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Fast corrective responses in redundant motor control are shaped by intrinsic constraints of movement patterns

Rapid movement corrections in redundant systems

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Abstract

In real-world motor tasks, body movements unfold in a high-dimensional space, whereas task errors are defined in a lower-dimensional space. How such low-dimensional errors propagate across redundant motor degrees of freedom to generate rapid corrective responses remains poorly understood. To address this question, we developed a redundant bimanual task in which human participants (males and females) manipulated a virtual stick with both hands to move its tip to a visual target. By shifting the tip position (task-relevant perturbation) or rotating the stick with the tip position fixed (task-irrelevant perturbation), we separated task-space errors from redundant-dimension errors. Participants rapidly corrected both types of perturbations using highly stereotyped movement patterns. Corrections to task-relevant errors consistently involved coordinated changes across redundant dimensions, and even perturbations that did not affect task success elicited systematic corrective responses. Together, these results demonstrate that fast corrective responses in redundant motor control are shaped by intrinsic coordination constraints that govern how visual errors propagate through the motor system.

Significance Statement

The motor system can correct a movement error within 200 ms of its occurrence. However, the compensatory movement pattern is not uniquely determined because of the many degrees of freedom in the body. How does the motor system rapidly select and execute an appropriate corrective pattern? Our bimanual stick-tip reaching task, in which participants controlled a cursor located at the tip of a virtual stick, allowed us to dissociate tip-displacing errors from stick-rotation errors. Tip displacements triggered fast corrections, but surprisingly, rotation-only perturbations also evoked rapid responses and biased the tip along its usual coordination between tip motion and stick tilt. Our findings show that fast corrections are constrained by intrinsic coordination patterns, limiting the ability to ignore goal-irrelevant perturbations.

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55 Introduction

56 Accurate control of limb end-effectors, such as the hand, is essential for interacting with the
57 external environment and relies on multiple error correction processes operating at different
58 timescales. One such process is rapid feedback control, which allows ongoing movements to be
59 corrected in response to unexpected perturbations with latencies faster than voluntary reactions
60 (Day & Lyon, 2000; Scott, 2016). Another process involves updating motor plans based on past
61 errors, enabling feedforward compensation in subsequent movements and promoting motor
62 learning (Shadmehr & Mussa-Ivaldi, 1994; Thoroughman & Shadmehr, 1999; Takiyama et al.,
63 2015). These error correction processes have been predominantly studied using unimanual
64 reaching tasks that constrain movement to a two-dimensional plane and limit kinematic degrees
65 of freedom to the shoulder and elbow (Morasso, 1981; Flash & Hogan, 1985; Gordon et al.,
66 1994). Importantly, these paradigms involve relatively limited kinematic redundancy, as the
67 dimensionality of the control variables matches that of the task space.

68 In contrast to these constrained paradigms, the motor system typically possesses more
69 degrees of freedom than are strictly necessary to control an end-effector (Bernstein, 1996). In
70 such redundant systems, multiple body configurations can produce the same end-effector
71 outcome, giving rise to dimensions of movement that directly affect task success as well as
72 dimensions that do not. A central challenge for motor control is therefore how task-relevant
73 errors, defined in a low-dimensional task space, are distributed across high-dimensional motor
74 degrees of freedom to achieve reliable control. One influential framework for addressing
75 redundancy is optimal feedback control theory, which proposes that motor behavior follows a
76 minimal intervention principle: variability is actively corrected in task-relevant dimensions while
77 being tolerated in task-irrelevant dimensions (Todorov & Jordan, 2002; Todorov, 2004; Scott,
78 2004). Diedrichsen (2007) provided empirical support for this framework by showing that
79 feedback control and adaptation in a redundant bimanual task were flexibly adjusted according

80 to the task goal, and interpreting these task-dependent changes as consistent with optimal
81 feedback control.

82 To investigate how redundancy is resolved during movement, we previously developed a
83 redundant bimanual task in which participants manipulated the endpoint of a virtual stick using
84 both hands (Kobayashi & Nozaki, 2024). Although the same endpoint position could be
85 achieved through multiple stick configurations, participants consistently adopted stereotyped
86 movement patterns involving stick tilt, indicating intrinsic coordination constraints linking
87 movement dimensions that directly affect the control of the end-effector with those that do not.
88 Based on this background, we defined the terms 'end-effector relevant' and 'end-effector
89 irrelevant', thereby distinguishing them from the commonly used terms 'task-relevant' and 'task-
90 irrelevant' (Kobayashi & Nozaki, 2024). The constraints between end-effector relevant and
91 end-effector irrelevant movements appear to shape how adapted motor commands are
92 organized during movement planning. However, it remains unknown how these coordination
93 constraints influence the rapid propagation of end-effector relevant errors through redundant
94 motor spaces during ongoing movement. The present study addresses this question by
95 examining how the motor system rapidly reconfigures redundant effectors to correct movement
96 errors via feedback control.

97

98 **Materials and Methods**

99 **Participants**

100 A total of 65 healthy adults (33 females and 32 males, aged 25.2 ± 7.2 years old; mean $\pm$ SD)
101 participated in the study. The participants were recruited at The University of Tokyo or by the
102 online recruiting system (<https://www.jikken-baito.com>). All participants were right-handed
103 according to the laterality score (84.0 ± 16.1 ; mean $\pm$ SD) obtained by the Edinburgh

Handedness Inventory (Oldfield, 1971). They gave written informed consent to an experimental protocol approved by the ethical committee of The University of Tokyo (#19-225).

Experimental apparatus and task

Participants performed a bimanual reaching task using a virtual stick displayed on a horizontal screen while manipulating two handles of a robotic manipulandum (KINARM End-Point Lab; Kinarm, Kingston, Canada) (Scott, 1999; Kobayashi & Nozaki, 2024) (Fig. 1a). The display occluded direct vision of the participants' arms and the handles. Instead, it displayed a starting position, a target (1.4 cm in diameter), and a virtual stick (length: 40 cm; width: 0.5 cm). The two handles were linked by a stiff virtual spring generated by the manipulanda (spring constant: 2000 N/m), thereby creating the virtual stick. Handle positions and velocities were digitized at 1.129 kHz and recorded at 1 kHz for offline analysis.

Depending on the experimental condition, participants controlled either the right tip or the left tip of the virtual stick. In the right-tip control condition, 21 participants held the left tip of the stick with the left hand and grasped a point 15 cm from the left tip with the right hand, thereby controlling the right tip of the stick (Fig. 1a). In the left-tip control condition, 20 participants performed the corresponding task in a left-right mirrored workspace and controlled the left tip of the stick (Fig. S1a). This task was kinematically redundant because identical tip trajectories could, in principle, be generated by many different combinations of hand movements. For example, participants could translate the stick by moving both hands in parallel without changing its orientation, or they could achieve the same tip displacement by tilting the stick (Fig. 1b). An additional 24 participants performed non-redundant single-hand control tasks, the details of which are described below.

All experimental conditions comprised a baseline phase (280 trials) (Fig. 1c), which was common to all conditions, followed by a perturbation phase (stick-tip shift condition: 360 trials, or stick-angle shift condition: 160 trials) (Figs. 1d, 1e).

Baseline phase

The baseline phase was performed to investigate the basic strategy of how the participants moved the stick to reach the targets with the controlled tip. At the beginning of each trial, the participants were asked to move the stick to its home position (hands and stick in Fig. 1c). After maintaining the home position for 0.5–1 s, a gray target was pseudo-randomly chosen from seven possible targets (0° : horizontal direction, $\pm 30^\circ$, $\pm 60^\circ$, $\pm 90^\circ$; Fig. 1c) appearing 15 cm away from the initial right (or left) tip position of the stick. After waiting for another 0.5–1 s, the color of the target changed to pink, indicating that they should immediately start moving the tip to the target. The participants were instructed to maintain the peak velocities of the tip as constant as possible across the trials. When the tip reached the target, a feedback message, “FAST” or “SLOW,” was presented on the monitor if the peak speed was higher or lower than the range of 400–550 mm/s, respectively. After maintaining the tip at the target for 0.5 s, the visual feedback of the stick and target disappeared. Then, the handles automatically returned to their home position, and the next trial began.

