Motor control and adaptation in a redundant motor task manipulating a stick with both hands

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Main Text

Abstract

Redundancy is a prevalent feature of practical motor tasks. However, how the motor system learns to control multiple variables to achieve low-dimensional task goals remains unclear. To address this issue, we designed a novel redundant motor task in which participants held a virtual stick implemented by a robotic manipulandum with both hands and reached a cursor at the tip toward targets. Participants exhibited a stereotypical movement pattern: the cursor movement directions were uniquely associated with the stick tilting angle. This inherent relationship might have contributed to minimizing energy expenditure. Importantly, this task enabled a direct investigation of how the motor system adapts to movement patterns when implicitly introducing task-relevant perturbations to the cursor, task-irrelevant perturbations to the stick angle, and both types of perturbations. Contrary to the prevailing view that the motor system is only concerned with the task goal, the motor system corrected not only the task-relevant perturbation (cursor) but also the task-irrelevant perturbation (stick angle). Furthermore, these corrections had a mutual influence through the inherent relationship between the cursor movement and the stick tilting angle. Our results provide new insights into how the motor system corrects for redundant movement patterns when movements in both dimensions are constrained by an inherent relationship.

Introduction

If a movement error occurs while reaching a target, the motor system automatically and implicitly updates the motor command for the next movement to reduce the error. This remarkable motor learning ability contributes not only to maintaining accurate movements in the presence of noise but also to flexibly adapt the movement to new environments. In the standard planar arm-reaching task, which has been widely used to study the mechanisms of motor learning, participants manipulate a visual cursor with their hands primarily by moving their shoulder and elbow joints (Flash & Hogan, 1985; Gordon et al., 1994). Notably, in this task, the position of the hand is uniquely determined by the joint angles (Fig. 1a). Consequently, when the motor system adapts the reaching movement to the visual rotation imposed on the cursor representing the hand position, the adapted pattern is uniquely determined (Fig. 1b).

However, our body is inherently redundant (Bernstein, 1996), and the task goal is constrained to a low dimension (e.g., hand position), while there are many control variables to achieve the goal (e.g., joint angles). For example, in golf swings, countless patterns of whole-body configurations exist to realize identical clubhead positions. Previous studies have decomposed redundant degrees of freedom in the body into task-relevant and task-irrelevant dimensions (Scholtz & Schoner, 1999; Scholtz et al., 2000). The motor system actively corrects the variability that affects the task goal (task-relevant dimension), while allowing the variability that does not affect the task goal (task-irrelevant dimension or “uncontrolled manifold”) (Domkin et al., 2002; Mosier et al., 2005; Latash, 2012; Sternad, 2018). Optimal feedback control theory suggests that the strategy based on such a “minimal intervention principle” is optimal in terms of achieving the task goal (e.g., movement accuracy) (Todorov & Jordan, 2002; Todorov, 2004; Scott, 2004; Diedrichsen, 2007; Valero-Cuevas et al., 2009; Ronsse et al., 2010; Sternad et al., 2011; Selgrade & Chang, 2015).

However, how the motor system adapts to change the multiple body variables when encountering task-relevant and/or task-irrelevant errors has not been directly investigated. This lack of understanding can be illustrated by considering the reaching movement of a hypothetical limb with three joints (Fig. 1c). When visual rotation is imposed on the cursor, the movement patterns can be corrected in multiple ways (Fig. 1d). How does the motor system select a unique movement pattern? Furthermore, a redundancy problem exists for movement correction when there is no movement error. If joint movements change while the hand position remains unchanged (Fig. 1e), does the motor system attempt to correct the joint movements? Alternatively, as proposed

by the minimal intervention principle (Todorov & Jordan, 2002; Todorov, 2004; Scott, 2004), does the motor system simply ignore the change in the joint movement?

The standard planar reaching task has contributed to uncovering many important properties of error correction by evaluating the changes in the cursor position (Thoroughman & Shadmehr, 1999; Mazzoni & Krakauer, 2006; Taylor & Ivry, 2011; Takiyama et al., 2015). However, this task is not useful for investigating the redundancy problem because there is no redundancy between the task goal and control variables (Figs. 1a and 1b). In a previous study (Singh et al., 2016), reaching movements were modified to include multi-joint movements (shoulder, elbow, clavicle, and wrist, i.e., 4D) to investigate the importance of variabilities in task-irrelevant dimensions on motor learning performance. However, the task design did not enable testing how the motor system dealt with task-irrelevant errors (Fig. 1e).

Hence, to investigate movement correction using a redundant body system, a new experimental approach is required. This study introduces a novel bimanual stick manipulation task specially developed to address this issue (Fig. 2a). In this task, the participants manipulated a virtual stick held with both hands to reach visual targets by a cursor at the end of the stick. This is a redundant task because the same cursor position can be achieved using various stick angles (Fig. 2b). Importantly, this task enabled us to visually perturb the cursor position (i.e., task-relevant perturbation) and stick angle (that is task-irrelevant perturbation) either separately or simultaneously. Using this approach, we can directly investigate how movement patterns in the task-relevant and task-irrelevant dimensions adapt to different types of perturbations.

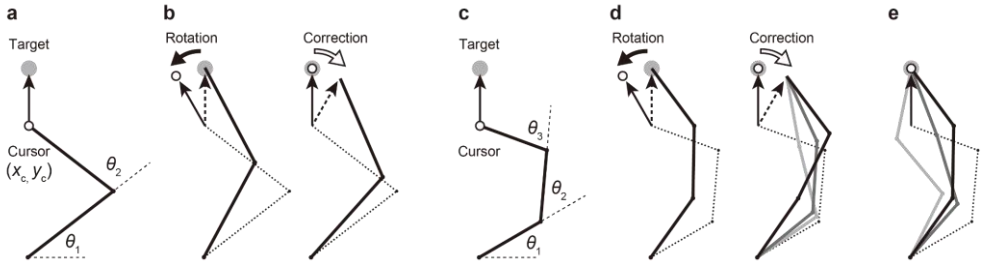

Figure 1. Redundancy and movement correction patterns. (**a**) In the ordinary arm-reaching movement task, there is no redundancy between the task goal (x_c, y_c) and the control variables (θ_1, θ_2). (**b**) Therefore, the corrective patterns against visual rotation are uniquely determined. (**c**) In the case of planar reaching movement by a hypothetical limb with three joints, the cursor can reach the target in infinite patterns (θ_1, θ_2, θ_3). (**d**) Accordingly, there are various corrective patterns to a visual rotation imposed on the cursor. (**e**) Infinite patterns are allowed to achieve the task; however, it has not been directly tested if these task-irrelevant patterns can be ignored.

