

The cost of moving with the left hand

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Abstract Precise left-hand movements take longer than right-hand movements (for right-handers). To quantify how left-hand movements are affected by task difficulty and phase of movement control, we manipulated the difficulty of repetitive speeded aiming movements while participants used the left or right hand. We observed left-hand costs in both initial impulse and current control phases of movement. While left-hand cost during the initial impulse phase was small, left-hand cost during the current control phase varied from 10 to 60 ms, in direct proportion to the movement's difficulty as quantified by Fitts' law ($0.77 < R^2 < 0.99$, across three experiments). In particular, in comparison with a difficult task for the right hand (Fitts' $ID_R = 6.6$), the left hand's task would have to be made easier by 0.5 bits ($ID_L = 6.1$) to be performed as quickly. The left-hand cost may reflect the time required for callosal transfer of information between the left and right hemispheres during the current control phase of precision left-hand movements or reflect movement control differences in the current control phase of movement that are inherent to the hemispheres. Overall, the present results support multiphase models of movement generation, in which separate specialized processes contribute to the launching and completion of precision hand movements.

Keywords Laterality · Movement time · Left hand · Fitts' law · Corpus callosum · Hemispheric dominance · Reaction time

Introduction

Understanding what determines how quickly we can move has been an enduring goal of experimentation for more than a century. Woodworth (1899) first described the speed–accuracy trade-off in reciprocal movements, by observing that requiring faster movements produced greater endpoint error. The speed–accuracy trade-off was quantified by Fitts (1954), who measured the effect of required movement distance and accuracy on movement time. Both discrete movements to individual targets and reciprocal movements between paired targets take longer if they have larger amplitudes or require greater accuracy, in direct proportion to the difficulty in the movement (Fitts 1954; Fitts and Peterson 1964; Keele 1968; Elliott et al. 2001).

Fitts' quantification of the effects of target width (W) and movement amplitude (A) on movement time (MT), now commonly known as Fitts' law, is:

$$MT = a + b \times ID \quad (1)$$

where ID is the index of difficulty (in bits),

$$ID = \log_2(2A/W). \quad (2)$$

The speed–accuracy trade-off encapsulated in Fitts' law has been variously attributed to the need for visuomotor guidance for more accurate movement (Woodworth 1899); for one or more corrective submovements because of the inaccuracy of initial movements (Crossman and Goodeve 1963/1983; Keele 1968; Jagacinski et al. 1980); to the amount of information that must be processed to achieve particular levels of accuracy (Fitts 1954; Fitts and Peterson 1964); to delays in visuomotor feedback (Beamish et al. 2009); to minimization of endpoint positional variance (Harris and Wolpert 1998), and to submovement

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optimization (Meyer et al. 1988). Fitts' law applies not only to linear hand or stylus movements (as in most of the studies above) but also to rotational movements (Jagacinski et al. 1980; Meyer et al. 1988) and to movements of a tool around obstacles (Jax et al. 2007; Vaughan et al. 2010).

Another observation about the control of precision movements to a target first made by Woodworth (1899) is that movement duration can be decomposed into two phases: An *initial impulse phase*, in which the hand is brought close to the target, and a *current control phase*, in which the hand's position is precisely adjusted using visual feedback. Variations on this biphasic model of movement control have been further developed by Crossman and Goodeve (1963/1983), Keele (1968), Meyer et al. (1988), Sainburg and Schaefer (2004), and Elliott et al. (2010).

Finally, Woodworth (1899) observed that the accuracy decrement for speeded movements in right-handers was greater for the left hand than the right, which Woodworth attributed to the more rapid and uniform movement control of the right hand (and possible better proprioception).

Despite the superficial symmetry of the motor system, in which each hemisphere controls the movements of the contralateral limbs, there is converging evidence that there is hemispheric specialization in the control of movement. A hemispheric asymmetry in movement control was first noted by Liepmann in the early 20th century (Rothi and Heilman 1996). Half of Liepmann's left-hemisphere (LH) lesion cases (all with right-hand paralysis) also showed apraxia in the left hand, whereas almost all of his right-hemisphere (RH) lesion cases were able to perform most tasks adequately with the non-paralyzed right hand. For Liepmann, this indicated that LH structures were involved in the control of both contralateral and ipsilateral movements; that is, the LH tends to be dominant for movement control (in typical right-handers) regardless of the hand used.

A wide variety of recent behavioral and neurophysiological evidence supports the role of the LH in movement control of both hands. Consistent with Woodworth's observations, movements of the right hand tend to be faster than those of the left (Flowers 1975; Kabbash et al. 1993). Sainburg (2002) showed that the dominant hand adapts better than the non-dominant to disruption of the dynamics of limb movements (even though the hands adapt equivalently to rotational visual displacement). Furthermore, fMRI studies (e.g., Johnson-Frey et al. 2005) have shown substantial LH activation during the *preparation* of both right-hand and left-hand movements (though some studies, including Johnson-Frey et al. 2005, and Cramer et al. 1999, show bilateral activation during *execution* of tasks with either hand). LH trans-cortical magnetic stimulation (TMS), applied just before a response is to be made, impairs performance of both hands, whereas RH TMS impairs only left-hand performance (Terao et al. 2005).

The end-state comfort effect (Rosenbaum et al. 1992) represents the tendency to begin a multistep action so as to minimize the awkwardness of a posture later in the sequence. Janssen et al. (2009) observed stronger end-state comfort effects in movements of the right hand than in those of the left hand, a difference that was observed even in left-handers (Janssen et al. 2011). Hemispheric specialization for different aspects of movement is also observed in adaptation tasks. Mutha et al. (2011) compared visuo-motor adaptation in patients with LH or RH lesions and observed adaptation only in those with an intact LH. Left-hand adaptation to prism displacement transfers to performance with the right, but right-hand adaptation does not transfer to the left hand (Redding and Wallace 2008, 2009).