Perturbation phase

During the subsequent perturbation phase, the target was presented only in the 0° direction, and visual perturbations were introduced. The home positions, visual feedback, target size, inter-trial interval, and criteria for the velocity feedback were the same as those used in the baseline phase. The controlled tip side remained unchanged through the experiment.

Nineteen participants (right-tip control: $N = 10$, left-tip control: $N = 9$) performed the end-effector relevant stick-tip shift condition (360 trials; Fig. 1d). Participants experienced four perturbation types (Fig. 1d), each presented in two opposite directions, resulting in eight perturbation conditions. Perturbations were introduced pseudo-randomly every three trials (15 repetitions per perturbation condition). The four perturbation types were as follows: (1) the entire stick was displaced perpendicularly to the target direction (normal shift); (2) the stick was shifted and disappeared except for the controlled tip (disappearing shift); (3) the stick was shifted and rotated in the inner direction by 6° (inner shift); and (4) the stick was shifted and

rotated in the outer direction by 6° (outer shift). In all four perturbation types, the controlled tip was displaced by 3 or -3 cm when it had moved 1 cm from the home position.

Twenty-two participants (right-tip control: $N = 11$, left-tip control: $N = 11$) performed the end-effector irrelevant stick-angle shift condition (160 trials) (Fig. 1e). The stick was rotated about the controlled tip without changing its position. Participants experienced two perturbation conditions, namely clockwise (-6°) and counterclockwise ($+6^\circ$) rotations. As in the stick-tip shift perturbations, these perturbations were introduced when the controlled tip had moved 1 cm from the home position. Perturbations were presented pseudo-randomly every four trials (20 repetitions per perturbation direction).

To test learning effects of these perturbations, we examined trial-by-trial aftereffects following perturbation trials, using a single-trial perturbation paradigm similar to that employed in previous studies of trial-by-trial motor learning (Diedrichsen et al., 2005; Wei & Körding, 2009, 2010; Fine & Thoroughman, 2006; Albert & Shadmehr, 2016; Kim et al., 2022; Hayashi et al., 2020; Makino et al., 2023; Makino et al., 2026). The trials following a perturbation were normal trials without any visual perturbation.

Single-hand control task

Twenty-four participants performed the single-hand control task (left-hand task: $N = 12$; right-hand task: $N = 12$) (Fig. 1f). The home position, target configuration, visual feedback, target size, inter-trial interval, and velocity-feedback criteria were identical to those used in the bimanual task. Each experiment consisted of a baseline phase (280 trials) followed by a perturbation phase (160 trials). In the left-hand task, participants held the left tip of the virtual stick with the left hand (Fig. 1f, left). In the right-hand task, participants grasped a point 15 cm from the left tip of the virtual stick with the right hand (Fig. 1f, right). In both tasks, participants controlled the position of the right tip of the virtual stick. Because stick orientation was not under participants' control, the stick remained horizontal throughout the experiment except during the stick-angle perturbation trials.

During the perturbation phase, clockwise and counterclockwise 6° stick-angle perturbations around the control tip were introduced pseudo-randomly every four trials (20 repetitions per perturbation direction). The perturbation was imposed when the controlled tip had moved 1 cm from the home position, producing a dissociation between the visually displayed stick orientation and the actual hand position without changing the position of the controlled tip (Fig. 1g).

Data analysis

Data analyses were performed using MATLAB R2025a (Mathworks, Natick, Massachusetts). Before analysis, the kinematic data were low-pass filtered (10 Hz, fourth-order Butterworth). No participant was rejected from the analyses.

Movement onset was detected as a time point when the tip velocity exceeded 1% of the peak velocity for at least 0.1 s. Similarly, movement offset was defined as a time when the tip velocity fell below the same criteria. With respect to the feedback response, we quantified the response at the movement endpoint, where the response to the perturbation had fully accumulated. In contrast, with respect to the learning response, we quantified the response at peak velocity rather than at the endpoint to avoid contamination by online corrective components during the movement. When calculating feedback responses and their aftereffects, to correct for participant-specific movement biases, we subtracted the mean data of the pre-perturbation null trials from the perturbation and aftereffect trials for each participant.

Latency of the corrective responses to the visual perturbations was defined as the time point at which responses to opposite perturbations split, and was estimated using a receiver-operator characteristic (ROC) knee method (Pruszynski et al., 2008; Yang et al., 2011; Crevecoeur et al., 2012). To increase detection sensitivity, latency was derived from the time derivatives of the tip position or stick-tilt angle profiles. The area under the ROC curve (AUC) for each time step was generated to calculate the probability that two responses to the distinct perturbations could be distinguished. A discrimination time point was defined as the first time

point when the AUCs were < 0.25 or > 0.75 for five consecutive samples. We then calculated the fitting line to 30 samples (30 ms) of the AUCs, centered on the discrimination time point. Latency was defined as a time point when the fitting line intersected with the chance level (AUC = 0.5) line.

Statistical analysis

To statistically evaluate the behavioral data, we conducted ANOVAs, t-tests, and a linear mixed-effects model using MATLAB. A mixed-design ANOVA applied to the baseline stick-tilt angles revealed no significant difference in the movement patterns between the left-tip and right-tip control groups (Fig. S1f). For statistical analyses, the two groups were treated separately using mixed-design ANOVAs. For visualization, however, the kinematic data from the left-tip control group were left-right mirrored and pooled with those from the right-tip control group because no significant main effects of controlled tip side were found.

Paired t-tests were used to test whether the perturbations induced significant feedback responses and aftereffects. If no perturbation-evoked response occurred, there should be no difference between the responses to the two opposing perturbations (e.g., changes in the stick-tilt angle in response to +3 cm and -3 cm stick shifts); conversely, a significant difference would indicate the presence of a perturbation-specific response.

For inner/outer shift perturbations, to test whether the direction of the stick-angle perturbation

systematically modulated the peak correction velocity of the tip, we fitted a linear mixed-effects model with perturbation condition, controlled tip side, and their interaction as fixed effects, with participant included as a random intercept. Perturbation condition was coded as a linear contrast: inner shift = -1, normal shift = 0, and outer shift = 1. A linear mixed-effects model was also applied when testing how the different discrepancy between the hand and stick affected the hand compensative response.

Results

Stereotyped movement patterns manipulating a stick with both hands

During the baseline phase, 21 participants moved the right tip of the stick from a starting point to a target located in one of seven directions. Despite the availability of multiple movement solutions, participants exhibited highly consistent movement patterns. The trajectories of the tip and both hands were approximately straight, and the right hand was consistently moved farther than the left hand (Fig. 2a). Notably, participants rarely translated the stick by moving both hands in parallel, except when aiming at the 0° target. Instead, they systematically tilted the stick during movement execution, with stick tilt gradually increasing from movement onset (Fig. 2b). This tilting strategy was present from the very first trial, and the amplitude of the stick-tilt angle was clearly greater than zero for all non-zero target directions (Fig. 2c). The stick-tilt angle was strongly modulated by target direction, increasing monotonically with the angular deviation of the target from the horizontal (Fig. 2d).

These stereotyped movement patterns may simply reflect a strategy of reducing reliance on the non-dominant hand while relying on the dominant hand. To examine this possibility, 20 different right-handed participants performed a similar task in which they controlled the left tip of the stick (Fig. S1a). If participants relied primarily on the dominant hand while minimizing movements of the non-dominant hand, they would be expected to control the left

tip by rotating the stick around the left hand. In that case, the resulting movement patterns should be asymmetric relative to those observed when controlling the right tip. However, the participants exhibited movement patterns that were kinematically symmetric to those observed in the right-tip control condition (Fig. S1b). They moved the tip while systematically tilting the stick according to the target direction (Figs. S1c–e), and there was no significant main effect of controlled tip side (mixed-design ANOVA, $F(1, 39) = 0.005$, $p = 0.945$), and no target direction $\times$ controlled tip side interaction ($F(1.10, 42.78) = 0.91$, $p = 0.355$) (Fig. S1f). These results suggest that the stereotyped stick-tilt pattern did not simply reflect a strategy of relying on the dominant hand, but rather that the hand closer to the controlled tip was consistently moved farther than the other hand.