Results

Movement strategy to manipulate the stick

A total of 72 healthy participants participated in the study (Experiments 1–3). They were asked to manipulate a virtual stick with both hands (length = 40 cm; distance between hands = 15 cm) to move the cursor at the right end of the stick toward the targets (Fig. 2a). This task is redundant because the same target can be reached in countless movement patterns. The participants could move both hands in parallel without tilting the stick (Fig. 2b, top). Alternatively, they could perform the task by tilting their sticks (Fig. 2b, bottom). During the first half of the task (baseline phase: 360 trials) in all the experiments (Experiments 1–3), the participants moved the cursor from a starting point to a target (movement distance = 10 cm) that appeared in one of nine directions (0°: horizontal direction, ±10°, ±20°, ±30°, and ±40°) (Fig. 2c).

The trajectories of the cursor and both hands appeared to be almost straight, but both hands were not moved in parallel, except when aiming at the 0° target. Instead, the participants tilted the stick slightly to reach the target (Fig. 2d, top). The velocity profiles of the hands and cursor were bell-shaped (Fig. 2d, bottom), similar to a normal unimanual reaching movement (Flash & Hogan, 1985; Gordon et al., 1994). We defined two indices to characterize the movement pattern: the cursor-movement direction (CMD) from the starting point relative to the horizontal direction, and the stick tilting angle (STA) relative to the initial horizontal state (Fig. 2e). Changes in the STA

over time showed that the participants moved the cursor while slightly tilting the stick (Fig. 2f). This tendency was observed from the beginning of the task (Fig. 2g). This stereotyped strategy can be expressed as a monotonically increasing curve on the CMD–STA plane (Fig. 2h): The STA was significantly modulated by the CMD (paired *t*-test compared with the STA at peak velocity when aiming at the 0° target, STA(-40°): $t(71) = -20.926$; STA(-30°): $t(71) = -24.515$; STA(-20°): $t(71) = -28.761$; STA(-10°): $t(71) = -28.139$; STA(+10°): $t(71) = 24.037$; STA(+20°): $t(71) = 25.310$; STA(+30°): $t(71) = 23.652$; STA(+40°): $t(71) = 23.580$, Bonferroni corrected $P < 0.01$; paired *t*-test compared with the STA at movement offset when aiming at a 0° target, STA(-40°): $t(71) = -24.886$; STA(-30°): $t(71) = -26.594$; STA(-20°): $t(71) = -31.530$; STA(-10°): $t(71) = -33.755$; STA(+10°): $t(71) = 30.516$; STA(+20°): $t(71) = 31.024$; STA(+30°): $t(71) = 27.235$; STA(+40°): $t(71) = 24.913$, Bonferroni corrected $P < 0.01$). This curve, referred to as the “baseline CMD–STA relationship,” indicates a constraint between the CMD and STA movements. The relationship showed that clockwise (CW) CMD was accompanied by CW STA, and counterclockwise (CCW) CMD was accompanied by CCW STA. This constraint was likely created by minimizing the movement distance of the hands. If both hands are moved in parallel, the total distance between the initial and final positions of the hands should be 20 cm (10 cm for each); however, the experimentally observed distance was a near-minimal value (Fig. 2i) (see Materials and Methods).

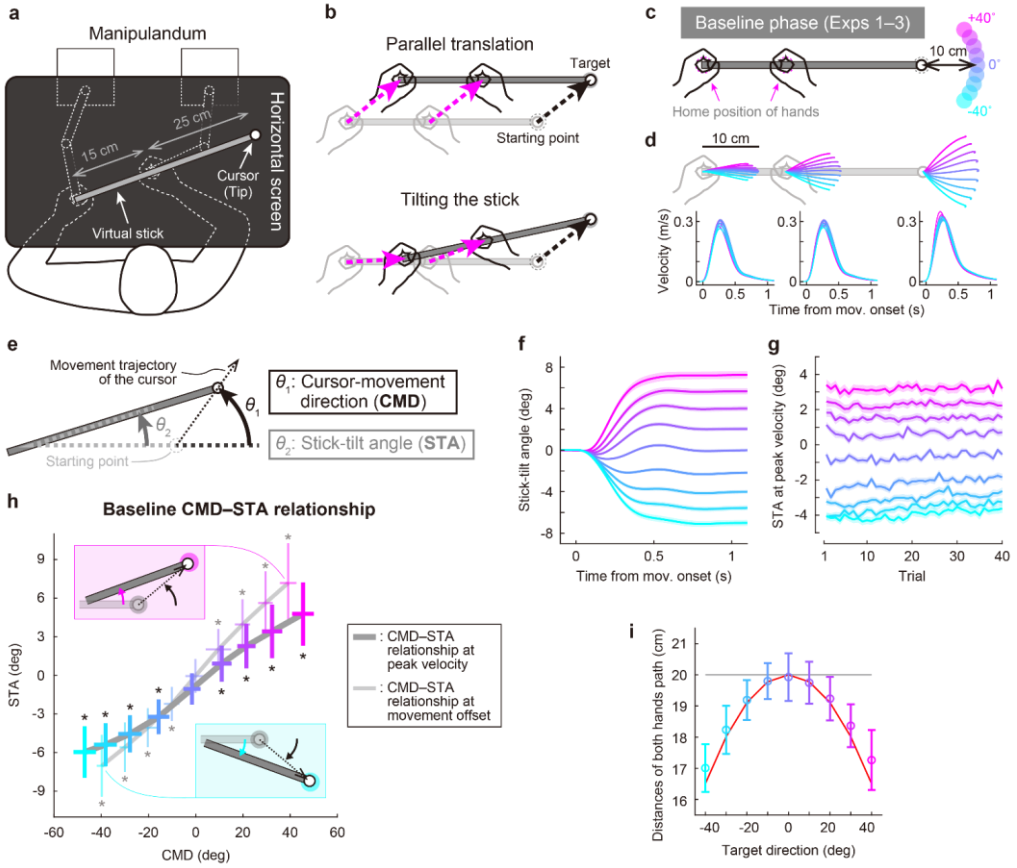

Figure 2. Bimanual stick manipulation task. (**a**) Participants held handles of manipulandum with both hands and moved a cursor positioned on the right tip of a virtual stick on the monitor. (**b**) In this redundant task, there are countless movement patterns to move the cursor to the target. Two representative strategies are shown: parallel translation (*top*) and tilting the stick (*bottom*). (**c**) During the baseline phase, the participants were instructed to move the cursor from a starting point to a target that appeared in one of nine directions. (**d**) Movement trajectories (*top*) and velocity profiles (*bottom*) of the left hand, right hand, and cursor averaged across participants. Each color corresponds to the target direction shown in **c**. The shaded areas represent the standard error of the mean across participants. (**e**) To characterize the movement pattern of the stick, we defined two indices: the cursor-movement direction (CMD, angle shown by the black arrow) and the degree of stick tilt (STA, angle shown by the gray arrow). (**f**) Time-course changes in the STA showed that the participants moved the cursor while tilting the stick. The shaded areas indicate the standard errors of the mean. (**g**) Trial-to-trial change in the STA at the peak velocity of the cursor, showing that the strategy of tilting the stick was observed from the beginning of the task. The shaded areas indicate the standard deviation. (**h**) The relationship between the CMD and STA at the peak velocity (dark plots) and movement offset (light plots) is plotted as a curve (baseline CMD–STA relationship). The STA was significantly modulated by CMD (*: paired *t*-test compared with the STA(0°), Bonferroni-corrected $P < 0.01$). Error bars indicate the standard deviation. (**i**) Sum of the distances between the initial and final positions of both hands (i.e., the sum of the lengths of pink arrows in **b**). The gray line indicates the distances when both hands are moved in parallel, whereas the red line indicates the mathematically derived minimum distances by tilting the stick. The error bars denote the standard deviation.

