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Report

Responsibility Assignment in Redundant Systems

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Summary

Redundancy is a fundamental feature of biological motor systems. For example, when touching an object, many different combinations of movements of the shoulder, elbow, wrist, and finger joints result in the same movement at the fingertip [1]. Exploiting this redundancy, the motor system distributes work across effectors to minimize signal-dependent noise and effort [2–4]. When an error occurs, however, the motor system must assign the error to specific effectors, even though it may be ambiguous which effector caused them. Here, we studied the principles of responsibility assignment by using a bimanual task, in which the left and right hands jointly moved a visual cursor. We found that participants assigned errors, which were induced by visual rotation of the cursor, in a unified manner for correction and adaptation; the hand that corrected more for the error within the current movement also showed a bigger adaptive change in the next movement. Right-handed participants corrected errors more with their left hands, even though they corrected faster with their right hands in nonredundant tasks. Further experiments show that the motor system assigns responsibility preferentially to the hand that was previously exposed to larger errors. Our results show that responsibility assignment is a flexible process that attributes errors to the most likely cause.

Results and Discussion

When an error occurs in a redundant movement, the motor system faces a situation akin to a teacher supervising two students working on a joint project. The teacher could let the more experienced student determine and repair the mistake. Although this may be an efficient remedy for the situation, it is more likely that the less experienced student caused the error. Therefore, it may be a good idea to let that student correct and learn from the mistake. This analogy makes clear that responsibility assignment is important for two, possibly associated, processes. First, the motor system needs to determine which effector should correct the current movement online. Second, the system needs to decide which effector should learn from the error and change its motor command on the next trial. We therefore distinguished between the reactions to errors occurring in the late component of the same movement (correction) and the early component of the consecutive movement (adaptation).

To study the principles of responsibility assignment, we used a bimanual redundant task, in which a single cursor was presented at the midpoint between the two hands. Participants moved the cursor to a target with a combined bimanual action (Figure 1A). To induce errors, we visually rotated the cursor on each trial by a random angle around its start location. Because participants could not see their hands, the origin of the error was ambiguous and could be attributed to either the right or left hand.

For each trial we determined the angular deviation of the initial movement of the cursor (y_C) and of the two hands (y_L, y_R) from straight ahead. We also determined the subsequent correction, the change between the initial and overall movement direction (c_L, c_R). To estimate the correction gains for each hand (g_L, g_R), we took the slope of the regression line of the correction onto the initial cursor error (Figure 1B). Although these correction gains must average to 1.0 to bring the cursor to the target, their relative distribution is free to vary.

To measure adaptation, we determined how much each hand changed its initial movement direction in response to the visual error on the previous trial. We estimated adaptation rates by fitting a state-space model to the initial movement directions (Figure 1C; Supplemental Experimental Procedures available online).

The motor system may assign responsibility for adaptation according to the same principles as those used in online correction. Alternatively, it may follow different rules for the two processes. Given that among right handers, the dominant right hand is usually more skilled [5–8], it would make sense to use the better right effector for corrections, thereby increasing performance on that trial. In contrast, because the left, less skilful, hand is more likely to cause errors, one might expect to observe more adaptation for this hand.

To our surprise, however, we found that our right-handed participants (n = 25) showed a tendency to correct more with the left, nondominant hand (Figure 1D). To quantify this observation, we calculated the asymmetry index $g_R/(g_R + g_L)$. These were significantly smaller than 0.5, $t(24) = -3.63$, $p = .001$. Averaged over all experiments in this study, the asymmetry index for corrections to visual rotation was 0.45 (n = 61, SD = 0.11). We also reanalyzed data from three previous studies [9, 10] in which a force field perturbed one or both hands. Again, we found a bias toward left-hand correction with an average asymmetry index of 0.47 (n = 38, SD = 0.03). For force field perturbations, the asymmetry was present even when visual feedback was withdrawn. Thus, the left-hand preference for movement corrections is consistent across a range of perturbation types.