Thus, although the task allowed many equivalent solutions in terms of end-effector kinematics, participants consistently adopted a specific coordination pattern linking end-effector displacement to systematic changes in an end-effector irrelevant dimension. These stereotyped movement patterns indicate the presence of intrinsic coordination constraints between end-effector relevant and irrelevant dimensions. Consistent with previous work, this baseline coordination structure likely reflects minimization of overall hand movement distance (Kobayashi & Nozaki, 2024).

Rapid corrective responses to end-effector perturbations

During the second half of the task, visual perturbations were introduced while participants reached a target located at 0° . Nineteen participants (right-tip control: $N = 10$; left-tip control: $N = 9$) performed perturbation trials in which the position of the stick-tip was unexpectedly shifted by ± 3 cm during movement execution (normal shift: Fig. 1d). Participants can correct the error using various movement patterns. Because movements toward the 0° target were typically performed without stick tilt during baseline, participants could correct the perturbation by translating the stick in parallel (Fig. 3a, left). Alternatively, if feedback corrections were

constrained by the baseline coordination structure, correcting the tip position error would necessarily involve systematic changes in stick tilt (Fig. 3a, right).

Participants initiated corrective responses to the stick-tip shifts with a latency of 136 ms (Figs. 3b, 3c), consistent with rapid visuomotor feedback control (Day & Lyon, 2000; Scott, 2016). Importantly, these corrective responses were accompanied by systematic rotations of the stick. Upward corrections of the tip position were consistently associated with counterclockwise stick rotation, whereas downward corrections were accompanied by clockwise rotation (Fig. 3d). These feedback-induced changes in stick tilt closely matched the direction-dependent coordination patterns observed during unperturbed baseline movements (Fig. 2d). Thus, although the perturbation affected only the end-effector position, corrective responses propagated into the redundant stick-tilt dimension in a highly stereotyped manner. At the end of the movement, the stick remained significantly tilted in the direction induced during the corrective response (Fig. 3e). A mixed-design ANOVA revealed a significant main effect of perturbation (Table S1a; $F(1, 17) = 3221.30$, $p < 0.001$, partial $\eta^2 = 0.995$). Neither the main effect of controlled tip position ($F(1, 17) = 1.93$, $p = 0.183$, partial $\eta^2 = 0.102$) nor the perturbation $\times$ controlled tip position interaction ($F(1, 17) = 0.02$, $p = 0.899$, partial $\eta^2 = 0.001$) was significant, indicating that the observed movement patterns did not depend on the laterality of the controlled tip position.

The results demonstrate that rapid corrective responses to end-effector relevant perturbations are shaped by intrinsic coordination constraints and thus are accompanied by end-effector irrelevant errors. To further examine this speculation, we performed an additional analysis to test whether the feedback response pattern followed the relationship between tip movement and stick angle in the baseline phase. The accompanying changes in tip position and stick-tilt angle during the feedback response were aligned with the baseline relationship between these two dimensions (Fig. 3f; Figs. S2a, S2b).

An important question is how such corrective responses influence subsequent motor learning. Specifically, with respect to the secondary deviations which were resulted from feedback correction to a perturbation, does the motor system attempt to compensate for the deviations in the following trial, or are they left uncorrected? Participants showed aftereffects biased the initial tip position downward (upward), consistent with predictive compensation for the perturbation (Fig. 3g). A mixed-design ANOVA revealed a significant main effect of preceding perturbation (Table S1b; $F(1, 17) = 40.53$, $p < 0.001$, partial $\eta^2 = 0.705$). They also showed systematic aftereffects of the stick angle that matched the direction of the corrective response expressed in the preceding trial, rather than counteracting it (Fig. 3h). A mixed-design ANOVA revealed a significant main effect of preceding perturbation (Table S1c; $F(1, 17) = 12.27$, $p = 0.003$, partial $\eta^2 = 0.419$). Similar to the feedback response, these movement biases followed the baseline relationship (Fig. 3f; Figs. S2a, S2b). Additionally, participants who rotated the stick more during the corrective response exhibited larger stick-tilt aftereffects (Fig. S2c; $r = 0.725$, $p < 0.001$), suggesting that the feedback response affected the subsequent learning.

Finally, we examined whether visual information about stick-tilt was necessary for these corrective responses by introducing a perturbation in which the stick disappeared except for the controlled tip (disappearing shift: Fig. 1d). Despite the absence of visual information about stick orientation, feedback corrections exhibited the same systematic coupling between tip correction and stick tilt as observed when the full stick was visible (Figs. 4a–c; Table S1d). Moreover, aftereffects in both tip position and stick angle were indistinguishable from those observed in the normal shift (Figs. 4d, 4e; Tables S1e, S1f). These results indicate that the propagation of end-effector errors into stick-tilt does not depend on explicit visual feedback about the end-effector irrelevant dimension.

Rapid corrective responses to the end-effector irrelevant perturbation

To examine whether the motor system maintains an implicit goal for stick tilt and, if so, how this goal is expressed, we introduced perturbations in an end-effector irrelevant dimension. Twenty-two participants (right-tip control: $N = 11$; left-tip control: $N = 11$) performed a perturbation phase including trials in which the stick angle around the controlled tip was unexpectedly rotated by $\pm 6^\circ$ during movement execution (stick-angle shift: Fig. 1e). Importantly, these perturbations altered the stick-tilt without directly affecting the tip position. According to the minimal intervention principle, such end-effector irrelevant perturbations might be ignored, as they do not affect achievement of the task goal (Fig. 5a, left). Alternatively, the stereotyped baseline relationship between tip motion and stick tilt may provide an implicit reference angle for stick tilt, even though stick orientation was not explicitly specified as a task goal. A deviation from this reference would constitute a stick-tilt error. If correction of this error follows the baseline coordination pattern, it may systematically induce changes in tip position (Fig. 5a, right).

Participants initiated corrective responses to the stick-tilt perturbation with a latency of 125 ms (Figs. 5b, 5c). The peak magnitude of the correction during the reaching movement was $-1.90 \pm 0.14^\circ$ and $1.79 \pm 0.13^\circ$ (mean $\pm$ SEM) for the $+6^\circ$ and -6° perturbations, respectively. Although the perturbation did not affect the tip position, corrective responses to the stick-tilt error were accompanied by systematic deviations of the tip trajectory (Fig. 5d). Specifically, counterclockwise corrections of the stick angle were associated with upward deviations of the tip (0.9 ± 0.1 cm, when the correction of the angle was peak), whereas clockwise corrections were associated with downward tip deviations (-0.9 ± 0.1 cm, when the correction of the angle was peak). These coordination patterns closely matched those observed during baseline movements, indicating that corrective responses followed the same intrinsic relationship between stick tilt and tip position. Both the perturbation-evoked changes in stick-tilt angle and tip position persisted until the movement endpoint (Fig. 5e). With respect to the stick-tilt angle, a mixed-design ANOVA revealed a significant main effect of perturbation ($F(1, 20) = 40.55$, $p < 0.001$, partial $\eta^2 = 0.670$) and a significant perturbation $\times$ controlled tip position interaction (Table S1g; $F(1, 20) = 14.26$, $p = 0.001$, partial $\eta^2 = 0.416$). The main effect of controlled tip

position was not significant ($F(1, 20) = 3.52$, $p = 0.075$, partial $\eta^2 = 0.150$). Bonferroni-corrected post hoc comparisons showed the significant difference between perturbations in the right-tip control condition ($p < 0.001$), whereas the change was not significant in the left-tip control condition ($p = 0.082$). With respect to the tip position, a mixed-design ANOVA revealed a significant main effect of perturbation (Table S1h; $F(1, 20) = 11.01$, $p = 0.003$, partial $\eta^2 = 0.355$). Neither the main effect of controlled tip position ($F(1, 20) = 3.50$, $p = 0.076$, partial $\eta^2 = 0.149$) nor the perturbation $\times$ controlled tip position interaction ($F(1, 20) = 3.53$, $p = 0.075$, partial $\eta^2 = 0.150$) was significant.

Plotting the corrective movement patterns on the plane representing the relationship between the tip position and the stick-tilt angle revealed that they were still biased toward the baseline relationship (Fig. 5f; Figs. S3a and S3b). The stick-tilt correction was significantly and positively correlated with the accompanying deviation of the tip position (Fig. S3c; $r = 0.855$, $p < 0.001$). These results suggest that end-effector control is partly constrained by sensory information in the end-effector irrelevant dimension.