Although overall MT is usually longer with the left hand, the time to *initiate* movements (reaction time) shows smaller and less consistent hand differences. Some have observed a left- or right-hand advantage in reaction time for ballistic movements (Zuoza et al. 2009), depending on whether the movement overshoots a target, whereas others have found that hand differences in reaction time are small and unsystematic (Annett and Annett 1979) and may depend on the uncertainty of movement or whether the target is in ipsilateral or contralateral space (Mieschke et al. 2001).

We can therefore distinguish three measurable components of the time to move to a target: Response initiation time (the time until movement begins, designated as response latency or reaction time, depending on whether an imperative cue signals movement) and the two phases of movement (initial impulse and current control) distinguished by Woodworth (1899) as ballistic or feedback-controlled, respectively. While there has been much work on hand differences in movement (e.g., Flowers 1975; Kabbash et al. 1993) and on adaptation to perceptuomotor distortions (Sainburg 2002; Redding and Wallace 2009), the interaction between task difficulty and hand in the different phases of movement has not been measured in detail, to our knowledge.

Given the frequently observed differences in manual performance between the dominant and non-dominant hands, and insofar as MT depends on task difficulty, one might ask how the relative ease of movements with the dominant hand is related to movement difficulty across the components of movement. To address this question, we conducted three experiments using a movement task similar to that of Vaughan et al. (2010), in which participants used a tool to alternately touch two targets. Across the three experiments, we investigated the effect of required speed and directional uncertainty on the initiation of the movement (response latency or reaction time). Within each experiment, we varied difficulty (movement amplitude and target width) and examined response initiation time and

movement times in the initial impulse phase and the current control phase, to evaluate how they reflected hand differences.

If there are hand differences in performance, we can ask a number of specific questions: Are the hand differences similar in movement initiation (i.e., response latency or reaction time) and in movement duration? Are hand differences affected by task difficulty? And finally, if hand differences are observed to vary with task difficulty, does difficulty affect the hands similarly in the initial impulse and current control phases of movement?

Experiment 1

The first experiment manipulated movement amplitude and target width, while right-handed participants made reciprocal movements using a handheld tool to alternately touch two targets as rapidly as possible. The primary goal of the experiment was to determine whether there was a consistent difference in MT between the dominant (right) and non-dominant hands. A pilot study (Keating unpublished, Hamilton College Senior Thesis) showed no significant difference between left- and right-handed movement times in a task with discrete, self-paced movements (a paradigm used in much of the work on Fitts' law, including Vaughan et al. 2010); therefore, a speeded reciprocal movement task was used in the present study, with the goal of making the dependent measure as sensitive as possible to potentially small response initiation and movement duration differences between the hands.

Method

Participants

Six participants (all women), aged 18–21 years, were recruited from psychology courses, served after giving informed consent, and were compensated with experiment-participation credit. All reported primarily right-hand use for everyday tasks. All procedures were reviewed and approved by the Hamilton College Institutional Review Board.

Apparatus and procedure

Participants sat at arm's length plus 25 cm from the front edge of a bookcase from which two parallel 22-cm rods extend horizontally 91 cm above the floor, separated by a distance (*A*) of 20, 40, or 80 cm. A target disk with a diameter (*W*) of 1.6, 4.1, or 10.5 cm was mounted on the end of each rod, parallel to the frontal plane, approximately at the participant's shoulder level, making nine unique

amplitude-width target pairs, representing ID values (Eq. 2) ranging from 1.9 to 6.6 bits.

In each hand, the participant held a 35-cm baton (an aluminum rod 1 cm in diameter, weighing 175 gm, with a 1.6-cm rubber tip), whose form-fitting handle was individually molded to accommodate the left or right hand with a unique grip that constrained hand motion but did not impede wrist movement. A Nest of Birds (www.ascension-tech.com) motion-capture sensor mounted on the shaft of each baton recorded the position of the sensor with 6 degrees of freedom (*x*, *y*, *z* position and pitch, roll, and yaw), from which the tooltip location could be computed at 101 samples/s with a precision of 0.25 mm.

Because of the need to manually change the rods that supported the targets as target size and separation were varied, the experimental conditions were ordered hierarchically, rather than completely randomly. In each of nine four-trial blocks, one of the nine amplitude-width target conditions (in random order) was run in each of the four hand-direction combinations (left or right hand, initially moving leftward or rightward, in random order). These 36 unique trials were then repeated in a different random order for a total of 72 trials per participant.

At the beginning of each trial, participants placed the tooltip of the indicated hand on the appropriate starting target as instructed by a computer-controlled verbal prompt. A ready signal (.125 s, 75 db, 260 Hz) sounded when the tooltip was detected in the correct starting location, and the participant then moved to alternately touch the two targets following the general imperative, "Move as quickly as possible to touch each of the targets, without sacrificing accuracy." Participants were free to move as soon as the tooltip had been placed in the correct position for the start of the trial. (To distinguish the response initiation measure in Expt. 1 from that of Expts. 2 and 3, which used an explicitly speeded initial response to a separate imperative signal, the time to begin moving on each trial will be referred to as "response latency," RL.) The participant then moved the tooltip between the two targets as quickly as possible, briefly touching each target, until eight movements had been made.

Data analysis

The same analysis paradigm was used in all three experiments. Tool movements were easily identified from the velocity of the tooltip (low-pass filtered using a stationary filter with half-amplitude value of 15 Hz) as it was moved from one target to the other. Response initiation time for each trial was the interval between the "go" signal and the first horizontal displacement in the direction of the opposite target that began a period of monotonically increasing velocity. Overall movement time (MT) was subdivided into two