To determine whether the bias in correction depends on handedness, we also included 10 left-handed participants in our study. On average, this group corrected slightly more with the right hand. The handedness score correlated negatively with the asymmetry index for corrections (Table S1). Thus, participants who used the left hand more in everyday activities corrected less with this hand in a redundant task.

Importantly, the asymmetry index for corrections correlated positively with asymmetry index for subsequent adaptations (Figure 1D). This observation was significant when both groups were combined ($r = 0.6$, $p < .001$) in the right-handed group alone ($r = 0.61$, $p < .001$), and was marginally significant

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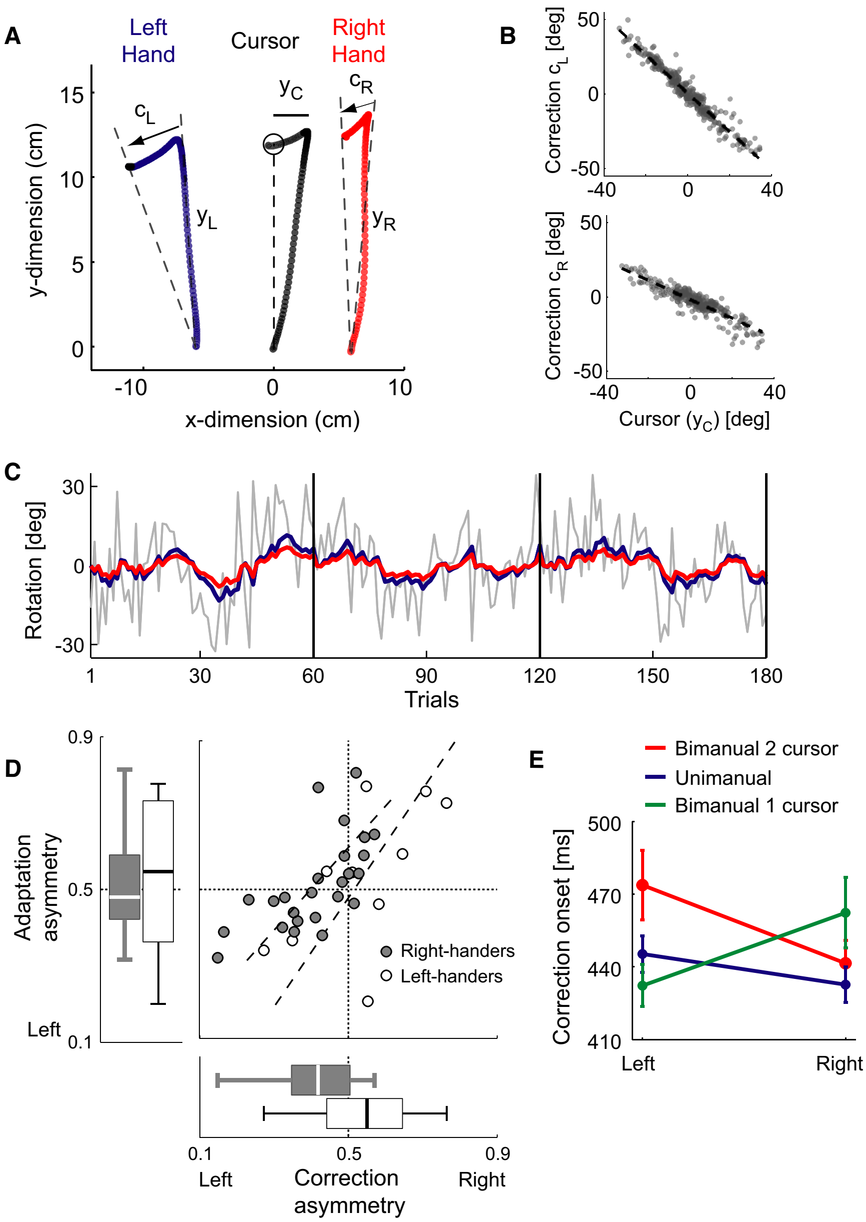

Figure 1. Responsibility Assignment in a Bimanual One-Cursor Task

Data are from Experiments 1a and 1b.