In trials after the perturbation, participants exhibited aftereffects in stick angle, consistent with predictive compensation for the preceding perturbation (Fig. 5g). A mixed-design ANOVA revealed a significant main effect of perturbation (Table S1i; $F(1, 20) = 17.40$, $p < 0.001$, partial $\eta^2 = 0.465$). Neither the main effect of controlled tip position ($F(1, 20) = 0.31$, $p = 0.583$, partial $\eta^2 = 0.015$) nor the perturbation $\times$ controlled tip position interaction ($F(1, 20) = 0.40$, $p = 0.536$, partial $\eta^2 = 0.019$) was significant. Additionally, the aftereffect in tip position did not act to counteract the tip deviation accompanied by the feedback correction. Instead, tip position was biased in the same direction as the deviation in the previous trial (Fig. 5h). A mixed-design ANOVA revealed a significant main effect of perturbation (Table S1j; $F(1, 20) = 14.61$, $p = 0.001$, partial $\eta^2 = 0.422$). Neither the main effect of controlled tip position ($F(1, 20) = 0.06$, $p = 0.804$, partial $\eta^2 = 0.003$) nor the perturbation $\times$ controlled tip position interaction ($F(1, 20) = 0.25$, $p = 0.624$, partial $\eta^2 = 0.012$) was significant. Again, the biases in movement patterns

observed as aftereffects were consistent with the baseline relationship (Fig. 5f; Figs. S3a and S3b); however, contrary to the results of the stick-tip shift perturbation, the feedback correction was not correlated with the aftereffect observed in the subsequent trial (Fig. S3d; $r = -0.030$, $p = 0.895$). Thus, even when the perturbation acted solely on an end-effector irrelevant dimension, the resulting learning did not compensate for end-effector deviations generated during feedback correction.

Together, these results demonstrate that even errors that are irrelevant to task success evoke rapid and systematic corrective responses. Importantly, these responses propagate into end-effector relevant dimensions according to the same coordination constraints observed during unperturbed movements, indicating that fast feedback control in redundant motor systems is governed by intrinsic movement coordination structure rather than by selective correction of end-effector relevant errors alone.

Dissociation between the stick and hand position alone does not elicit corrective responses

One possible alternative explanation for the corrective responses to stick-angle perturbations observed in the bimanual task is that they were driven not by errors in stick-tilt per se, but by a positional discrepancy between the hand and the visually displayed stick. To test this possibility, we conducted control experiments using single-hand stick manipulation tasks (Fig. 1f). Twenty-four naïve participants performed either a left-hand task or a right-hand task ($N = 12$ each), following the same protocol as the bimanual task (baseline phase: 280 trials; perturbation phase: 160 trials). Crucially, in the single-hand tasks, participants could not control the stick orientation: the stick angle remained fixed at zero except during perturbation trials. During the perturbation phase, we applied the same stick-angle shifts ($\pm 6^\circ$) as in the bimanual task, which introduced a dissociation between the visual stick-tilt and the actual hand position without affecting the tip position (Fig. 1g).

If the positional discrepancy between the hand and the stick were sufficient to induce corrective responses, participants should have exhibited compensatory changes in movement even in the single-hand condition (Fig. 6a). However, no such corrective responses were observed: The time course of tip position showed no systematic deviation following the perturbation (Fig. 6b), and there was no significant difference in tip position at movement end for either perturbation direction (Fig. 6c; paired t-tests; left-hand task: $t(11) = 1.318$, $p = 0.214$; right-hand task: $t(11) = -1.103$, $p = 0.294$). One possible explanation for the absence of corrective responses is that participants gradually learned that stick orientation was uncontrollable and therefore suppressed unnecessary corrective responses. However, the magnitude of the compensatory response did not differ significantly between the first and second halves of the perturbation phase, suggesting that the present data do not support this possibility (Fig. S4).

Together, these results indicate that a dissociation between the hand position and the visual representation of the stick alone is insufficient to elicit corrective responses. Instead, the corrective responses observed in the bimanual task likely depend on the ability to actively control and predict stick orientation. This supports the interpretation that corrective responses to stick-angle perturbations arise from intrinsic coordination between end-effector relevant and end-effector irrelevant dimensions, rather than from positional discrepancies at the level of the hand.

End-effector irrelevant perturbations modulate corrective responses to end-effector errors

To further examine whether perturbations in end-effector irrelevant dimensions influence the correction of end-effector errors, we simultaneously applied a stick-tip perturbation and a stick-angle perturbation (inner/outer shift: Figs. 1d, 7a). According to the minimal intervention principle, corrective responses should primarily target the tip position error while ignoring the stick-angle perturbation, as the latter does not directly affect task success. Under this

account, corrective responses should be similar across conditions. In contrast, if intrinsic coordination constraints couple end-effector relevant and end-effector irrelevant dimensions, the structure of the corrective response should depend on the relationship between the two perturbations. Specifically, in the inner-shift condition, the stick-angle correction biases the tip movement toward the target, potentially facilitating tip correction. Conversely, in the outer-shift condition, the stick-angle correction biases the tip movement away from the target, potentially slowing the correction.

Participants rapidly corrected the perturbed tip position in both conditions and appeared to largely ignore the stick-angle perturbation at the level of task outcome (Figs. 7b, 7c). Consistent with this, the latency of the corrective response to the tip position error did not differ between the inner- and outer-shift conditions (Fig. 7d). Despite similar response latencies, the kinematic structure of the corrective movements differed between conditions (Figs. 7d, 7e). These differences were reflected in the velocity profile of the tip correction (Fig. 7f). Actually, the direction of the stick-angle perturbation systematically modulated the peak correction velocity (Fig. 7g). We fitted a linear mixed-effects model with perturbation condition, controlled tip side, and their interaction as fixed effects, with participant included as a random intercept. Perturbation condition was coded as a linear contrast: inner shift = -1, normal shift = 0, and outer shift = 1. This analysis revealed a significant main effect of perturbation condition ($F(1, 36) = 61.45, p < 0.001$), indicating that peak correction velocity decreased systematically from the inner-shift condition to the outer-shift condition. The main effect of controlled tip side was not significant ($F(1, 17) = 0.73, p = 0.404$), and neither was the perturbation condition $\times$ controlled tip side interaction ($F(1, 36) = 1.62, p = 0.211$). Thus, stick-angle perturbations systematically modulated the velocity profile of the tip-position correction regardless of the controlled tip side.

Discussion

The present study addressed a fundamental challenge in motor control posed by kinematic redundancy: how low-dimensional sensory errors are translated into coordinated changes across high-dimensional motor degrees of freedom. Traditional arm-reaching paradigms provide limited access to this problem because end-effector position is tightly constrained by limb posture. Using a redundant bimanual task that dissociated end-effector relevant and irrelevant dimensions, we showed that visual errors propagated through the motor system in stereotyped patterns shaped by intrinsic coordination constraints. This propagation occurred not only when perturbations directly affected task success but also when they acted solely on end-effector irrelevant dimensions. Aftereffects in the subsequent trial also reflected the coordination structure expressed during the preceding corrective response.

Kinematic symmetry for the laterality of stick-tip manipulation

In the present stick-manipulation task, participants consistently adopted a stereotyped strategy involving stick tilt despite the availability of multiple movement solutions (Figs. 1b, 2c, 2d), consistent with our previous finding that this pattern minimizes the combined movement distance of both hands (Kobayashi & Nozaki, 2024). Although all participants were right-handed, those controlling the left tip exhibited the mirror-symmetric coordination pattern (Fig. S1), indicating that the baseline coordination structure depended on the controlled end-effector rather than hand dominance. This symmetry is notable given previous evidence for lateralized roles of the two arms during bimanual motor learning (Yokoi et al., 2014; Schaffer & Sainburg, 2021). At the same time, it is consistent with work showing that functional roles can be flexibly exchanged between the two hands according to task demands in redundant bimanual tasks (Johansson et al., 2006).

Rapid corrections to end-effector relevant perturbations in a redundant motor system

When the stick was suddenly shifted, participants rapidly corrected the resulting tip error by tilting the stick (Fig. 3). The short corrective latency of approximately 140 ms indicates that this correction pattern was not the result of an explicit strategy, but rather an automatic feedback process (Scott, 2016). Specifically, tip-position corrections were accompanied by stick rotations that preserved the baseline relationship between tip movement direction and stick-tilt angle (Figs. 3f and 5f), suggesting that rapid feedback corrections recruit pre-existing coordination patterns established during unperturbed movements.