Experiment 1: Motor adaptation to reduce the task-relevant error

During the second half of the experiment (adaptation phase: 240 trials), the target appeared only in the 0° direction, and three types of visual perturbations were introduced. Most importantly, this task enabled the introduction of task-relevant errors (Exp. 1), or task-irrelevant errors (Exp. 2), or a combination of both error types (Exp. 3). In Experiment 1A (N = 13), the CMD was visually rotated by 30° about the starting position (CMD rotation), whereas the STA remained unchanged (Fig. 3a). Figure 3b illustrates how this visual perturbation changes the stick movement in visual and physical spaces. The movement in the visual space was the one visible to the participants, whereas the movement in the physical space was the actual hand movement, which was invisible to them. Owing to the redundant nature of this task, participants could adapt to correct the visual cursor errors using different strategies. For example, they could change the cursor movement without changing the STA (Fig. 3c, left) or by changing the STA as if they were aiming at the target at -30° (Fig. 3c, right). These strategies can be expressed as a shift in the CMD–STA plane along the CMD axis or the baseline CMD–STA relationship (Fig. 3d).

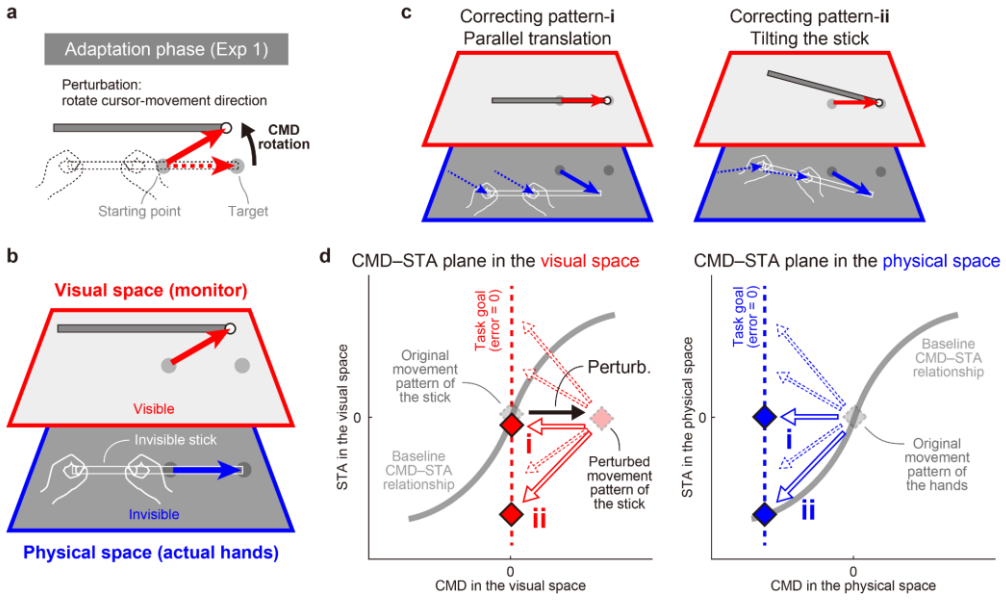

Figure 3. Experiment 1: Task-relevant visual perturbations. (**a**) During the adaptation phase of Experiment 1, the cursor-movement direction was rotated by 30° about the starting point (CMD rotation). The red dotted and solid arrows indicate the intended and actual cursor trajectory, respectively. (**b**) Movement pattern in the visual space (red square) and in the physical space (blue square). (**c**) The participants could correct the cursor error without (pattern-i, *left*) or by (pattern-ii, *right*) altering the stick-tilting angle. (**d**) The corrective strategies are expressed as the shift on the CMD–STA plane (*left*: visual space, *right*: physical space). The vertical bold dashed lines denote the task goal. The visual error caused by the perturbation (a black arrow) could be compensated by various adaptation patterns (dashed arrow): Representative adaptation patterns are expressed by arrows (patterns i and ii).

The experimental results demonstrated that the participants corrected the error by tilting both hands (Fig. 4a). The adaptation appeared to be constrained along with the baseline CMD–STA relationship (Fig. 4b). There was no significant difference between the adapted hand movements and those aimed at the -30° target in the baseline phase (CMD: paired *t*-test, $t(12) = -1.628$, $P = 0.129$, STA: paired *t*-test, $t(12) = -0.490$, $P = 0.633$; Fig. 4b). Notably, owing to this adaptation pattern, the STA that the participants saw (i.e., in the visual space) was different from that observed during the baseline phase (paired *t*-tests, $t(12) = 7.529$, $P < 0.01$; Fig. 4a). Therefore, the motor adaptation system was likely to correct the task-relevant cursor movement while ignoring the task-irrelevant stick tilt, which supports the minimal intervention principle. In this experiment, however, because a 30° CMD rotation was suddenly imposed, the participants recognized the presence of a CMD error. Under these conditions, the adaptation pattern of tilting the stick reflects the explicit downward strategy.

To eliminate the effect of such an explicit strategy, Experiment 1B (N = 19) was performed by gradually increasing the CMD rotation up to 30° by 1° per trial. This manipulation made the participants unaware of the presence of rotation throughout the experiment. The adapted hand tilting (i.e., STA in the physical space) was again similar to that when aiming at the -30° target in the baseline phase (paired t-test, $t(18) = -1.081$, $P = 0.294$). The stick on the monitor was visually tilted more in the final phase than when aiming at the 0° target in the baseline phase (paired t-test, $t(18) = 10.003$, $P < 0.01$; Fig. 4c). However, a significant difference in CMD in the visual space was observed (paired t-test, $t(18) = -10.053$, $P < 0.01$; Fig. 4d). Additionally, the participants who tilted their stick more when aiming at the -30° target during the baseline phase exhibited a greater stick tilt in the adapted movement patterns ($R = 0.599$, $P < 0.001$; Fig. 4e). Therefore, the residual CMD error remained only when CMD rotation was implicitly imposed. One possible explanation for this residual CMD error is that the motor system attempted to correct the STA error resulting from CMD adaptation, although correcting the task-irrelevant STA error was unnecessary. If the STA correction is coupled with the CMD correction via the baseline CMD–STA relationship, this STA correction interferes with the CMD adaptation, which might lead to a residual CMD error.

