagined walking experiments, participants were required to stand in place while imagining walking forward. The lack of any motor component of walking left participants rooted in place, relying solely on a mental simulation of imagined walking. There is evidence from Stevens (2005) that supports the idea that biomechanical information that conflicts with the action required for locomotion affects imagined walking performance. In a number of experiments, Stevens demonstrated that biomechanical and cognitive interference affected imagined walking times, yielding imagined walking times that were shorter than real walking times. Although these experiments utilized interfering actions or stances that clearly conflicted with the biomechanical components of gait, the result may apply to the present Experiments 1 through 4 and Experiment 8. Actions (or lack of actions) that conflict with the imagined updating task impair performance while actions that resemble the biomechanics of the imagined action improve performance, at least in spatial updating. Our perceptual-motor recalibration findings of Experiment 5 also support the notion that biomechanical information may be drawn on during an imagined locomotion task, although in this case it is prior to and not concurrent with imagined locomotion. Imagined walking time was clearly affected by the adaptation to a new perceptual-motor mapping, consistent with the change in distance walked found in previous studies of recalibration of physical locomotion.

As introduced earlier, it is difficult to directly compare the neural mechanisms involved in real and imagined walking and spatial updating in humans because of limitations of mobility inherent to functional neuroimaging methods. However, an fMRI study comparing imagined standing, walking, and running lends support to our conclusions of both motor and cognitive aspects to imagined locomotion. In an imagined walking task, Jahn et al. (2004) found bilateral activation in the fusiform and parahippocampal gyri, regions previously identified as supporting representations of place and spatial navigation (Ekstrom et al., 2003; Epstein & Kanwisher, 1998) and real movement based path integration in human lesion patients (Philbeck, Behrmann, Levy, Poltacicchio, & Caputy, 2004), supporting the notion that environmental spatial updating occurs with imagined locomotion. A second dominant region of activation was found in the cerebellar vermis, previously identified in human PET studies just following locomotion, and identified in humans and nonhuman animals as critical to the timing of stance and locomotion. More interesting, the activity in the cerebellum increased respectively with increasing speed of locomotion, showing the highest level with imagined running, parallel to findings in animal electrical stimulation of what has been termed the locomotor cerebellar region (Mori et al., 1999; Mori, Matsuyama, Mori, & Nakajima, 2001). Thus, the cerebellar activity in the Jahn et al. study may well reflect the necessary processing of timing of leg movement involved in imagined locomotion, consistent with our present claims. Finally, Jahn et al. found minimal and variable activity in the premotor
cortex during imagined walking, a finding that is inconsistent with the dominant premotor activity found in tasks such as imagined grasping and further supports the claim that the mechanisms of imagined locomotion may be partially distinct from those underlying imagined arm and hand movements.

Conclusions

Generalized claims about the role of motor simulation in imagined movement must include an examination of a range of imagined actions, including the whole-body locomotion and spatial updating task presented here. Our results show evidence for shared motor mechanisms in real and imagined locomotion and a bias in the absolute timing of imagined locomotion that we attribute to a lack of biomechanical information available to provide a metric for the corresponding spatial updating process. It is unknown if this bias extends to other imagined actions. For example, in imagined performance of athletic routines (e.g., mental rehearsal), some degree of biomechanical mimicry of the physical feat may provide additional benefits over purely cognitive rehearsal. Given the present results and the apparent influence of task demands on imagined actions (Guillot & Collet, 2005; Stevens, 2005), it is important to analyze task components of motor imagery and to avoid overgeneralization of claims. Similarly, future research should systematically examine the effects of task demands, potential influences of research populations, training, and task instructions when comparing real and imagined actions. Particularly for real and imagined locomotion, instructions or imagery strategy may have a significant effect on absolute performance (Bakker et al., 2007).

Our results have additional practical implications for measurement of distance perception with imagined walking. The systematic timing effects make it a viable alternative to the overt visually directed action tasks that are more typically used. The addition of a relevant action such as stepping in place may make the measure even more useful, as it more closely mimics real walking time. Imagined walking while stepping in place might be particularly useful in experimental conditions in which walkable space is limited, as when judging far distances or navigating in a large rendered virtual space viewed while standing in a smaller physical room (Razzaque, Swapp, Slater, Whitton, & Steed, 2002; Usóh et al., 1999). Imagined actions are also useful in experimental situations in which physical movement is problematic or not feasible, as in functional neuroimaging methodology. The relevance of imagined movement for everyday functions of motor planning, prediction, and memory is highly related to the utility of imagined actions for research in spatial perception and cognition. Imagined walking is one example of a spatial task that involves motor simulation in the context of complex relations between the self and environment and can contribute to an understanding of the processes underlying both motor imagery and spatial updating.

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