components, an initial impulse phase and a current control phase. Since each movement from one target to the other began with an epoch of smooth tooltip acceleration, the beginning of the initial impulse phase of each movement was identified as the first horizontal displacement in the direction of the opposite target that began a period of monotonically increasing velocity, and the end of the initial impulse phase was operationalized as the instant of peak velocity during the movement. The beginning of the current control phase for each movement was defined by the end of the initial impulse phase, and its end was the beginning of the next movement. (The peak velocity might be considered a liberal, “early” marker of the separation of the initial impulse and current control phases and was chosen for its theoretical consistency with the model of Sainburg and Schaefer (2004). A separate analysis of all three experiments using a more conservative, “late” marker of phase separation, the first reversal of horizontal displacement near the current movement target, produced a pattern of left-hand costs in the current control phase essentially identical to those reported here.) In each trial, the two movement phases of the second through seventh movements were measured. The first and last movements were excluded from this computation, so that every movement contributing to the analysis was itself preceded and followed by a movement, and because in Expts. 2 and 3, the first movement was half the amplitude of the others. (A separate analysis of only the first movement produced effects qualitatively similar to those of movements 2–7). For the overall measures of performance, all effects on each dependent variable (response initiation or movement time) were evaluated by an omnibus two-way repeated-measures ANOVA with factors Hand (left/right) and ID, with Huynh–Feldt correction where indicated. Movement direction had no significant effects related to the dependent measures, so all results were collapsed across leftward and rightward movements. The response latency and the median durations of the initial impulse phase, current control phase, and total movement were recorded for each trial and then averaged across all trials of each condition.

Results

The measure of response initiation, mean RL, did not differ between the left hand (342 ± 26 ms [M \pm SE]) and the right hand (354 ± 25 ms), $F(1, 6) = 3.71$, ns. RL varied with ID, $F(4.8, 29.0) = 4.64$, $p = .003$ (in all ANOVAs, the degrees of freedom have been adjusted for lack of sphericity using a Huynh–Feldt correction), tending to be longer by 8 ms/ID (Fig. 1a). There was no Hand \times ID interaction, $F(8, 48) < 1$, ns.

As expected from Fitts’ law, overall MT varied with ID, $F(4.18, 25.1) = 65.68$, $p < .001$, with a slope of 81 ms/ID (see Fig. 1b):

$$MT_L = 120 + 86 \text{ ID ms}; \quad R^2 = .85 \quad (3)$$

$$MT_R = 114 + 76 \text{ ID ms}; \quad R^2 = .85 \quad (4)$$

Overall MT of the left hand (489 ± 38 ms) was longer than that of the right hand (441 ± 34 ms), $F(1, 6) = 17.1$, $p = .006$, demonstrating a left-hand cost (LHC, Fig. 1b), especially at higher values of ID, as indicated by a Hand \times ID interaction, $F(7.3, 19.2) = 3.148$, $p = .008$.

For detailed analysis of the LHC, overall MT was partitioned into an initial impulse phase and a current control phase, as described above. In this and the following experiments, the duration of the initial impulse phase ranged from about 100 to 240 ms, depending on ID (Table 1). The duration of the current control phase ranged from about 140 ms at ID values of 2 to values near 550 ms at ID values near 7 (Table 2).

Because the two movement phases are complementary proportions of total movement time, they are not independent measures, and so they were submitted to an omnibus ANOVA with the factors Hand, ID, and Phase, to address the question of whether variation in Hand (i.e., the magnitude of LHC) with ID differed between the two phases of movement. Such a difference would be apparent in the Hand \times ID \times Phase interaction. This interaction was significant, $F(8,40) = 2.201$, $p = .048$.

To elucidate this 3-way interaction, a post hoc 2-way ANOVA with factors Hand and ID was computed separately for each movement phase. (Here, and in Expts. 2 and 3, a Bonferroni correction was applied to the significance levels for the post hoc analyses.) In the initial impulse phase, there was a mean LHC of 14 ms, $F(1, 6) = 24.7$, $p = .006$, and a strong effect of ID, $F(5.9, 35.5) = 49.8$, $p < .002$, but no Hand \times ID interaction, $F(8, 48) = 1.5$, ns (Fig. 2a). For both hands, difficulty added about 18 ms/bit to the initial impulse phase (Table 1). In the current control phase, the mean LHC was 35 ms, as shown by the main effect of Hand, $F(1, 6) = 14.0$, $p = .020$, and there was a strong main effect of ID, $F(5.2, 31.3) = 56.4$, $p < .002$. Difficulty added about 58 ms/bit to the left hand, and 68 ms/bit to the right hand (Table 2). As a consequence, the LHC for the current control phase varied with ID, as shown by the Hand \times ID interaction, $F(7.0, 42.2) = 3.94$, $p = .004$, and as indicated by a strong linear relationship between ID and LHC (Fig. 2b):

$$\text{LHC} = -10.3 + 10.6 \text{ ID ms}, \quad R^2 = .77 \quad (5)$$

Discussion

As expected, Expt. 1 replicated the central observations of Fitts and Peterson (1964): There was a small (8 ms) effect of ID on RL (Fig. 1a), but a large (81 ms) effect of ID on total MT (Fig. 1b). Expt. 1 also showed a modest (14 ms) LHC in the initial impulse phase of each movement

Fig. 1 Response latency (RL, Expt. 1), reaction time (RT, Expts. 2 and 3), and overall duration of reciprocal movements (MT) in Expts. 1, 2, and 3. Note that the values of ID are smaller for the RTs than for the MTs in Expts. 2 and 3, because the amplitude of each trial's initial movement was half that the subsequent reciprocal movements. *Black open circles and dashed regression line: Left hand. Red filled circles and solid regression line: Right hand*