Our previous work proposed that baseline coordination patterns serve as a scaffold that implicitly guides how corrective commands are distributed across redundant degrees of freedom during motor adaptation (Kobayashi & Nozaki, 2024). The present findings extend this principle to rapid feedback correction and trial-by-trial learning. This interpretation is consistent with Hayashi et al. (2016), who showed that experimentally altering the visuomotor mapping between target direction and movement direction systematically enhanced or reduced both motor adaptation and rapid feedback correction. Importantly, our findings suggest that pre-existing coordination structures, analogous to the visuomotor mapping in a standard reaching task, constrain how corrective commands propagate through redundant motor systems.

Why end-effector irrelevant perturbations cannot be ignored in redundant motor control

We introduced an end-effector irrelevant perturbation by rotating the stick around the controlled tip, leaving end-effector position unchanged (Fig. 5a). Such perturbations could be ignored without compromising task performance. According to the minimal intervention principle, the motor system should therefore be indifferent to errors confined to task-irrelevant dimensions. However, the stereotyped relationship between tip motion and stick tilt observed during baseline movements may provide an implicit reference for stick tilt, even though stick orientation was not

explicitly specified as a task goal. The stick-angle perturbation therefore allowed us to test whether such an implicit stick-tilt goal exists and, if so, how correction toward that goal is expressed. Participants rapidly corrected the deviation in stick tilt during movement (Figs. 5b, 5c, and 5e). Although this correction was partial, reaching approximately one-third of the imposed perturbation, the presence of a clear corrective response indicates that the perturbation was not completely ignored. Relatedly, corrective responses to visual perturbations have been reported even when the perturbation could be tolerated without compromising target attainment because of goal redundancy. Veyrat-Masson et al. (2010) observed substantial corrections to cursor perturbations even when a large target made correction unnecessary, whereas Cross et al. (2019) found attenuated but persistent early feedback responses when a wide target reduced the need for correction.

Previous work has shown that visual feedback corrections during tool use can incorporate the kinematic mapping between hand motion and tool-endpoint motion, enabling task-appropriate online corrections (Baugh et al., 2012). One possible explanation is that the corrective response was driven by a discrepancy between visual information about stick orientation and proprioceptive information about hand position. More broadly, tool use can modify representations of the manipulated object and body-object relationship (Iriki et al., 1996; Ganesh et al., 2014), consistent with a sense of agency over self-generated object motion (Haggard, 2017). Perturbations to stick orientation may therefore generate sensory prediction errors known to drive both visuomotor adaptation (Wolpert et al., 1995; Flanagan & Rao, 1995; Mazzoni & Krakauer, 2006; Schaefer et al., 2012; Kim et al., 2019) and rapid feedback responses (Nashed et al., 2012; Franklin et al., 2016).

However, our results did not support the hypothesis that visuo-proprioceptive mismatch was a primary driver of the observed responses. If such local mismatch were the main cause, larger positional dissociations should have elicited larger corrective responses. However, corrective responses did not scale consistently with the local dissociation of each

hand (Fig. S5). In addition, in the single-hand stick manipulation task, a comparable dissociation between visual stick orientation and hand position was introduced, yet participants showed no clear corrective responses (Fig. 6).

A related possibility is that the corrective responses arose from uncertainty in state estimation. The motor system estimates the state of the body and environment by integrating sensory signals according to their reliability (van Beers et al., 1999; Körding & Wolpert, 2004). In our task, stick orientation and tip position were strongly coupled throughout baseline movements (Fig. 2d), such that stick orientation provided information about the likely state of the controlled tip. An unexpected perturbation to stick orientation may therefore have transiently biased the estimated state of the controlled tip, even though its actual position remained unchanged. Under this interpretation, corrective responses to stick-tilt perturbations may have arisen from altered end-effector state estimation rather than from explicit correction of stick orientation itself.

Interaction between end-effector relevant and end-effector irrelevant error corrections

Rapid stick-tilt corrections were accompanied by systematic tip-position deviations that followed the baseline relationship between stick tilt and tip position (Fig. 5f), consistent with our previous finding for adaptive corrections (Kobayashi & Nozaki, 2024). Thus, a common coordination structure may constrain corrective responses across end-effector relevant and irrelevant dimensions.

Notably, under this coordination constraint, correcting a stick-tilt error would itself generate a task-relevant tip-position error (Figs. 5d, 5e). Thus, the partial correction of the stick-tilt perturbation (Figs. 5b, 5c) may reflect not only prioritization of task-relevant tip position, but also partial cancellation by subsequent corrective responses that reduce the induced tip-position error and oppose ongoing stick-tilt correction. Consequently, the net stick-tilt

correction may underestimate the corrective response to the stick-tilt error, helping explain why it remained smaller than the imposed perturbation.

To directly examine how corrections in the two dimensions interact, we simultaneously perturbed tip position and stick tilt (Fig. 7a). Participants rapidly corrected the tip-position error, consistent with the minimal intervention principle, which predicts prioritization of end-effector errors (Fig. 7d). However, stick-tilt corrections occurred concurrently (Fig. 7e), and the resulting movement patterns followed the baseline coordination structure. Although response latency was unchanged, the velocity profile of tip correction was significantly modulated depending on whether stick rotation facilitated or opposed the correction (Figs. 7f, 7g). These findings suggest that end-effector errors determine when corrections are initiated, whereas intrinsic coordination constraints shape how they are distributed across redundant degrees of freedom.

Visuomotor mapping-dependent error correction

The single-hand stick manipulation task showed that a positional discrepancy between the hand and stick alone was insufficient to elicit corrective responses (Fig. 6). Because stick orientation remained fixed regardless of hand movement, participants lacked a visuomotor mapping between their movements and stick rotation. This suggests that visual errors evoke corrective responses only when an appropriate action–outcome mapping has been established (Schmidt, 1975; Hayashi et al., 2016).

The present findings also indicate that visuomotor mappings contribute to both within-trial feedback correction and across-trial motor learning. According to the feedback error learning hypothesis, feedback corrections serve as teaching signals for subsequent movements (Kawato et al., 1987). Consistent with previous studies showing that feedback-related motor output is reflected in the subsequent trial (Albert & Shadmehr, 2016; Fine & Thoroughman, 2006; Makino

et al., 2026), the corrective patterns of tip position and stick angle were reflected as aftereffects in the following trial (Figs. 3f–h and 5f–h).

In summary, our findings suggest that the motor system exploits a baseline coordination structure to propagate low-dimensional visual errors across high-dimensional movement degrees of freedom, thereby generating rapid corrective responses. This coordination structure couples end-effector relevant and end-effector irrelevant dimensions and shapes both within-trial feedback correction and across-trial motor learning.

Author Contributions

Conceptualization, Methodology, Investigation, Formal Analysis, Writing: TK, DN, Supervision: DN.

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Figures

Figure 1. Experimental protocols. (a) Participants held handles with both hands and moved the tip of a virtual stick on the screen. (b) They can reach a visual target by moving both hands parallel (*top*) or tilting the stick (*bottom*). (c) During the baseline phase, participants were instructed to move the tip from a home position to a target that appeared in one of seven directions. (d) The perturbation phase followed the baseline phase. For participants who received the stick-tip shift perturbation, the perturbation phase consisted of repeated cycles of two null trials and one visual perturbation trial. Participants in this group experienced eight types of perturbations (four shift types $\times$ two shift directions of ± 3 cm), with 15 trials for each type. First, the entire stick was displaced perpendicularly to the target direction (normal shift). Second, the stick was shifted and disappeared except for the tip (disappearing shift). Third, the stick was shifted and rotated in the inner direction by 6° (inner shift). Fourth, the stick was shifted and rotated in the outer direction by 6° (outer shift). In the perturbation trial, one of these was applied when the tip position was 1 cm away from the starting point. (e) For participants who received the stick-angle shift perturbation, the perturbation phase consisted of repeated cycles of three null trials and one visual perturbation trial. Participants in this group experienced two types of perturbations (shift directions of $\pm 6^\circ$), with 20 trials for each type. In the perturbation trial, the stick suddenly rotated around the tip by 6° when the tip position was 1 cm away from the starting point. (f, g) To investigate whether dissociation of the stick and holding position induced the responses to the stick-angle shift, we conducted single-hand stick manipulation tasks and introduced the stick-angle shift. Participants in the left-hand task held the left tip of the stick with a left hand, whereas participants in the right-hand task held a position 15 cm away from the left tip with a right hand.