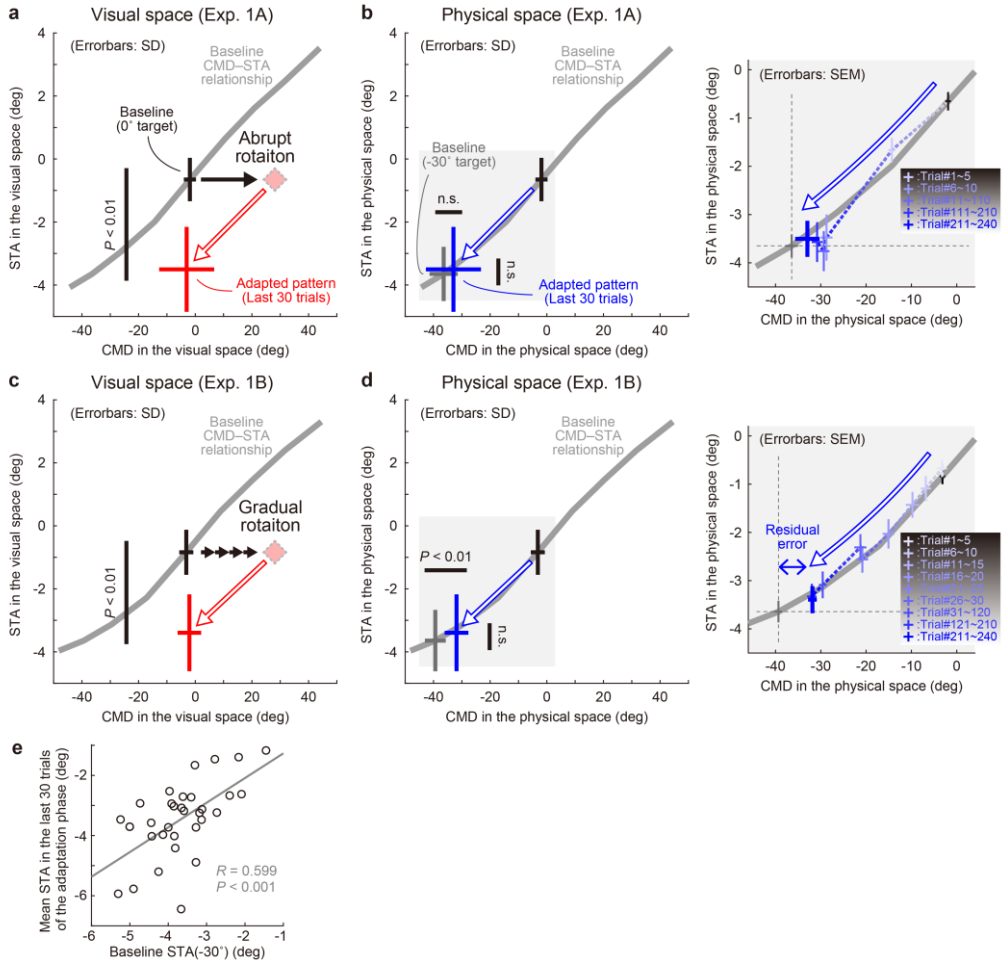

Figure 4. Experiment 1: Adaptation patterns to task-relevant visual perturbations. (**a**) The adaptation pattern in the visual space is shown in the CMD–STA plane. In Exp. 1A (abrupt rotation), the adaptation pattern is close to pattern-ii (Fig. 3d). The black and red crosses represent the movement patterns during the baseline phase when aiming at the 0° target and in the last 30 trials during the adaptation phase, respectively (mean ± SD, across participants). The STA is different from that during the baseline phase (paired *t*-tests, $t(12) = 7.529$, $P < 0.01$). (**b**) The adaptation pattern in the physical space is shown in the CMD–STA plane. *Left*: The pattern in the last 30 trials during the adaptation phase (blue cross) shows no significant difference compared with that during the baseline phase when aiming at the -30° target (gray cross) (paired *t*-test, CMD: $t(12) = -1.628$, $P = 0.129$, STA: $t(12) = -0.490$, $P = 0.633$). *Right*: The area indicated by the gray shade in the left panel is enlarged. The adaptive process (plots with a blue gradient) can be divided into five trial segments (Trials 1–5, 6–10, 11–110, 111–210, and 211–240). The black cross represents the baseline movement when aiming at the 0° target. The gray cross indicates the baseline movement when aiming at the -30° target. Error bars indicate SEM. (**c**) In Exp. 1B (gradual rotation), the adapted STA in the visual space differed from the baseline STA(0°) (paired *t*-tests, $t(18) = 10.003$, $P < 0.01$). The formats are the same as **a**. (**d**) In the physical space, the adapted CMD shows a significant difference compared with the baseline CMD when aiming at the -30° target (paired *t*-test, $t(18) = -10.053$, $P < 0.01$), while the STA did not (paired *t*-test, $t(18) = -1.081$, $P = 0.294$). In the enlarged left panel, the adaptive process can be divided into nine trial segments (trials 1–5, 6–10, 11–15, 16–20, 21–25, 26–30, 30–120, 121–210, and 211–240). (**e**) Participants who showed a larger STA when aiming at the -30° target (STA(-30°) also exhibited a larger STA correction ($R = 0.599$, $P < 0.001$).

Experiment 2: Examining whether the motor system ignores the task-irrelevant error

The presence of residual CMD errors in Experiment 1B implied that the motor system does not necessarily ignore task-irrelevant STA. Experiment 2 (*N* = 20) was designed to directly test this possibility by imposing an STA rotation about the cursor (Fig. 5a). As the cursor moved from the starting point, the stick started to rotate around the cursor up to ±6° when the cursor reached the target (the rotation amount was proportional to the cursor's distance from the starting point). The ±6° rotation was chosen according to the stick rotation at the movement offset when reaching the ±30° target (see Fig. 2h). Ten participants participated in the CCW (E2CCW-group: 6°) STA rotation condition (Fig. 5a, left; Fig. 5b), and the remaining ten participants took part in the CW (E2CW-group: -6°) STA rotation condition (Fig. 5a, right). Because the rotation amount was small, the participants did not notice the presence of rotation throughout the experiment. According to the minimal intervention principle, the motor system need not change STA because STA perturbation did not affect the cursor position (i.e., the task goal) (Figs. 5c and 5d, pattern-i). Alternatively, if the motor system predicts not only the cursor movement but also the stick-tilting angle, the dissociation between the predicted and actual STA could lead to STA correction (Figs. 5c and 5d, pattern-ii).