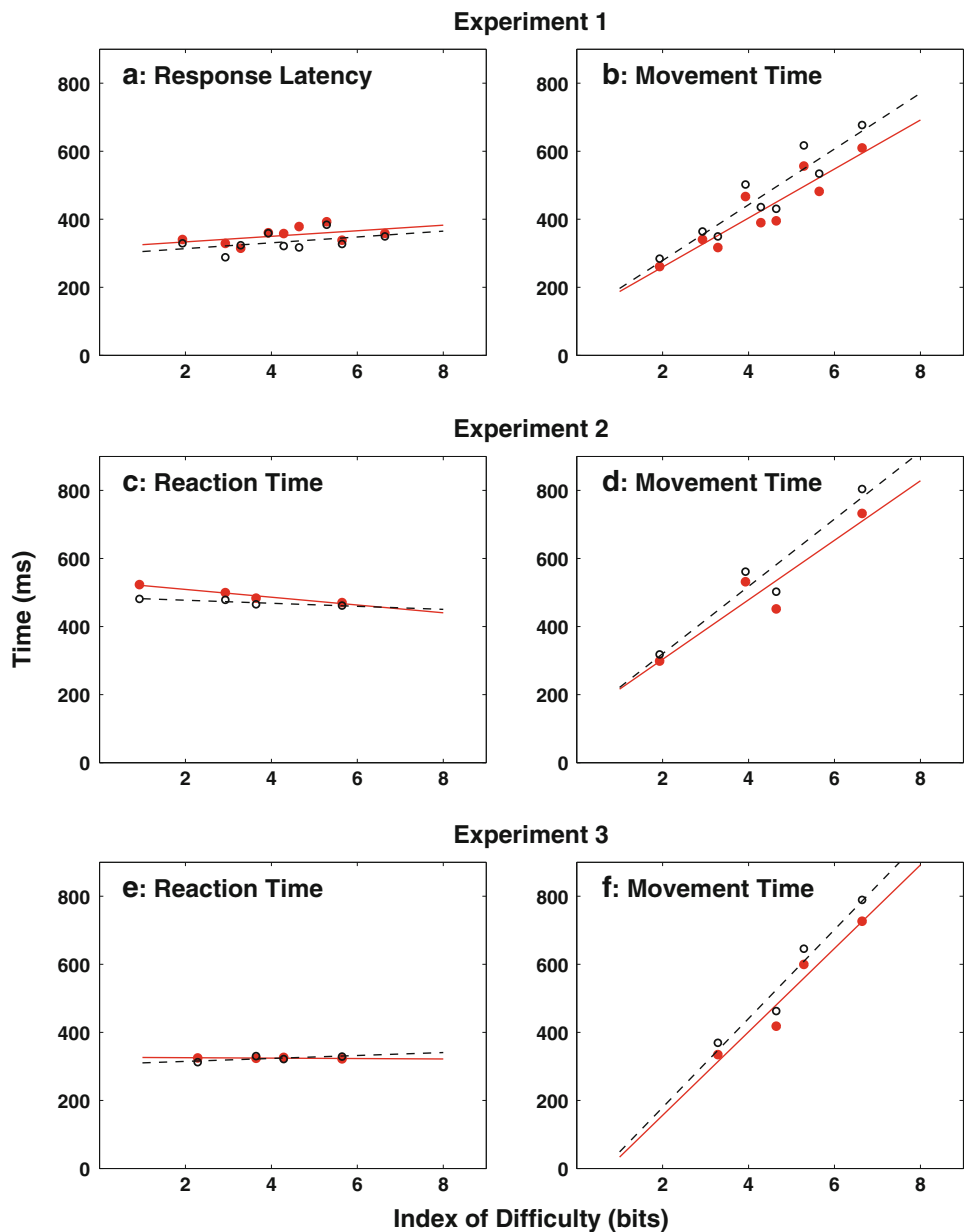


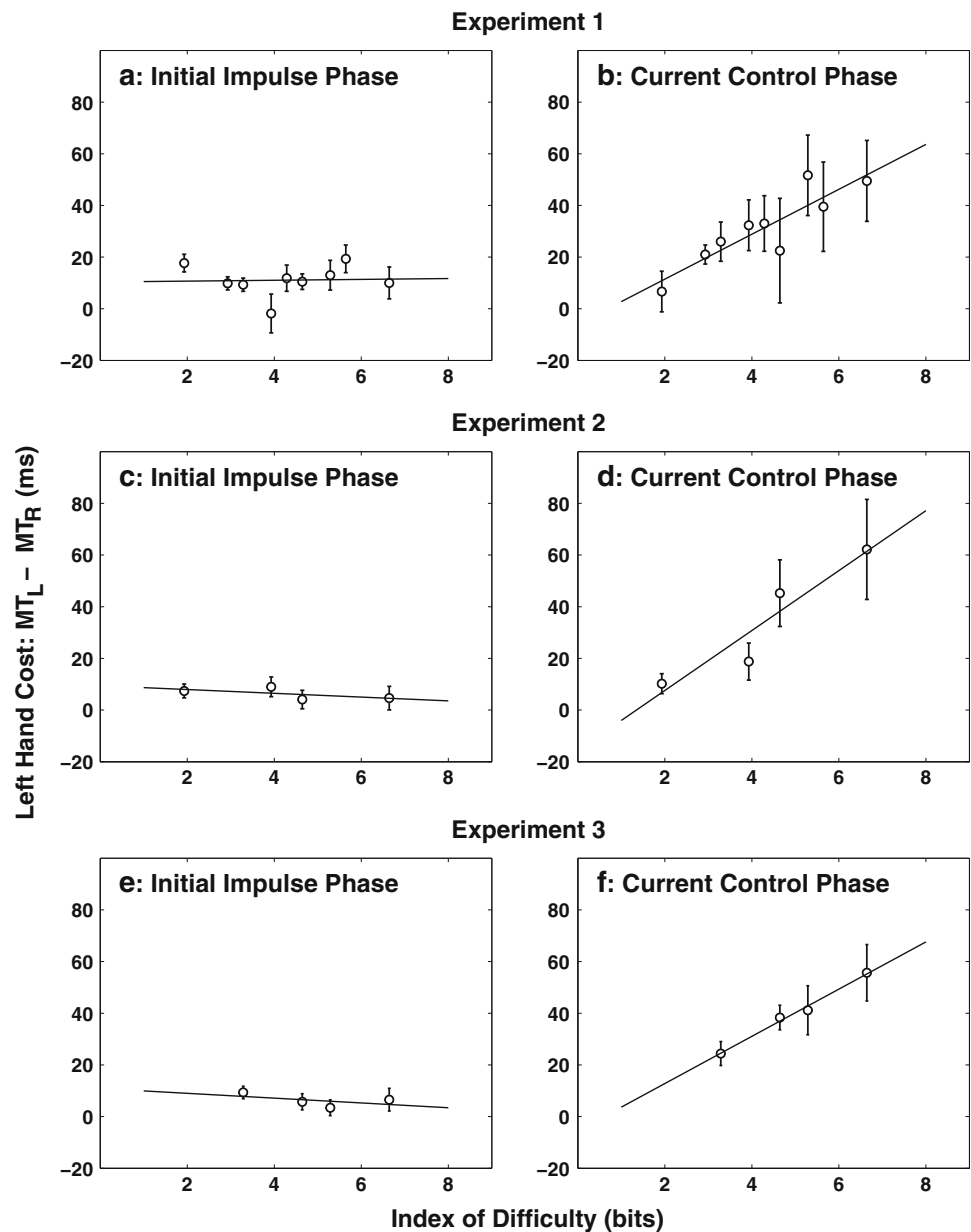
Table 1 Linear fit to the movement time during the initial impulse phase