(A) Example trial. The cursor position is calculated as the average position of the two hands, and then rotated to the right, inducing an initial cursor error (y_C, in deg). The angle of correction of the left (c_L) and right (c_R) hand is measured as the difference between initial (y_L and y_R, measured at 150 ms) and overall movement direction.

(B) The regression slope of the correction of the left (c_L, top) and right (c_R, bottom) hand against the initial cursor error (y_C) served as a measure of the correction gain for that hand (g_L, g_R). Exemplary data from a single participant with larger correction gain of the left hand is shown.

(C) Adapted state of the left (z_L, blue) and right (z_R, red) hand from the state-space model fit to the initial movement directions, in response to the imposed visual rotation on the cursor (gray) that followed a damped random walk. In this particular example, the adaptation rate for the left hand (B_L) is bigger than for the right hand (B_R).

(D) The correction asymmetry [$g_R/(g_L+g_R)$] < 0.5 indicates that right handers (gray circles) preferentially corrected with the left hand. Participants from Experiments 1a and 1b are shown together. Left handers (white circles) did not show a significant bias. The adaptation asymmetry [$B_R/(B_L + B_R)$] is correlated with the correction asymmetry within each group.

(E) The onset of correction was measured at the time when the hand had achieved 20% of the total correction. Results are shown for right-handed participants only. In both the bimanual two-cursor (red) and unimanual (blue) condition, the right hand corrected faster. The left hand corrected faster only in the redundant one-cursor condition (green).

in the left-handed group alone (r = 0.63, p = .0518). Participants that corrected the ongoing movement to a greater degree with the left hand also adapted motor commands on the next trial more for the left hand. Thus, rather than employing separate principles, the motor system appears to assign responsibility jointly for correction and adaptation. The positive correlation could be taken as evidence for the idea that online corrections serve as a teaching signal for adaptation [11, 12]. Although our findings are congruent with this hypothesis, it is also possible that adaptation and online correction are independent processes [13], for which responsibility assignment is solved according to similar principles.

What are the factors that determine this common responsibility assignment? Asymmetries in corrections may arise if the two hands independently worked to reduce the error. That is, if the nondominant hand were faster to correct than the dominant hand, it would reduce the error before the dominant hand could do so, and thus perform more of the overall correction. For our right-handed participant, the left hand initiated the correction before the right hand in the redundant one-cursor task (Figure 1E, green line, $t(24) = -2.19$, p = .039). In contrast, in the unimanual task, participants consistently initiated the correction sooner with the right than with the left hand (Figure 1E, blue line, $t(24) = 2.85$, p = .009). In Experiment 1b (10 right-handed participants), we also observed this right-hand advantage when participants moved their hands simultaneously to two separate targets (red line, $t(9) = 4.37$, p = .002).

These results show that responsibility assignment is not determined by the speed with which each effector makes corrections in nonredundant tasks. Other variables, such as a small asymmetry in movement extent and the temporal asynchrony between the hands, cannot explain the distribution of corrections either (Table S2). What then is the underlying cause of the asymmetry? We consider two possible hypotheses, both motivated by optimal feedback control theory [14]. In this framework, feedback corrections involve two processes—state estimation and control—both of which could give rise to the asymmetric corrections.

During state estimation, the system combines different sources of sensory information with internal predictions,

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each weighted by the inverse of its uncertainty, to form an optimal estimate of the controlled body and environment [15, 16]. In the one-cursor task, the motor system estimates the position of the two hands and the cursor. Participants could not see their hands and proprioception has higher uncertainty than vision [17, 18]. Therefore, the system would use visual information about the cursor position to infer the position of the hands (see Supplemental Experimental Procedures).