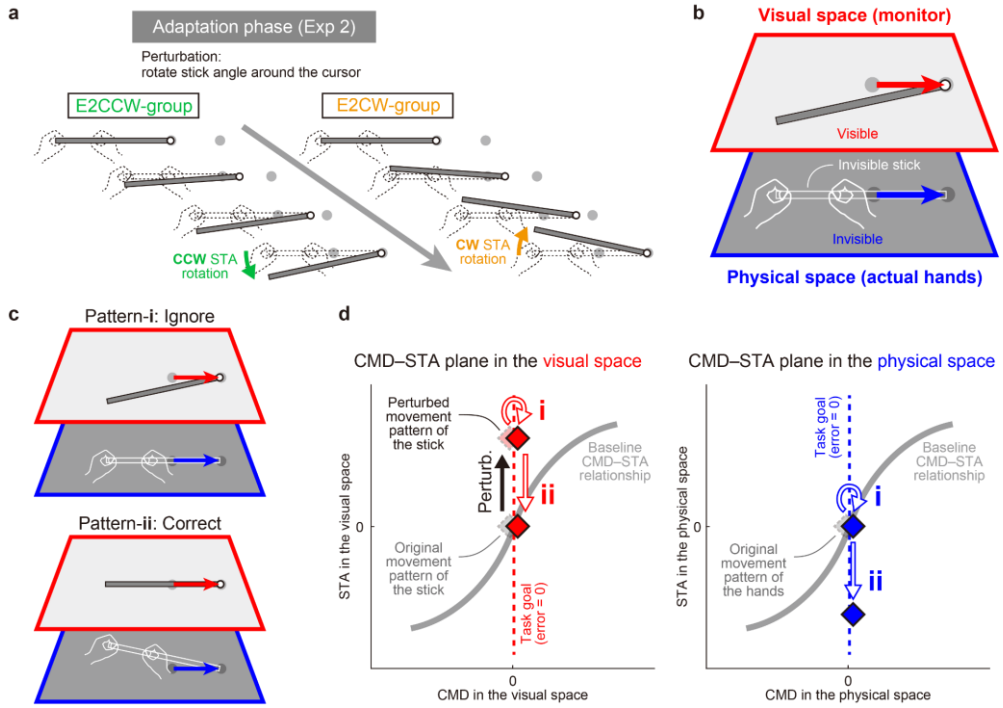

Figure 5. Experiment 2: Task-irrelevant visual perturbations. (**a**) During the adaptation phase of Experiment 2, the stick-tilting angle was rotated about the cursor. The participants performed either the counterclockwise (E2CCW-group, *left*) or the clockwise (E2CW-group, *right*) rotation. The amount of STA perturbations in the figure is exaggerated for clarity. (**b**) The visual (red) and physical (blue) movement patterns in the case of the CCW rotation are shown. (**c**) The participants may not change the movement pattern because the perturbation does not affect the cursor position (pattern-i, *top*). Alternatively, the perturbation may lead to stick-tilting angle correction (pattern-ii, *bottom*). (**d**) These corrective strategies are expressed as a shift on the CMD–STA plane (*left*: visual space, *right*: physical space). The formats are the same as that shown in Fig. 3d. Note that pattern-i means that there is no change in the movement pattern.

The experimental results clearly demonstrated that the motor system did not ignore the STA. Indeed, the participants implicitly changed the STA in the direction opposite to that of the perturbation from the early adaptation phase (Fig. 6a): Without the correction, the data of the E2CW and E2CCW groups should have largely overlapped. However, with respect to the STA, two-way (direction of STA rotation (i.e., groups), trial phase (first 30 trials or last 30 trials)) repeated-measures ANOVAs revealed the main effect of STA rotation direction ($F(1, 18) = 12.483$, $P < 0.01$; Fig. 6b) but did not reveal the main effect of the trial phase ($F(1, 18) = 3.331$, $P = 0.085$). The interaction between these factors was not significant ($F(1, 18) = 1.362$, $P = 0.258$).

Unexpectedly, this unnecessary STA correction resulted in task-relevant CMD errors. With respect to the CMD, two-way (direction of STA rotation (E2CW and

E2CCW), trial phase) repeated-measures ANOVAs revealed the main effect of the direction of STA rotation ($F(1, 18) = 5.104$, $P = 0.037$; Fig. 6b) but did not reveal the main effect of the trial phase ($F(1, 18) = 1.288$, $P = 0.271$) (the interaction between these factors was not significant: $F(1, 18) = 0.804$, $P = 0.382$). Notably, these correction patterns were consistent with the patterns predicted from the baseline CMD–STA relationship, and the CCW (CW) STA correction to the CW (CCW) STA perturbation slightly shifted the CMD in the CCW (CW) direction (Fig. 6c). These results indicate that the motor system corrected the task-irrelevant STA error at the expense of slightly increasing the task-relevant CMD error, and that this interaction might have been produced according to the baseline CMD–STA relationship.

Additional evidence to support our interpretation was obtained by considering individual differences in how the stick was tilted when aiming at the ±30° target (i.e., the steepness of the baseline CMD–STA relationship). The 6° STA perturbation should be insignificant for participants who tilt the stick at a larger angle; thus, this perturbation can be ignored. Conversely, for participants who did not tilt the stick, a 6° STA perturbation should be significant and must be corrected. Figures 6d and 6e show how the amount of STA correction and CMD change depend on the amount of STA when aimed at ±30° target in the baseline phase. As predicted, we observed a negative correlation (STA correction: $R = -0.572$, $P < 0.01$, Fig. 6d; CMD change: $R = -0.440$, $P = 0.052$, Fig. 6e), although the CMD change was not significant.