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Figure 2. Kinematics to move the right tip of the stick with both hands. (a) Movement trajectories of the left hand, right hand, and tip were drawn over the home position of the stick (averaged across participants). (b) The time-course of the stick-tilt angle during the reaching movements. They achieved the task while tilting the stick. Each color represents the direction of the target, as shown in a. The shaded areas indicate SEM. (c) Trial-to-trial changes in the stick-tilt angle at the movement end. They adopted the strategy of tilting the stick from the beginning of the experiment. The shaded areas indicate SEM. (d) The stick-tilt angle at the movement end differs compared to that when aiming at a horizontal target. Gray plots indicate individual data. The error bars mean SD.

Figure 3. Corrective rapid response to the end-effector relevant perturbation. (a) The movement pattern for correcting the tip error is not uniquely determined. Participants could correct the error by translating both hands in parallel (left). Alternatively, they could correct the error by tilting the stick (right). (b–h) For clarity of presentation, data from the right- and left-tip control conditions were combined by left-right mirroring the left-tip data, because mixed-design ANOVAs revealed no significant main effect of controlled tip side or interaction involving controlled tip side (Tables S1a–c). (b) The time-course changes in the tip position orthogonal to the target direction. The red (blue) plot shows average data when the stick was shifted by 3 cm (-3 cm). The shaded areas indicate the SD. (c) Changes in the correction amount of the tip position error. The participants rapidly corrected errors with a latency of 136 ms. Latency was derived from the time derivative of the position profiles (i.e., the velocity profiles). (d) Changes in the stick-tilt angle show that the correction of the tip position was accompanied by a stick rotation. Insets depict the stick on the monitor, exaggeratedly drawn for clarity. (e) Changes in the stick-tilt

angle at the movement end show that the stick rotation significantly accompanied the correction of the tip position. A mixed-design ANOVA revealed a significant main effect of perturbation ($F(1, 17) = 3221.30, p < 0.001$). The error bars indicate the SD. (f) A plane representing the relationship between the tip position and the stick-tilt angle. The tip Y position denotes the Y-coordinate relative to the starting position, that is the deviation orthogonal to the target direction. The bold gray line indicates the relationship in the baseline phase. The red (blue) filled circles and red (blue) open circles represent the feedback responses at the movement end and aftereffects at the peak velocity, respectively. The red (blue) small dots in the inset represent trajectories from perturbation onset to movement end at 50 ms intervals. All plots show data averaged across participants. (g, h) In trials following the perturbation trials, biases of the tip position and stick-tilt angle were observed as aftereffects of the perturbations. (insets: mixed-design ANOVA; a significant main effect of perturbation, tip position: $F(1, 17) = 40.53, p < 0.001$, stick-tilt angle: $F(1, 17) = 12.27, p = 0.003$). **: $p < 0.01$. ***: $p < 0.001$.

Figure 4. Corrective rapid response to the end-effector relevant perturbation in which the stick disappeared except for the right tip. (a–d) The left-tip data were left–right mirrored and combined with the right-tip data as described in Fig. 3 (see Tables Sd–f for statistical results). (a) Changes in the correction amount of the tip position error. The red (blue) plot shows average data when the stick was shifted by 3 cm (-3 cm). The participants rapidly corrected errors with a latency of 152 ms. Latency was derived from the time derivative of the position profiles. The shaded areas indicate the SD. (b) Changes in the hands-tilt angle show that the correction of the tip position was accompanied by a hands rotation. Insets depict the state of the hands, exaggeratedly drawn for clarity. (c) Changes in the hands-tilt angle at the

movement end show that the hands rotation significantly accompanied the correction of the tip position. A mixed-design ANOVA revealed a significant main effect of perturbation ($F(1, 17) = 2461.40, p < 0.001$). The error bars indicate the SD. **(d, e)** In trials following the perturbation trials, biases of the tip position and stick-tilt angle were observed as aftereffects of the perturbations (insets: mixed-design ANOVA; a significant main effect of perturbation, tip position: $F(1, 17) = 31.80, p < 0.001$, stick-tilt angle: $F(1, 17) = 15.99, p < 0.001$). ***: $p < 0.001$.

Figure 5. Corrective rapid response to the end-effector irrelevant perturbation.

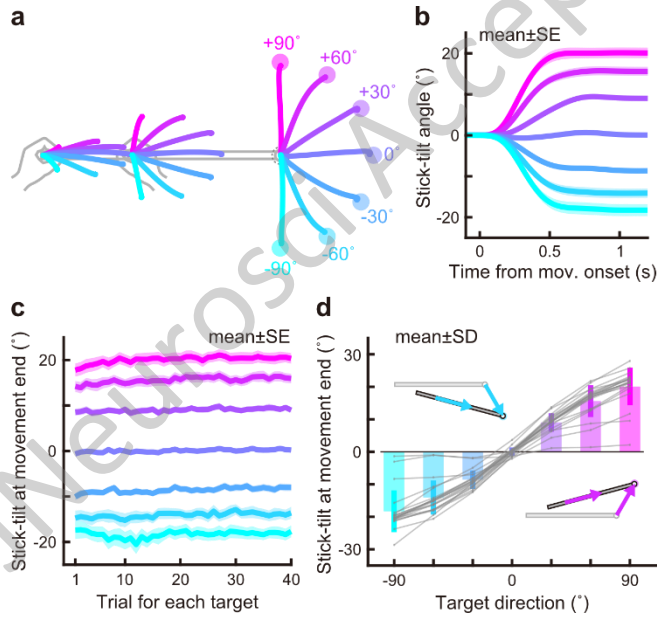
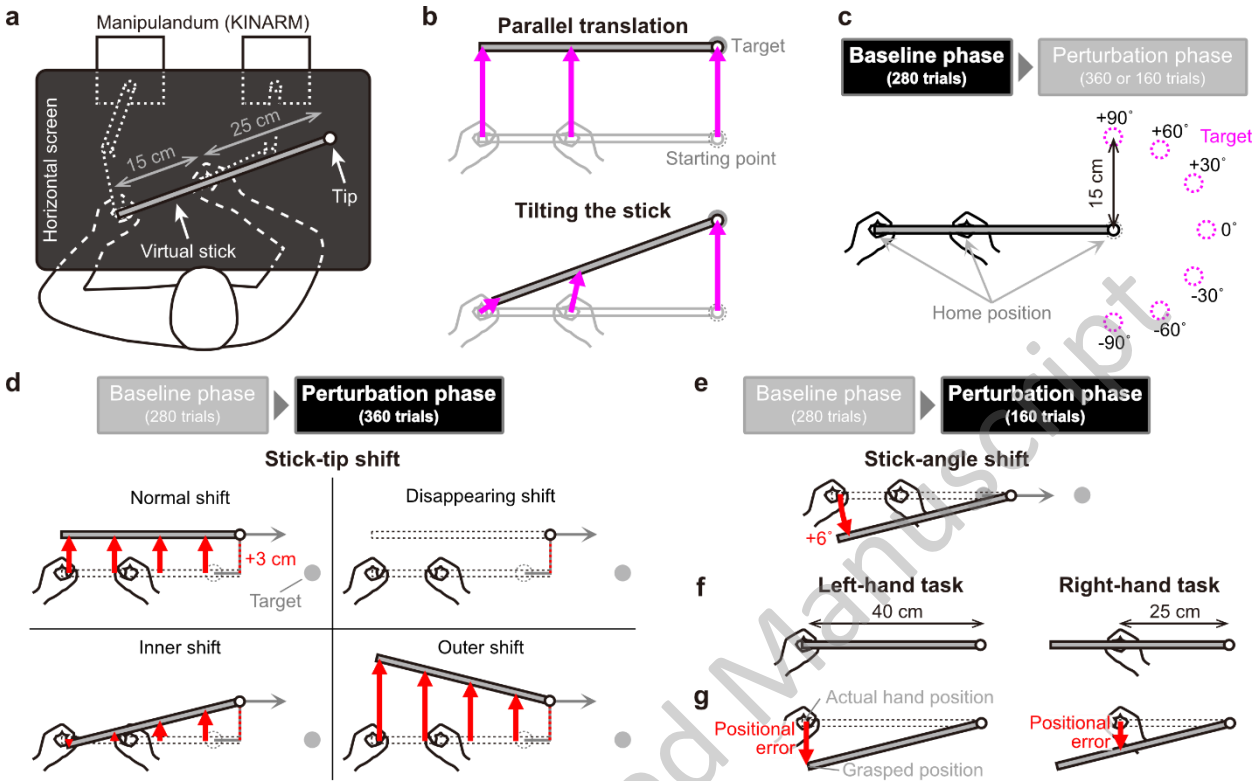
(a) Participants may not change the movement pattern because the perturbation did not affect the tip position (left). Alternatively, if corrective responses are constrained by intrinsic coordination between end-effector relevant and end-effector irrelevant dimensions, correcting the stick-tilt error may systematically induce changes in tip position (right). **(b–h)** The left-tip data were left–right mirrored and combined with the right-tip data (see Tables S1g–j for statistical results). **(b)** The time-course changes in the stick-tilt angle. The red (blue) plot shows average data when the stick was rotated by 6° (-6°). The shaded areas indicate the SD. **(c)** Changes in the correction amount of the stick-tilt error. The participants rapidly corrected errors with a latency of 125 ms. Latency was derived from the time derivative of the angle profiles. **(d)** Changes in the tip position orthogonal to the target direction show that the correction of the stick-tilt angle was accompanied by a deviation of the tip during the reaching movement. Insets depict the stick on the monitor, exaggeratedly drawn for clarity. **(e)** Changes in the stick-tilt angle (*left*) and the deviation of the tip (*right*) at the movement end show that the tip position error significantly accompanied the compensative stick rotation. The error bars indicate the SD. **(f)** A plane representing the relationship between the tip position and the stick-tilt angle. The formats are the