Experiment	Hand	Movement time (ms)	
		Intercept and slope	R^2
1	Left	$120.91 + 17.18 \text{ ID}$	0.70
	Right	$101.25 + 18.64 \text{ ID}$	0.66
2	Left	$130.23 + 16.97 \text{ ID}$	0.65
	Right	$120.84 + 17.70 \text{ ID}$	0.70
3	Left	$87.09 + 24.00 \text{ ID}$	0.83
	Right	$76.20 + 24.93 \text{ ID}$	0.82

Table 2 Linear fit to the movement time during the current control phase

Experiment	Hand	Movement time (ms)	
		Intercept and slope	R^2
1	Left	$-0.11 + 68.46 \text{ ID}$	0.88
	Right	$10.20 + 57.90 \text{ ID}$	0.88
2	Left	$-7.80 + 81.27 \text{ ID}$	0.96
	Right	$7.86 + 69.67 \text{ ID}$	0.92
3	Left	$-167.17 + 105.85 \text{ ID}$	0.96
	Right	$-161.69 + 96.71 \text{ ID}$	0.95

Fig. 2 Left-hand cost (LHC) for the initial impulse phase and current control phase of reciprocal movements in Expts. 1, 2, and 3. *Error bars* indicate the standard error of the difference between the left- and right-hand MTs



(Fig. 2a). Most centrally, the experiment observed a variable LHC (mean 35 ms) in the current control phase, which was directly related to ID (Fig. 2b). The different effect of task difficulty on left- and right-hand performance suggests a number of hypotheses related to hemispheric specialization and intercommunication, which we will address in detail in the general discussion.

We next sought to extend the results using a speeded initial response and different ID values.

Experiment 2

Expt. 2 was designed to replicate the observation of LHC in response initiation and the current control phase and to

further explore the effect of hand on response initiation. In Expt. 1, response latency may have been less sensitive to ID because it was not a speeded response and its direction was known in advance, so to test that hypothesis, a variable foreperiod and randomly lateralized imperative cue were used to initiate the first response.

Method

Participants

The 14 undergraduates (twelve female) were all right-handed, as confirmed by scores of +70 or greater on a modified Oldfield (1971) handedness test, where +100 is exclusive right-hand use in all tasks and -100 is exclusive

left-hand use. They were recruited from summer research students and were compensated with research participation credit or \$10 for a 40-min session.

Procedure

As in Expt. 1, participants were instructed at the beginning of each trial whether to use the left or right hand. They began each trial by placing the tip of the specified tool on a central starting location, which was indicated by a vertical dowel that ended just above the midpoint between the two targets, so the tool was not in contact with anything at the beginning of the trial. When the tooltip was detected in the starting location, a binaural ready signal sounded, followed by a variable foreperiod (1.50–2.25 s). After the foreperiod, a monaural imperative signal (.125 s, 75 db, 435 Hz) in the left or right ear indicated to begin moving to alternately touch the two targets, starting with the target on the side of the imperative signal, as quickly as possible without sacrificing accuracy. Because of the variable foreperiod and imperative cue, the time of movement initiation was controlled and the direction of the required movement was unknown until the imperative signal was delivered. (Because of the variable foreperiod, imperative cue, and speeded instructions in Expts. 2 and 3, the measure of movement initiation will be referred to as “reaction time,” RT, rather than RL). Only the 1.6- and 10.5-cm targets and the 10- and 80-cm movement amplitudes were used (again representing IDs ranging from 1.9 to 6.6 bits), in a hierarchical order similar to Expt. 1, so each of the four amplitude-width target conditions was run with all four hand-direction combinations. These 16 unique trials were repeated a total of 6 times in different orders for 96 trials per participant. Trials with movements initially in the wrong direction were later excluded from analysis. Because the initial movement began at the midpoint between the targets, its amplitude was half that of the subsequent reciprocal movements, and so ID values for RT ranged from 0.9 to 5.6 bits.

Results

While there appeared to be a modest left-hand advantage in mean RT ($RT_L = 472 \pm 20$ ms, $RT_R = 494 \pm 21$ ms), particularly at the easier values of ID, the main effect of Hand fell short of significance, $F(1, 12) = 4.07$, $p = .066$, and there was no main effect of ID, $F(3, 36) = 2.32$, ns, nor a Hand \times ID interaction, $F(3, 36) < 1$, ns (Fig. 1c).

As in Expt. 1, overall MT for the left hand was longer (546 ± 28 ms) than that of the right (504 ± 22 ms), $F(1, 12) = 16.2$, $p = .002$, and MT varied with ID, $F(1.9, 22.7) = 120.2$, $p < .001$:

$$MT_L = 122 + 99 \text{ ID ms}; \quad R^2 = .92 \quad (6)$$

$$MT_R = 129 + 87 \text{ ID ms}; \quad R^2 = .89 \quad (7)$$

Additionally, as in Expt. 1, there was a Hand \times ID interaction, $F(2.6, 30.7) = 6.80$, $p = .002$ (Fig. 1d).