If the uncertainty of the internal prediction for one hand were higher than for the other, the system would attribute the error—and subsequent correction—to that hand (Figure S1A). Indeed, higher uncertainty for the left than right hand has been proposed as an explanation for the asymmetric transfer of force field learning across hands [15]. Because the discrepancy between intended and estimated hand position also serves as a signal for subsequent trial-to-trial adaptation [13], this would also lead to faster adaptation for the more uncertain hand. Therefore, the "estimation hypothesis" provides an elegant explanation for why correction and adaptation rates are closely related.

Alternatively, according to the "control hypothesis," asymmetries between the hands could arise from an asymmetric setting of feedback control gains. Feedback gains multiply the difference between the estimated and desired state to determine the size of the corrective command for each effector (see Supplemental Experimental Procedures). For nonredundant unimanual movements, feedback gains are upregulated by exposing the hand to increased movement errors [19] (D.W. Franklin et al., 2009, Soc. Neurosci., abstract). Feedback control gains for the nondominant hand may be elevated due to the increased need to correct for errors that arise because of the greater variability in this hand (Table S3).

Can these explanations be distinguished? Our approach is based on the fact that reach errors can arise from different sources. Execution errors involve a discrepancy between the predicted and perceived state of the controlled object, for example because the cursor is rotated around the starting position. Target errors arise from a discrepancy between the predicted and perceived state of the movement goal, for example when the target is displaced at movement start. Although both types of errors evoke similar corrections, significant trial-by-trial adaptation to random perturbations is found only for visual rotations [20]. Thus, execution errors lead to an update of the state-estimate and the forward model of the hand, whereas target errors do not.

This distinction provides an opportunity to test the estimation and control hypotheses. Different uncertainties for the two hands, as proposed by the estimation hypothesis, can affect the distribution of feedback correction only if the error influences the estimated states of the hand (visual rotation). If the error signal changes only the estimate of the target location (target displacement), the difference in uncertainty should not influence the distribution of corrections (Figures S1B and S1D). In contrast, the control hypothesis predicts that the asymmetry should be observed in both conditions. Feedback gains multiply the difference between the desired and estimated state of the hand, and it therefore does not matter whether the estimate of the hand or of the target has changed (Figures S1E and S1F).

We tested these predictions in Experiment 2 ($n = 12$ right handers) by inducing corrections through visual cursor rotation (execution error) or through target displacement just after movement start (target error). Consistent with the idea that target errors are attributed to a noncontrollable external cause

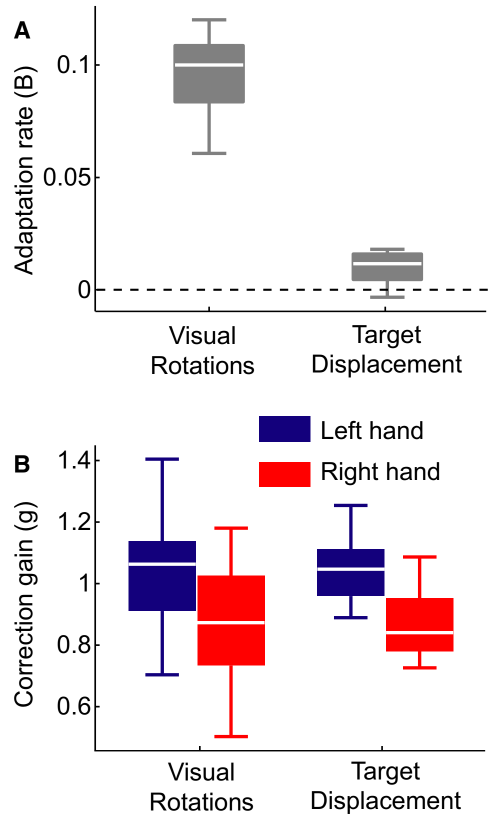

Figure 2. Results of Experiment 2

(A) The overall adaptation rate for random visual rotations was substantially higher than for random target displacements.