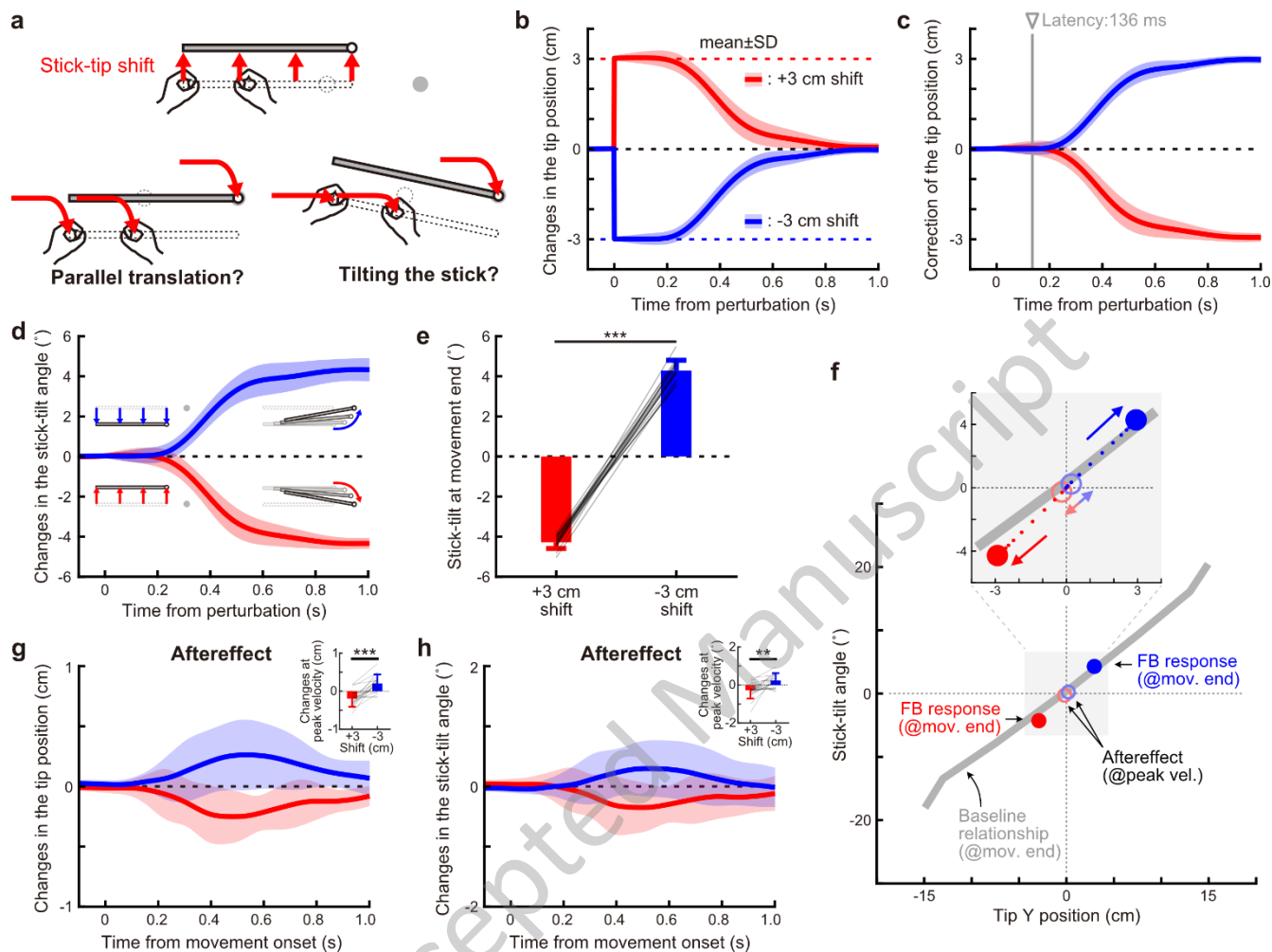
same as Fig. 3f. The plots of the aftereffects are shown only in the inset. **(g, h)** In trials following the perturbation trials, biases of the stick-tilt angle and tip position were observed as aftereffects of the perturbations. *: $p < 0.05$, ***: $p < 0.001$.

Figure 6. Single-hand stick manipulation task. **(a)** A total of 24 right-handers participated in the single-hand stick manipulation tasks. Twelve participants performed the left-hand task, whereas the rest twelve participants performed the right-hand task. During the perturbation phase, the stick-angle shift was introduced. Because the counterclockwise (clockwise) perturbation generates a backward (forward) error between the actual hand position and the grasped stick position, it may induce a corrective response by moving a hand forward (backward). **(b)** Changes in the tip position orthogonal to the target direction did not show such corrective responses depending on the perturbation direction. The red (blue) plots show average data when the stick was rotated by 6° (-6°). **(c)** There was no significant difference in the tip position at the movement end (paired t-test, left-hand task: $t(11) = 1.318$, $p = 0.214$, right-hand task: $t(11) = -1.103$, $p = 0.294$).