As in Expt. 1, the two movement phases were submitted to an omnibus ANOVA with factors Hand, ID, and Phase. The Hand \times ID \times Phase interaction was again significant, $F(2.05, 24.6) = 5.05$, $p = .014$, so a post hoc 2-way ANOVA with factors Hand and ID was computed (with Bonferroni correction) for each movement phase. In the initial impulse phase (Table 1), there was a LHC of 6 ms, $F(1, 12) = 7.96$, $p = .030$, and a strong effect of ID, $F(2.6, 31.5) = 204.8$, $p < .002$, but no Hand \times ID interaction, $F(3, 36) < 1$, ns (Fig. 2c). Difficulty added about 17 ms/ID to the initial impulse phase (Table 1). In the current control phase, the mean LHC was 34 ms, as shown by the main effect of Hand, $F(1, 12) = 14.8$, $p = .004$, and there was a strong effect of ID, $F(1.8, 21.6) = 92.0$, $p < .002$. The LHC for the current control phase was affected by ID, as shown by the Hand \times ID interaction, $F(2.1, 24.7) = 5.86$, $p = .016$. Difficulty added 81 ms/ID to the current control phase for the left hand, but only 70 ms/ID for the right (Table 2), as indicated by a strong linear relationship between ID and LHC (Fig. 2d):

$$\text{LHC} = -15.7 + 11.6 \text{ ID ms}, \quad R^2 = .89 \quad (8)$$

Discussion

Expt. 2 replicated the observation of Fitts' law in overall movement (Fig. 1d). There was a 6-ms mean LHC in the initial impulse phase, inversely related to ID (Fig. 2c; Table 1) and a variable LHC (mean 42 ms) in the current control phase, directly proportional to ID (Fig. 2d; Table 2), again showing that ID affected MT in the current control phase but not in the initial impulse phase. In short, the dependence of LHC on task difficulty was confined to the current control phase. In contrast to the small effect of ID on RL in Expt. 1, RT was not affected by ID in Expt. 2, and the effect of hand on RT was only marginal (Fig. 1c).

Experiment 3

Expt. 3 was designed to replicate the movement time observations of Expt. 2, using different values of ID. To increase the control over the RT measure, in Expt. 3 anticipatory or misdirected movement trials were immediately discarded, the participant was informed, and the condition was repeated later in the session so all data cells were completely filled. Thus, in view of the ambiguous RT

result of Expt. 2, Expt. 3 was optimized to detect any hand difference in RT.

Methods

Participants

Sixteen undergraduates (twelve female), all right-handed with scores of +75 or greater on the modified Oldfield (1971) handedness test, were recruited from summer research students and were compensated with research participation credit or \$10 for a 40-min session. Six had previously served in Expt. 2.

Procedure

Participants began each trial by placing the indicated tooltip on a central starting location, which was indicated by a vertical dowel that ended just above the midpoint between the two targets. When the tooltip was detected in the starting location, the ready signal sounded, followed by the variable foreperiod and the imperative signal, delivered monaurally to either the left or right ear. The imperative signal indicated to participants to begin moving as quickly as possible to alternately touch the two targets, without sacrificing accuracy, starting with the target on the side of the imperative signal, until 8 movements had been made. The 1.6- and 4-cm targets, and 20- and 80-cm movement amplitudes were combined with the hand-direction conditions as described for Expt. 2, for 96 trials, making 4 ID values ranging from 3.3 to 6.6. Because each initial movement began at the midpoint between the targets, it had half the amplitude of the subsequent repeated movements, and so its ID values for RT ranged from 2.3 to 5.6.

Results

As in Expt. 2, there were no significant main effects or interactions on RT, all F 's < 1 (Fig. 1e).

Overall movement durations of the left hand were longer (567 ± 27 ms) than those of the right (520 ± 24 ms), $F(1, 14) = 54.1$, $p < .001$. Movement duration varied with ID, $F(2.3, 31.6) = 235.7$, $p < .001$:

$$MT_L = -82 + 131 \text{ ID ms}; \quad R^2 = .95 \quad (9)$$

$$MT_R = -89 + 123 \text{ ID ms}; \quad R^2 = .94 \quad (10)$$

In addition, Hand interacted with ID, $F(2.3, 32.2) = 5.35$, $p = .007$ (Fig. 1f).

As in Expts. 1 and 2, the two movement phases were submitted to an omnibus ANOVA with factors Hand, ID, and Phase. The Hand \times ID \times Phase interaction fell just short of significance at the .05 level, $F(2.43, 34.02) = 3.01$,

$p = .053$. However, because the results (taken across all three experiments) are consistent, the post hoc 2-way ANOVA (with Bonferroni correction) with factors Hand and ID was computed for each movement phase as in Expts. 1 and 2. In the initial impulse phase, there was a LHC of 6 ms, $F(1, 14) = 8.5$, $p = .022$, and a modest effect of ID, $F(2.5, 34.5) = 243.2$, $p < .002$, again inversely related to ID; LHC did not vary with ID, $F < 1$ (Fig. 2e). In the current control phase, the mean LHC was 40 ms, as shown by the main effect of Hand, $F(1, 14) = 45.159$, $p < .002$, and there was a strong effect of ID, $F(2.1, 29.8) = 169.0$, $p < .002$. The LHC for the current control phase was affected by ID, as shown by the Hand \times ID interaction, $F(2.4, 33.7) = 4.41$, $p = .030$, reflecting a strong linear relationship between ID and LHC (Fig. 2f):

$$\text{LHC} = -5.5 + 9.1 \text{ ID ms}, \quad R^2 = .99 \quad (11)$$

In Experiment 3, an additional analysis explored whether there were differences between the hands in movement amplitude or variability that might be related to the left-hand cost. For each trial, median movement amplitude was computed from six movements in each trial, similar to the computation of movement time, and the standard deviation of these movements was also computed. Of necessity, given the manipulation of target distance, ID affected median movement amplitude, $F(3, 42) = 58,057.14$, $p < .001$, and it also affected movement variability, $F(3, 42) = 6.2314$, $p < .001$. However there were no main effects or interactions of variability involving Hand, all F 's < 1.