(B) The correction gains were higher for the left hand than for the right hand, both for the visual rotation and the target displacement conditions. Experiment 2 included right-handed participants only.

[20], the adaptation rates in the target displacement condition were close to zero and significantly lower than in the visual rotation condition, $t(11) = 13.35$, $p < .001$ (Figure 2A). In both conditions, however, right-handed participants still corrected more with their left hands (Figure 2B, $F(1,11) = 5.43$, $p = 0.04$), and there was no difference between task conditions, $F(1,11) < 0.01$, $p = .993$. Thus, these results favor the idea that the asymmetry arises from an asymmetric setting of feedback control gains rather than from asymmetries in the uncertainty associated with state estimation.

No matter whether the control or estimation hypothesis is correct, our core assumption is that the motor system assigns responsibility to the nondominant hand, because that hand encounters larger errors during everyday movements. If this is true, we should be able to modify the distribution of feedback corrections by exposing each hand to errors of different sizes before testing in the redundant task. We tested this prediction in Experiment 3. For the first 70 of 110 trials per block, participants alternated between unimanual right- and left-handed movements. For the last 40 trials, they performed the bimanual one-cursor task. During each unimanual movement, we imposed a random visual rotation of the cursor. The random process had high variance for one hand and low variance for the other hand (Figure 3A). Many participants were unaware of the manipulation and attributed their errors to poor ability to control the "treated" hand.

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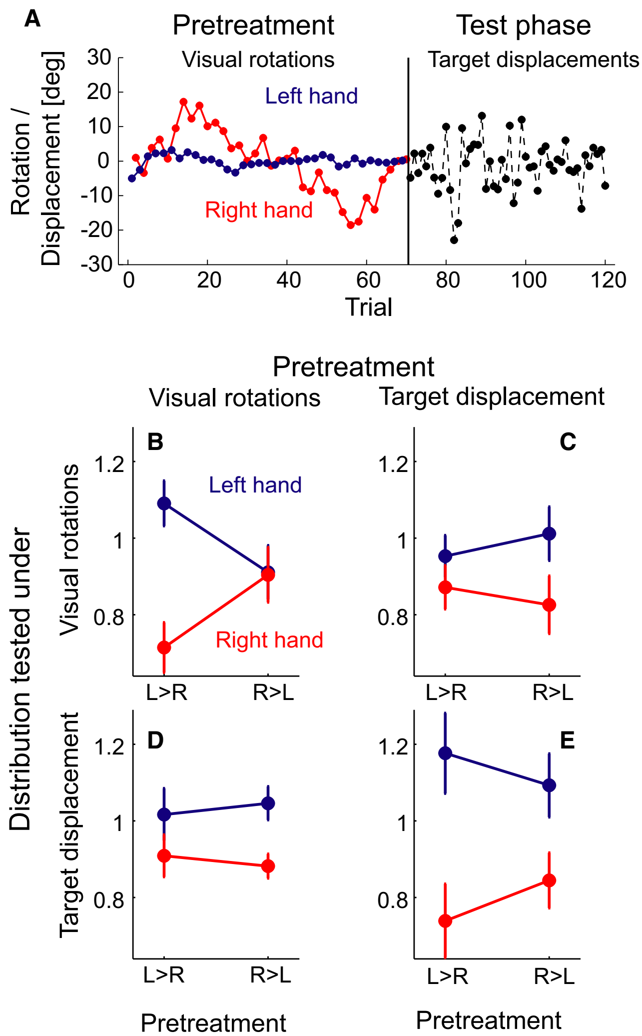

Figure 3. Modulation of Feedback Control Gains in Experiment 3

(A) In each block, participants performed 70 unimanual trials. Perturbations were caused either by visual rotations or target displacements, with different variances for the two hands. The distribution of feedback corrections was tested in the bimanual one-cursor task. The example shown is with high variance on the right hand.

(B) Correction gains of the left (blue) and right (red) hands. When the left hand experienced larger visual rotations during unimanual trials than the right (L > R), it corrected substantially more for visual rotation errors in the subsequent bimanual task. When the right hand experienced bigger rotation than the left (R > L), this difference cancelled out.