Figure 7. Effects of the end-effector irrelevant perturbation on the correction of the end-effector relevant error. **(a)** In the stick-tip shift conditions, we sometimes imposed the stick-angle shift at the same as the stick-tip shift. *Left*: the combination of ± 3 cm stick-tip shift and $\pm 6^\circ$ stick-angle shift (inner shift). *Middle*: the combination of ± 3 cm stick-tip shift and $\mp 6^\circ$ stick-angle shift (outer shift). *Right*: normal shift same as Fig. 3a (control). **(b–g)** The left-tip data were left–right mirrored and combined with the right-tip data. **(b)** The time-course changes in the tip position orthogonal to the target direction. The solid (dashed) plot shows averaged data when the stick was shifted by 3 cm (-3 cm), and the red (blue) plot

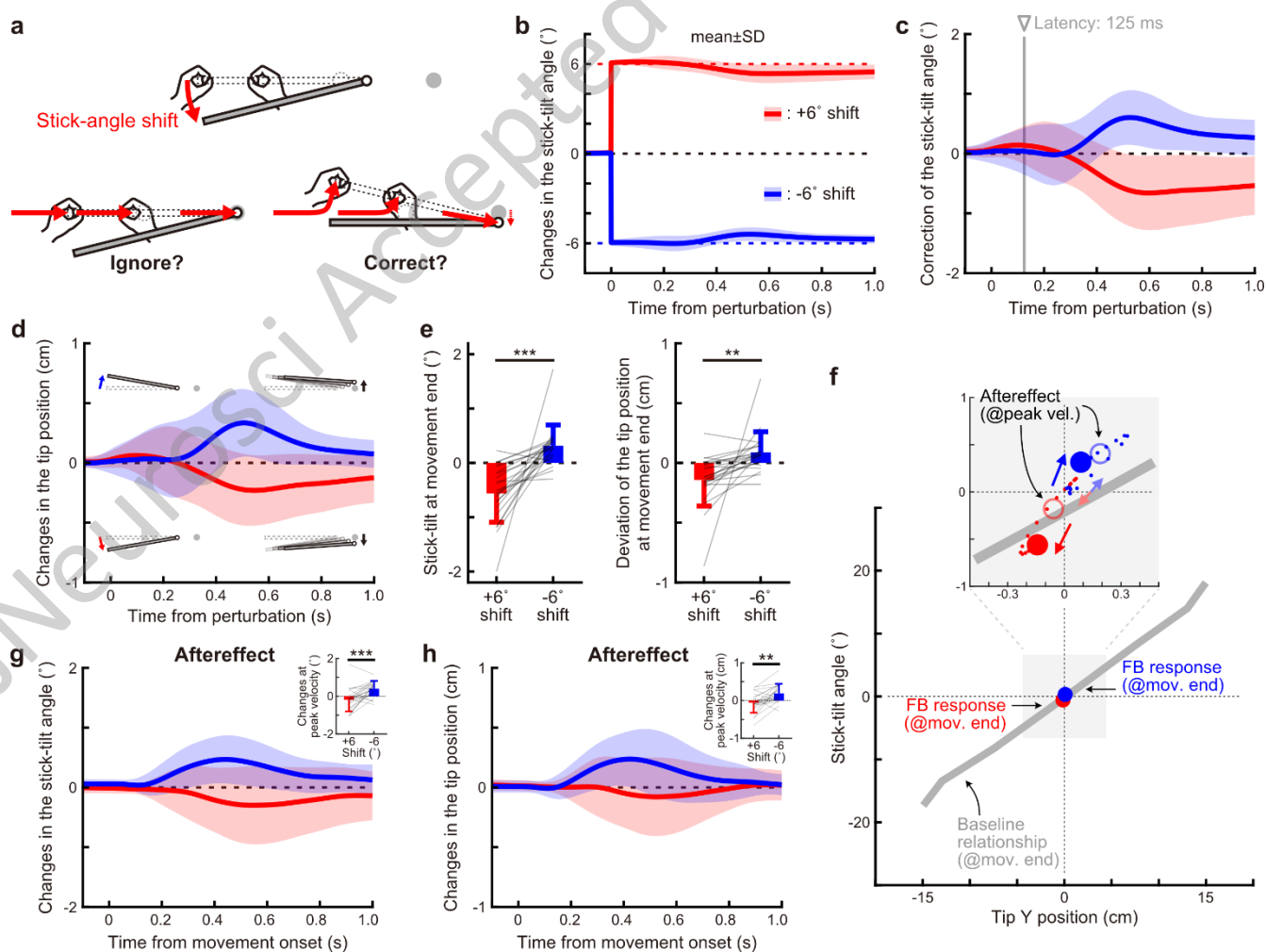
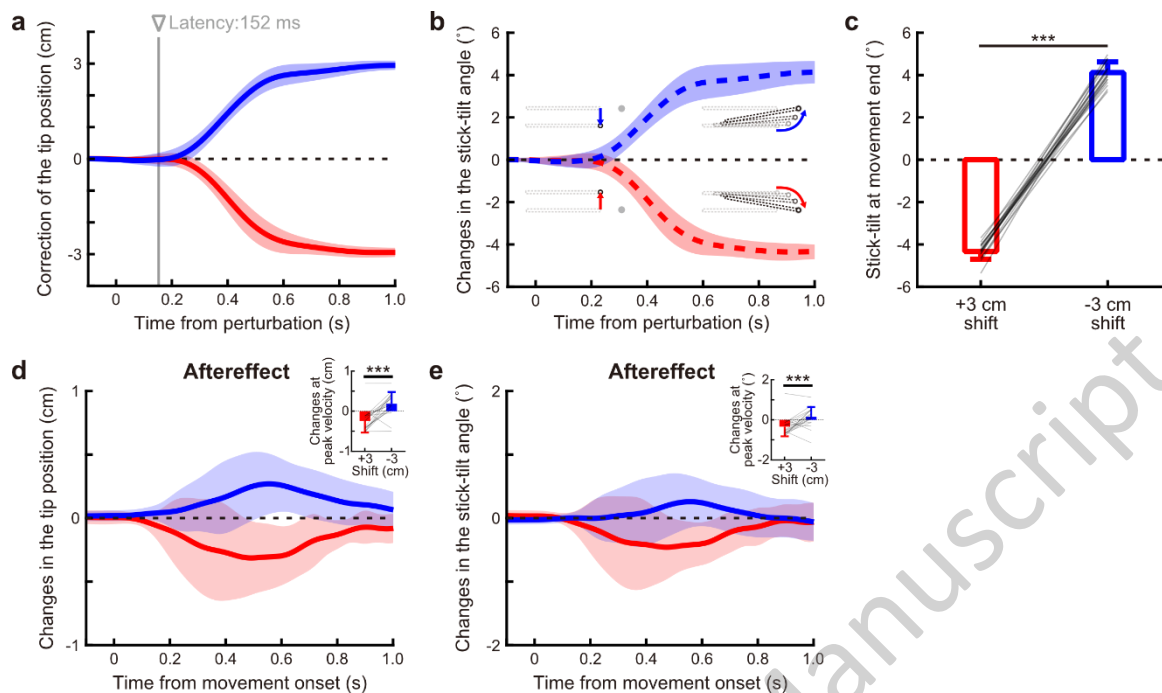
shows averaged data of the inner shift (outer shift). The shaded areas indicate the SD. (c) The time-course changes in the stick-tilt angle. (d) Changes in the correction amount of the tip position error. Regardless of the direction of the stick-angle shift, the participants rapidly corrected the tip position error with a latency of 166 ms (inner shift) or 151 ms (outer shift). Latency was derived from the velocity profiles. (e) Changes in the correction amount of the stick-tilt angle. (f) The correction velocity of the tip position was drawn by the derivative of the plots in d. Arrows in the figure indicate a peak of each velocity profile. The red, blue, and black plots indicate the result when the inner shift, outer shift, and normal shift were imposed, respectively. (g) The magnitude of peak velocity of the tip position correction varied depending on the direction of the stick-angle shift. A linear mixed-effects model applied to the combined data from the right-tip and left-tip control conditions revealed a significant main effect of perturbation condition ($F(1, 36) = 61.45, p < 0.001$).

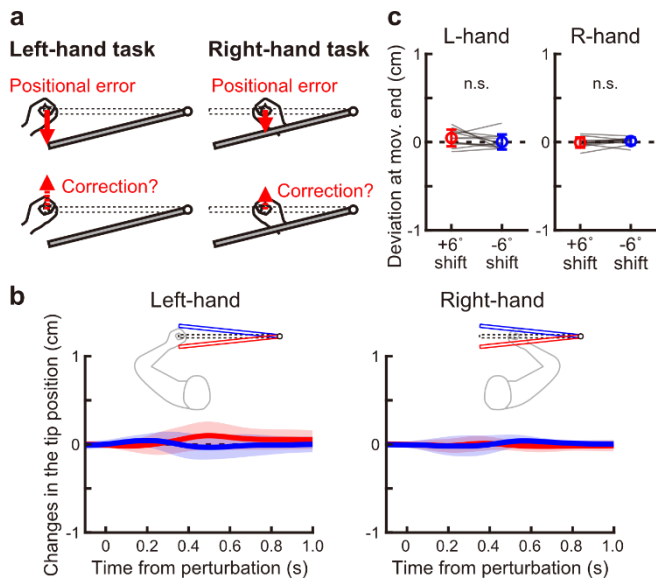




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