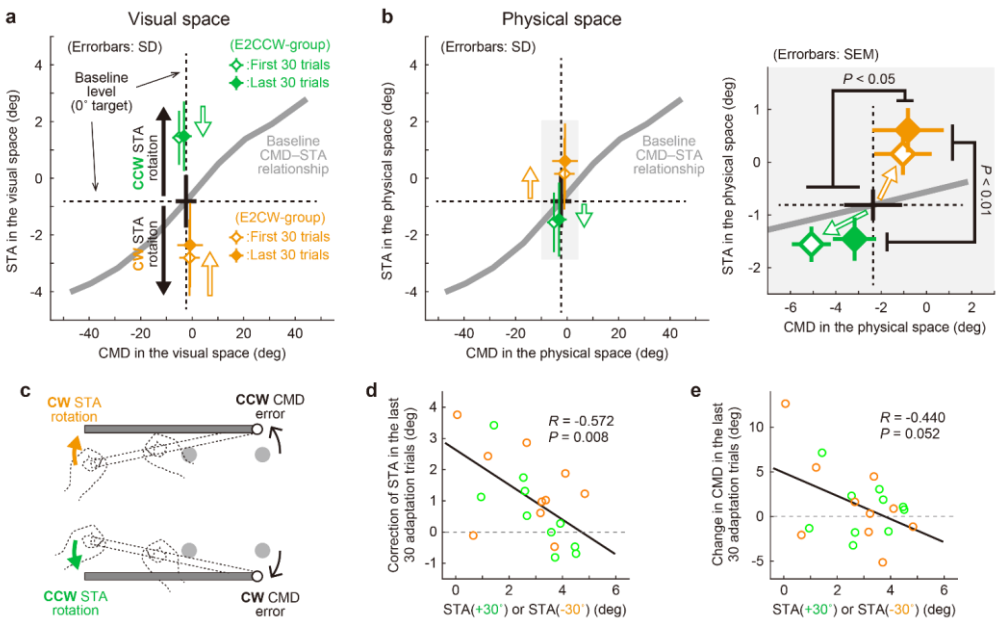

Figure 6. Experiment 2: Adaptation patterns to task-irrelevant visual perturbations. (**a**) The movement patterns in the visual space are shown (same formats as Fig. 4a). Green (orange) open and filled plots represent the averaged movement pattern of E2CCW-group (E2CW-group) in the first and last 30 trials during the adaptation phase, respectively. (**b**) The movement patterns in the physical space showed that the participants corrected the task-irrelevant STA errors. Moreover, the corrections were accompanied by task-relevant CMD errors. These effects remained until the end of the adaptation phase (two-way repeated-measures ANOVAs). (**c**) Schematics of the movement patterns altered by the STA rotation are shown (with exaggeration for clarity). (**d**, **e**) There are negative correlations between how the participants tilted the stick during the baseline and the adapted movement patterns. Each value was subtracted by the baseline STA or CMD when aiming at the 0° target.

Experiment 3: Effects of task-irrelevant error on motor adaptation

Experiment 3 (N = 20) was designed to further investigate the interaction between these two error types by simultaneously imposing both (Fig. 7a). As shown in the results of Experiment 2, STA error correction should accompany CMD correction along the baseline CMD–STA relationship (Fig. 6b). Therefore, we suppose that adaptation to CMD perturbation shows different adaptation patterns depending on the direction of the simultaneously applied STA rotation (Figs. 7b and 7c). Specifically, when the CCW CMD rotation is combined with the CCW STA rotation, corrections to these perturbations should be directed along the baseline CMD–STA relationship (Fig. 7b). In contrast, when CCW CMD rotation was combined with CW STA rotation, the corrections did not align with the baseline CMD–STA relationship (Fig. 7c). These differences were observed in the different adaptation processes on the CMD–STA

plane (Fig. 7c). This prediction was tested by simultaneously imposing CCW CMD rotation with CCW STA rotation (E3CCW-group: N = 10; Fig. 7a, left) or by imposing CCW CMD rotation with CW STA rotation (E3CW-group: N = 10; Fig. 7a, right). The CMD rotation was gradually increased by 1° per trial up to 30° and the STA rotation was the same as the STA rotation used in Experiment 2. Again, the participants did not notice perturbations throughout the experiment.

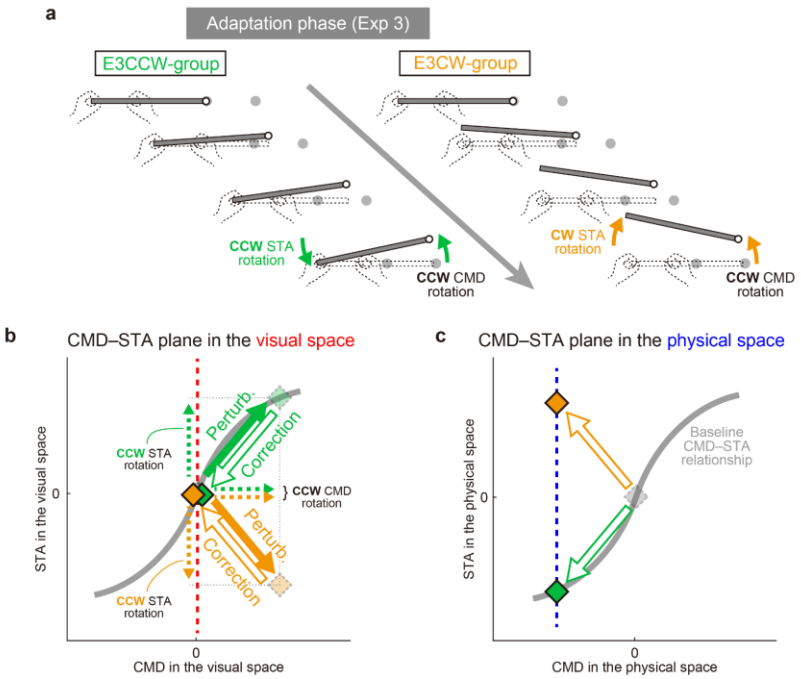

Figure 7. Experiment 3: Task-relevant and task-irrelevant visual perturbations. (**a**) During the adaptation phase of Experiment 3, both CCW CMD rotation and CCW (or CW) STA rotation were introduced. The participants were assigned to the CCW STA rotation condition (E3CCW-group, *left*) or the CW STA rotation condition (E3CW-group, *right*). The images are exaggerated for clarity. (**b**, **c**) The expected corrective pattern for each perturbation is represented on the CMD–STA planes in the visual and physical spaces. The visual perturbations (bold filled arrows, green: E3CCW-group, orange: E3CW-group) are composed of CCW CMD rotation (horizontal dotted arrows) and CCW or CW STA rotation (vertical dotted arrows).

The difference in the STA perturbations did not influence the final movement patterns correcting the CMD error, and there were no significant differences between the two groups (CMD: paired t-test, $t(18)$ = -0.479, P = 0.638, STA: paired t-test, $t(18)$ = -0.386, P = 0.704; Figs. 8a and 8b). However, consistent with our predictions, distinct corrective trajectories can be observed on the CMD–STA plane during the adaptation phase (Fig. 8c). Specifically, significant differences were observed in the movement patterns between the two groups during the entire adaptation phase, indicating that

STA perturbations influenced the adaptive process. Indeed, a repeated-measures multivariate analysis of variance (MANOVA) showed a significant effect of group (Pillai's Trace $F(8, 162) = 0.155$, $P < 0.001$) and trial segment (Pillai's Trace $F(8, 162) = 0.719$, $P < 0.001$); however, no significant interaction was observed (Pillai's Trace $F(8, 162) = 0.039$, $P = 0.982$).