(C) No effect on the distribution of correction for visual rotations was found when the pretreatment involved target displacements.

(D) No effect on the distribution of correction for target displacements was found when the pretreatment involved visual rotations.

(E) The effect occurred again when the hands were pretreated and tested with target displacements.

We found that the hand exposed to large errors during the unimanual task also increased its contribution to the feedback correction in the subsequent bimanual one-cursor task (Figure 3B, significant interaction, $F(1,16) = 5.383$; $p = .034$). These results clearly show that responsibility assignment is not fixed but influenced by recent experience. The findings are consistent with both the estimation and the control hypothesis. According to the estimation hypothesis, increased error will lead to increased state-uncertainty for the hand [21]; according to the control hypothesis, correcting for larger errors should lead to an increase in feedback gain for that hand [19] (D.W. Franklin et al., 2009, Soc. Neurosci., abstract).

To distinguish these two explanations, we replicated the experiment via target displacements instead of visual rotations for both unimanual and the subsequent bimanual trials. If increased errors lead to an increase in control gains, we should observe a similar effect for target displacements [19]. In contrast, target displacements should not lead to a change in the uncertainty of the hands, as shown by the fact that the motor system clearly attributes these errors, at least for the purpose of adaptation, to unpredictable target movements. During the subsequent bimanual movements, we again found that the proportion of the correction increased for the hand that had experienced larger errors in the preceding unimanual trials (Figure 3E, significant interaction, $F(1,7) = 9.419$, $p = .018$). Although the effect was numerically smaller than for visual rotations, a direct comparison of the effect size across these two conditions was not significant, $F(1,23) = 0.658$, $p = .426$. A parsimonious explanation for these results is that feedback gains were altered based on the asymmetric demand on corrections in the pretreatment phase [19] (D.W. Franklin et al., 2009, Soc. Neurosci., abstract). The estimation hypothesis, which states that these changes are based on the changed uncertainty in the visuo-motor mapping, can account only for the visual rotation findings.

According to the control hypothesis, the same feedback gain determines the size of the corrective command in both conditions. Therefore, increasing one type of error should increase feedback corrections for the other type of error. To test this, we pretreated the hands during unimanual movements with different amplitudes of visual rotations and then tested the distribution of feedback corrections in the one-cursor task for target displacements (Figure 3D). In the second condition, we pretreated with target displacements and tested with visual rotations (Figure 3C). In both conditions, we failed to observe an influence of pretreatment ($t(6) = 0.449$, $p = .669$ and $t(7) = 0.197$, $p = .850$). Indeed, the pattern was reversed for both visual rotations and target displacements, making it unlikely that these null effects reflect a lack of statistical power. Thus, the upregulation of feedback gains seems to be specific to the source of the error.

Taken together, our experimental results provide important insights into the process of responsibility assignment. First, the distribution of feedback correction is not a mere consequence of the independent actions of the two hands. Faster corrections for the nondominant hand were specific to the redundant tasks; indeed, for the nonredundant task, the dominant hand was faster to correct for movement errors. Furthermore, we show in Experiment 3 that responsibility assignment is a flexible process in which the distribution of corrections across effectors reflects the recent history of movement errors. According to this idea, the consistent left-hand bias in right-handed participants would arise because actions conducted with the left hand are more prone to errors [22, 23]. This could lead to higher uncertainty associated with state estimation of the left hand [15], which would also explain the correlation between correction and adaptation. However, the estimation hypothesis can account for the results in the visual rotation, but not in the target displacement conditions. Rather, a parsimonious explanation for both results would be that feedback gains are increased for the left hand [19] (D.W. Franklin et al., 2009, Soc. Neurosci., abstract).