Discussion

Expt. 3 replicated the observation of Fitts' law in overall movement (Fig. 1f) and again showed a 40-ms LHC that was closely related to the difficulty in the particular task during the current control phase of the movement (Fig. 2f). There was no effect of ID on LHC during the initial impulse phase of movement (Fig. 2e). As in Expt. 2, task difficulty did not affect RT (Fig. 1e), despite the better control of anticipatory and incorrect-direction responses. The analysis of movement amplitude and variability performed for Experiment 3 suggests that neither of these parameters was affected by the hand used, and so the LHC that was observed is not obviously mediated by amplitude or accuracy differences.

General discussion

Overall left-hand cost

Overall MT depended strongly on task difficulty in all three experiments, as expected based on the historical consistency

of Fitts' law. In addition, the difference in the hands' movement times (left-hand cost) was larger at the higher difficulty levels (Fig. 1b, d, f). This result is also consistent with earlier observations, including those of Woodworth (1899) who reported larger accuracy differences between the hands when faster movements were required. Flowers (1975) measured MT with the preferred and non-preferred hands in both right- and left-handers at several difficulty levels. The LHC function for right-handers (computed from Flowers 1975, Figs. 2, 3) was similar to that reported here in Eqs. 5, 8, and 11: $LHC = 13 + 16 ID \text{ ms}$, $R^2 = .75$. Similarly, Kabbash et al. (1993) reported larger movement time differences at higher difficulties in a between-group study comparing preferred and non-preferred hand performance using a computer mouse, trackpad, and trackball. Neither the Flowers (1975) nor the Kabbash et al. (1993) data allow us to localize the effects of ID to a particular phase of movement, however.

Left-hand cost in the current control phase

The largest LHC was observed in the current control phase, the part of the movement after the point of peak velocity, and the LHC was modulated by task difficulty, ranging from about 10 ms in the easiest condition to 60 ms in the most difficult. Todor and Cisneros (1985) also observed a LHC that was modulated by ID in the latter segment of movement (identified by accelerometry) of a stylus-placing task. Thus, the present results are qualitatively similar to prior observations of the effect of difficulty on hand differences in performance.

Two general mechanisms may be considered to account for the overall LHC and its modulation by ID: The first hypothesis is based on the observation that the LH contributes substantially to visuomotor control of both hands. As a consequence, the corpus callosum is a potential bottleneck for information exchange between visuomotor areas in the LH and motor areas in the RH during precision movements by the left hand. Supporting this anatomical distinction, fMRI evidence shows LH participation in movement control of both hands (see Johnson-Frey et al. 2005; Haaland et al. 2004). Serrien et al. (2006) review the evidence that the contribution of each hemisphere to a movement is dependent on the type and complexity of the movement.

In keeping with the larger LHC in the more difficult conditions, the rate of transmission of information across the corpus callosum might be slower when more precise information must be exchanged, for two reasons. Ringo et al. (1994) point out that the variation in axonal diameters could lead to different rates of colossal transfer depending on the information conveyed: Recruitment of smaller and slower fibers for the transfer of more complex information could produce a longer callosal delay (a "parallel" model). Alternatively, if more "packets" of information had to be

exchanged between the hemispheres in order to complete more difficult left-hand movements (an "iterative" model), then more time would be required. Callosal delays have been estimated to be long enough (tens of ms; Ringo et al. 1994) that the iterative exchange of *multiple* discrete "packets" of information for submovements in the corrective phase of a movement is an implausible explanation for the small differences (tens of ms *in toto*) that we observed. Nevertheless, insofar as information must be exchanged across the corpus callosum during left-hand movements, callosal delays are a factor to be considered.

The second hypothesis for the modulation of LHC by ID is that precise movements of the left hand might be inherently more time-consuming than those of the right, with or without callosal delays. Such an explanation is compatible with a recently proposed model of hemispheric specialization and functional asymmetry (Sainburg and Schaefer 2004; Yadav and Sainburg 2011). The model posits a serial hybrid control system for arm movements, comprising an initial rapid predictive control (i.e., ballistic) process followed by switch to a slower impedance control process (roughly parallel to Woodworth's initial impulse and current control phases, respectively). The two processes of movement control may be reflected in the specialization of the action systems of the two hands (Guiard 1987; Sainburg and Schaefer 2004). In two-handed tasks, the left hand appears to be specialized for maintaining postures by modulating stiffness (in gripping a bottle, for example, or fingering a stringed musical instrument), whereas the right hand is specialized for controlling dynamics (in uncapping the bottle or bowing the instrument). Effects of this hemispheric specialization might, then, appear in one-handed tasks as well.

Relatedly, Sainburg and Schaefer (2004) observed that, in moving different distances, the dominant hand modulated the peak of the accelerative impulse, whereas the non-dominant hand varied the duration of an impulse with relatively constant peak across amplitudes. As a consequence, the duration of the acceleration varied more during non-dominant arm movements than during those of the dominant arm. Such hemispheric differences in control strategies could be reflected in the left-hand cost that we observed in the current control phase. A specific prediction of this hypothesis, not yet tested, is that the time of switching from predictive to impedance control in the serial hybrid model would vary with task difficulty, contributing to the variation of LHC with difficulty. It remains to be seen whether this hypothesis is supported by formal modeling and empirical observations.