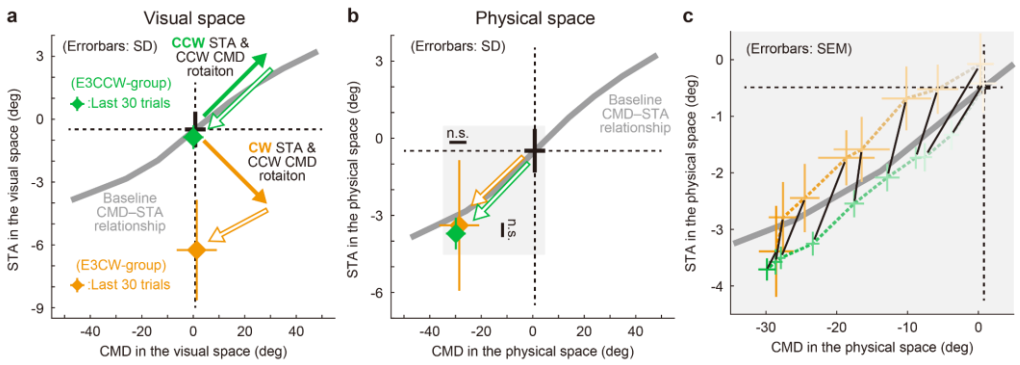

Figure 8. Experiment 3: Adaptation patterns to task-relevant and task-irrelevant visual perturbations. (**a**, **b**) Movement patterns in the visual and physical spaces are shown (same formats as shown Figs. 4a and 4b). Green (orange) plots represent the averaged movement pattern of E3CCW-group (E3CW-group) in the last 30 trials during the adaptation phase. The movement patterns did not show a significant difference between groups (*t*-test, CMD: $t(18) = -0.479$, $P = 0.638$, STA: $t(18) = -0.386$, $P = 0.704$). (**c**) However, the adaptive processes appeared to be different. The formats of the trial numbers for each plot are the same as those shown in Fig. 4d. The movement patterns of the two groups are compared using repeated-measures MANOVA. The definition of the trial segments is the same as that shown in Fig. 4d. A multivariate analysis revealed a significant effect of group (Pillai's trace $F(8, 162) = 0.155$, $P < 0.001$) and trial segment (Pillai's trace $F(8, 162) = 0.719$, $P < 0.001$); however, no significant interaction can be observed (Pillai's trace $F(8, 162) = 0.039$, $P = 0.982$). The black lines indicate identical trial segments.

Discussion

In this study, we employed a novel stick-manipulating reaching task designed specifically to investigate redundancy in motor control and learning (Fig. 2a). This redundant motor task enables the examination of adaptation patterns in the redundant motor system following the introduction of task-relevant, task-irrelevant, or both types of perturbations. First, we verified that the participants adopted a stereotypical strategy to reach the target with the stick, and that the movement pattern (movement of the stick's tip and stick tilting angle) was governed by an inherent CMD–STA relationship. Second, when only task-relevant perturbations were imposed on the

cursor, the motor system corrected the physical movement patterns along the inherent relationship to achieve the task goal (Exp. 1). Third, when perturbations were applied solely to the task-irrelevant dimension (i.e., stick tilting angle), the motor system still corrected the task-irrelevant error, which was accompanied by a task-relevant error (Exp. 2). Finally, when both types of perturbations were simultaneously imposed, movement correction was influenced depending on the combination of perturbations (Exp. 3).

Inherent relationship between task-relevant and task-irrelevant dimensions

Our body has more degrees of freedom than required to achieve a relatively low-dimensional task goal. Understanding how the motor system resolves this redundancy is challenging (Bernstein et al., 1996). One of the key observations to help us understand the problem is that the motor system attempts to reduce movement variability to directly affect the task goal but allows movement variability that does not affect the goal. This feature has been called “minimal intervention principle” that was demonstrated by decomposing the movement variability into the variability in task-relevant and task-irrelevant dimensions (Scholtz & Schoner, 1999; Scholtz et al., 2000; Mosier et al., 2005; Latash, 2012; Sternad, 2018). Importantly, as an optimal feedback control theory is proposed, this strategy contributes to optimizing the task performance (Todorov & Jordan, 2002; Todorov, 2004; Scott, 2004; Diedrichsen, 2007; Valero-Cuevas et al., 2009; Ronsse et al., 2010; Sternad et al., 2011; Selgrade & Chang, 2015).

In the current task, task-relevant and task-irrelevant dimensions are represented in the horizontal CMD axis and vertical STA axes on the CMD–STA plane, respectively (Fig. 2h). According to the minimal intervention principle, once the CMD is determined, arbitrary movements along the STA axis are allowed. However, this was not the case; the participants showed stereotypical patterns of moving the tip of the stick (i.e., the task goal) by tilting it. This pattern was not learned but observed from the beginning of the task (Fig. 2g). Notably, compared with the case where both hands moved in parallel, the movement distances of both hands were significantly reduced to a near-optimal level (Fig. 2i), which contributed to reducing the required work (Collins 1995; O'Sullivan et al., 2009). As a result of this optimization process, CMD and STA were constrained by an inherent relationship expressed as the baseline CMD–STA relationship (Fig. 2h).

Movement correction to task-relevant perturbation

When the task-relevant perturbation was imposed on the cursor only (visual rotation by 30° CCW), the participants corrected the CMD in the opposite direction, as reported in many previous studies using an ordinary reaching movement (Cunningham, 1989; Krakauer et al., 2000). Importantly, our task helped investigate how such movement corrections in the task-relevant dimensions (CMD) propagated to the task-irrelevant dimension (STA). The participants corrected the CMD by rotating the STA along the baseline CMD–STA relationship (e.g., CW CMD correction was accompanied by CW STA rotation; Figs. 4b and 4d). This correction pattern was observed not only for Exp. 1A in which the participants could use explicit strategy but also for Exp. 1B in which adaptation implicitly occurred, indicating that the implicit motor learning system exploits inherent movement patterns, even when correcting the movement. We previously demonstrated that correction of the reaching movement to a visual error was significantly influenced by the baseline relationship between the movement and target directions (i.e., a visuomotor map) (Hayashi et al., 2016). After the visuomotor map was distorted such that the movement direction was modulated with the target direction more (or less) sensitively, the movement correction increased (or decreased). The present finding that the baseline movement pattern constrains the adaptation pattern is consistent with this finding.