Responsibility assignment appears to also be sensitive to the type of the error, because pretreating the hand with target displacements did not change the distribution of the error correction during visual rotations—and vice versa. This surprising finding suggests that a simple change in control gain is not sufficient to explain our results. Rather, the motor system specifically assigns responsibility to the effector that was most probably associated with that specific type of error in the past.

Redundancy endows the motor system with the flexibility to distribute work across many effectors and to compensate after damage or injury. Responsibility assignment is a necessary process when learning from errors, and it will shape the final learned movements.

Experimental Procedures

Participants, apparatus, and stimuli are described in the Supplemental Experimental Procedures.

Experiment 1: Visual Rotation Task

To start a trial, participants positioned the cursors of the left and right hand (8 mm spheres) into the starting spheres (8 mm diameter), positioned 6 cm to the left and right of the body midline at chest height. In unimanual trials, a target was displayed 12 cm above either the left or right starting sphere. In the bimanual one-cursor condition, a single target was presented, and a single cursor was positioned at the spatial average of both hands. In the bimanual two-cursor condition, two targets were presented. Participants moved the cursor(s) to the target(s) by moving the left, the right, or both hands upward. The cursor(s) could be rotated around their respective starting position by a random angle; in the bimanual 2-cursor condition, rotations occurred independently for the left and right hands.

In Experiment 1a, participants performed 8 blocks of 60 trials: 2 unimanual left blocks, 2 unimanual right blocks, and 4 bimanual one-cursor blocks. Block order was counterbalanced across participants. In every trial, the cursor trajectory was rotated to the left or to the right by u_n degrees according to a damped random walk, described by the equations $x_{n+1} = 0.8x_n + \eta_n$ and $u_n = x_n + \varepsilon_n$ with the standard deviations set to SD(η) = 4 deg and SD(ε) = 8 deg. Only perturbation sequences within ±35 deg were used. The experiment began with one 15-trial training block for each condition.

In Experiment 1b, participants performed two unimanual left, two unimanual right, three bimanual one-cursor, and three bimanual two-cursor blocks. Rotations occurred randomly to the left or right (±18 deg, each 40% of the trials).

Experiment 2: Target Displacements versus Visual Rotations

Participants performed 8 blocks of 60 trials of the bimanual one-cursor task alternating between two blocked conditions. In the visual rotation condition, the cursor was rotated by ±18 deg. In the target displacement condition, the target was displaced at movement onset by ±18 deg. The movement of the target was clearly visible to the participants. Target displacements and visual rotations were determined independently on each trial, with a third of the trials perturbed to the right, a third perturbed to the left, and the remaining trials unperturbed.

Experiment 3: Pre-exposure of the Hands with Different Sizes of Errors

Participants (n = 40) performed 8 blocks of 110 trials, distributed over 2 experimental sessions, which were separated by at least one day. Each block started with a pretreatment phase of 70 trials during which participants alternated between unimanual left and unimanual right reaching movements. In the subsequent test phase of 40 trials, participants used both hands to reach the target with a single cursor. In condition 1, both pretreatment and testing phase involved visual rotations. In condition 2, we treated and tested the hands with target displacements. In condition 3, we treated the hands with visual rotations but tested with target displacements and vice versa in condition 4.

For visual rotations, the perturbation sequence for each hand was generated from a random walk [21], $u_{n+1} = u_n + \varepsilon_n$ with a SD (ε_n) of 1 deg for one hand and 4 deg for the other. Only perturbation sequences within ±35 deg and with the last 4 perturbations within ±2.5 deg of straight ahead were used. For the target displacements, the perturbations were generated from a Gaussian white-noise process with SD = 1 or 8 deg. Pilot experiments indicated that these values roughly matched the size of the errors between conditions. Note that in the visual rotation condition, the size of the errors was much smaller than the size of the cursor rotations, because participants adapted to the perturbation. For the test phase in the bimanual one-cursor task, we used random perturbations with a SD of 6 deg.

Supplemental Information

Supplemental Information includes one figure and three tables and can be found with this article online at doi:10.1016/j.cub.2010.05.069.

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