Left-hand cost in the initial impulse phase

In contrast to the relatively large LHC modulated by ID in the current control phase, the LHC in all three experiments

was small (6–14 ms) and not affected by task difficulty (Fig. 2a, c, e). As in the case of the current control phase, one plausible explanation for any LHC in the initial impulse phase might be the delay of information being transmitted through the corpus callosum (Ringo et al. 1994). Such a delay might come about because of the active involvement of the dominant hemisphere in initiating the movement (e.g., see Liepmann in the early 20th century, cited in Rothi and Heilman 1996), or because other specific information must be shared between hemispheres during the movement. We would expect that the effects of a callosal delay for response initiation would be equivalent at all levels of task difficulty. An alternative hypothesis for LHC in the initial impulse phase, based on the serial hybrid model (Sainburg and Schaefer 2004; Yadav and Sainburg 2011), is that the LHC observed in the initial impulse phase (as we have operationally defined it, analogous to the predictive control process of the serial hybrid model) results from impedance control rather than predictive control. Recall that our operational definition of the boundary between initial impulse and current control phases was the moment of peak velocity. The serial hybrid model (Yadav and Sainburg 2011) suggests that the switch from predictive to impedance control occurs before peak velocity for the left hand and after peak velocity for the right hand. An early switch to impedance control could impose a cost on left-hand movement time.

Response initiation time

While investigating response initiation was not the primary motivation of these experiments, and an exhaustive treatment of hand differences in response initiation is beyond the scope of the present paper, the lack of a consistent effect of ID on response initiation (especially the clearly null effect in Expt. 3; see Fig. 1e) deserves some scrutiny.

Hand differences in RT have been observed to be greater for speeded responses (Zuoza et al. 2009), responses that require the allocation of visuospatial attention (Barthélemy and Boulinguez 2002), and complex responses (Haaland et al. 2004), whereas hand differences are minimal for responses that require great accuracy (Carson et al. 1995).

In keeping with the variable results on the hand used and response initiation, in our observations, hand differences in initiation time fell short of significance in all three experiments. Thus, in contrast to the LHC of *completing* precise movements, no corresponding cost to *initiating* movements with left hand was observed, and there was an effect of task difficulty on response initiation time only for RL in Expt. 1. Insofar as first-response initiation time reflects processes similar to the initial impulse phase of the reciprocal movements that follow, the results are broadly consistent across the two measures.

The lack of hand differences in response initiation (Fig. 1a, c, e), a presumed index of LH involvement in left-hand movements, contrasts with tasks that are speeded or require visuospatial processing in the initiation of movement. The left and right hand's initiation time or initial impulse duration will not reflect the precision required by the task, which would be most salient only later in the movement when the effector must be adjusted by corrective movements (Woodworth 1899; Crossman and Good-ave 1963/1983; Meyer et al. 1988).

For example, Haaland, et al. (2004) observed substantial (40–50 ms) LHC in RT in their response sequencing task but no larger LHC in MT for the more complex sequential movement, whereas the present study showed no RT difference but larger LHC for the more precise movement. This distribution of LHCs therefore suggests a double dissociation between the effects of sequence complexity and endpoint precision on response initiation and movement time, possibly indicating a distinction between LHCs that are due to interhemispheric communication and LHCs that are due to inherent hemispheric differences.

Summary and conclusions

Overall, these differences in hand performance, observed using a hand-held tool, would be expected to generalize to reaching with the unencumbered hand as well. Many Fitts' law experiments have used a hand-held tool such as a pencil, stylus, or other pointing devices (Woodworth 1899; Fitts 1954; Fitts and Peterson 1964; Todor and Cisneros 1985; Kabbash et al. 1993). Similarly, Arbib et al. (2009) argue that the brain accommodates to tool use by extending the body schema to incorporate it.

Hypotheses based on central function notwithstanding, there might be more peripheral differences between the hands in the control of movement that have yet to be systematically explored. Consistent lateral differences in movement kinematics have been observed in other situations. Janssen et al. (2009) observed that during an object manipulation task, a comfortable end posture (Rosenbaum et al. 1992) was selected by the right arm more frequently than the left. Relatedly, if moving with either hand involved a different distribution of movement extent across the segments of the arm, MT might be affected (see Rosenbaum et al. 1991, for discussion of the movement times of different limb segments). It remains a question for further research to determine whether kinematics or joint trajectories differ between the arms in the present task, a factor that would need to be ruled out before all differences are definitively attributed to central mechanisms.

A variety of converging evidence supports a specialization of the two hemispheres in regulating precision

motor movements by the left and right hands. If specialization takes the form of LH dominance in motor execution, movements of the non-dominant hand (the left, for the right-handers who were tested) would either suffer in precision or require more time for communication between the hemispheres. Alternatively, the specific mechanisms inherent in each hemisphere might differ in the details of their execution processes that would produce hand differences in MT. In any case, the present experiments demonstrate, for a tool-based pointing task, that making precise movements with the left hand incurs a consistent and replicable cost on the order of tens of ms, in proportional to the difficulty in the movement as described by Fitts' Index of Difficulty.

In the three experiments, the slopes of the LHC as a function of ID range from 9 to 12 ms/bit. Thus, the effect of difficulty on dominant (right-hand) and non-dominant (left-hand) movement times in this task may be precisely quantified. Consider, for example, the observations of Expt. 3 (Eqs. 9 and 10). When ID is small, MT_L and MT_R are essentially equal, whereas at $ID = 6.6$, there is a 59-ms LHC: $MT_L = 782$, compared with $MT_R = 723$. If one were to adjust the left hand's difficulty (ID_L) so it could move as quickly ($MT_L = 723$ ms) as the right does at $ID_R = 6.6$, ID_L would have to be somewhat smaller to make the task a little bit easier. Solving for ID_L with $MT_L = 723$ in Eq. 9 produces $ID_L = 6.1$, a value just 0.5 bits smaller than ID_R in the logarithmic units of Fitts' law. A factor of "half a bit easier" corresponds to having the left-hand move (in 723 ms) to a target that is either closer or larger than that of the right, by $\Delta ID = 0.5$ bits. That is, the left hand's target would have to be $2^{0.5} = 1.41$ times as wide, or only $2^{-0.5} = .71$ as far away, to be touched as quickly as by the right hand. For less difficult tasks, the handicap required by the left hand for it to move as fast as the right would be correspondingly smaller.

Most generally, the present results support multiphase models of movement generation, in which separate processes, different for each hand, contribute to the launching and completion of precision hand movements.

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