Notably, this correction pattern changed the stick rotation that the participants saw during the reaching movement (i.e., the STA in the visual space). For the 0° target in the baseline condition, STA rotation was almost 0° (Fig. 2h). However, after adaptation, the STA rotation was equivalent to the STA rotation when aiming at the -30° target. Thus, the observed STA rotation differed from that observed in the baseline condition (Figs. 4a and 4c). Nevertheless, movement correction followed the baseline CMD–STA relationship, implying that the motor system signified task-relevant CMD and ignored task-irrelevant STA. Therefore, this movement correction pattern is likely consistent with the minimum intervention principle.

However, a slight difference in the correction patterns between Exp. 1A and Exp. 1B implies a violation of the minimum intervention principle. In Exp. 1A, in which a 30° visual rotation is suddenly imposed, the final adapted patterns of CMD and STA closely resembled the pattern when aiming at the target positioned at -30° (Fig. 4b, right). This result indicated a near-perfect adaptation. However, when cursor perturbation was implicitly introduced through a gradual increase in perturbation (Exp. 1B), the residual errors persisted in the final adaptive patterns (Fig. 4d, right). Visuomotor adaptation is often incomplete even after sufficient training (Krakauer et al.,

2000; Ethier et al., 2008; Malone et al., 2011; Vaswani et al., 2015). Although the presence of residual errors is believed to be due to the balance between learning and forgetting, a recent study demonstrated that only the implicit learning system is responsible for producing residual errors by modulating the error sensitivity with the consistency of errors in previous trials (Albert et al., 2021). However, we believe that an alternative mechanism was involved in producing a residual error in Exp. 1B. In contrast to the minimal intervention principle, if the motor system attempts to correct the task-irrelevant STA and this correction pattern is constrained by the baseline CMD–STA relationship, the STA correction could interfere with the CMD adaptation and lead to the generation of a residual error. As discussed below, the results of Experiments 2 and 3 support this hypothesis.

Movement correction to task-irrelevant perturbation

According to the minimal intervention principle, the motor system should ignore STA perturbations, because they do not influence task goal achievement. However, inconsistent with this idea, Experiment 2 clearly demonstrated that the motor system corrected STA perturbations (Figs. 6a and 6b). Therefore, the motor system predicts task-irrelevant STA when performing the task and corrects the dissociation between the observed and predicted STA (i.e., sensory prediction error). This idea was corroborated by the fact that participants who demonstrated a lower STA at baseline showed a greater amount of STA correction (Fig. 6d).

Previous studies have demonstrated that motor system corrects movements using task-irrelevant perturbations. For example, Wolpert et al. (1995) examined motor adaptation when a visual cursor trajectory was curved during a reaching movement. Although this perturbation did not affect the task goal, significant aftereffects were observed in subsequent trials. Schaefer et al. (2012) examined motor adaptation to visual rotation when the target was an arc rather than a point. In this case, visual rotation did not influence the task success. Nevertheless, they observed an after-effect. Thus, consistent with our results, these findings suggest that the motor system does not necessarily ignore task-irrelevant errors. However, notably, these studies imposed perturbations on task-relevant visual cursors. Thus, these results should be interpreted as evidence that the motor system can predict the entire movement of task-relevant visual feedback. Our experiment differs from these previous studies in that the true effect of task-irrelevant perturbation can be assessed because it enables task-irrelevant STA perturbation to be imposed independently of the task-relevant CMD perturbation.

Adaptation to task-irrelevant perturbation influences task-relevant performance

Experiment 2 demonstrates that adaptation to task-irrelevant perturbations degrades the task-relevant performance. Correction of the task-irrelevant STA error was accompanied by an increase in the task-relevant CMD error, which can be predicted from the baseline CMD–STA relationship (Fig. 6b, right). Specifically, when the STA is rotated about the cursor in the CW (or CCW) direction, the required CCW (or CW) STA correction produces a CCW (or CW) CMD error (Fig. 6c). This tendency was more pronounced in participants with a smaller stick-tilt angle at baseline phase, that is, those with a shallower baseline CMD–STA relationship (Fig. 6e). Such an interaction between the CMD and STA was also observed in Experiment 3. When the CMD and STA errors were imposed simultaneously, the CMD error correction was influenced by the combination type (Fig. 8c). If the motor system simply attempted to correct the STA to reduce the sensory prediction error, this spillover effect on the CMD would not have been observed. Therefore, these results indicate that the CMD and STA are strongly coupled.

There are two possible reasons why the motor system corrects task-irrelevant STA errors. As mentioned in the previous section, a possible simple interpretation is that the motor system predicts the sensory information generated by the action and attempts to correct the differences between the predicted and actual sensory information, even when the task is successfully achieved (Mazzoni & Krakauer, 2006; Schaefer et al., 2012; Morehead et al., 2017; Kim et al., 2019). Given that CMD and STA are tightly coupled, task-irrelevant STA error information should contain information concerning the task-relevant CMD error. Thus, the motor system interprets task-irrelevant STA errors as evidence that task-relevant CMD errors have been produced. When sensory information contains noise and/or uncertainty, the reliability of sensory information estimation can be improved by utilizing additional sensor information (Ernst & Banks, 2002). From this viewpoint, utilizing STA information may be useful for improving the accuracy of CMD error estimation.

In summary, this study directly examined how the motor system adapted to changing redundant movement patterns when errors were introduced in both task-relevant (CMD) and task-irrelevant (STA) dimensions. When only the task-relevant CMD error was introduced, the motor system could implicitly correct the CMD by altering the task-irrelevant STA (Exp. 1). However, when only task-irrelevant STA errors were introduced, the motor system attempted to correct the STA, although this correction

was unnecessary (Exp. 2). Importantly, this task-irrelevant STA correction interfered with task performance through the inherent baseline CMD–STA relationship. Furthermore, when CMD rotation was combined with STA rotation, the adaptation process was significantly influenced by the direction of STA rotation (Exp. 3). These results suggest that the motor system predicts sensory consequences, regardless of their task relevancy, and actively corrects any dissociation between predicted and actual sensory information. We speculate that, as long as the movement patterns are inherently constrained, the motor system can use task-irrelevant error information to obtain the task-relevant error information because an error in the task-irrelevant dimension may imply a task-relevant error.

Methods

Participants

A total of 72 healthy adults (25 females and 47 males, aged 22.1 ± 2.5 years old; mean ± SD) participated in the study. Participants were recruited using an online recruitment system (https://www.jikken-baito.com). All the participants were right-handed according to their laterality score (83.3 ± 13.7; mean ± SD) obtained using the Edinburgh Handedness Inventory (Oldfield, 1971). They provided written informed consent, and the experimental protocol was approved by the ethics committee of The University of Tokyo (#19-225).

Experimental apparatus

The participants performed reaching movements using a virtual stick displayed on a horizontal screen with both handles of a manipulandum (KINARM End-Point Lab; Kinarm, Kingston, Canada) (Scott, 1999) (Fig. 2a). This screen prevented the participants from directly seeing their arms and handles, and displayed a start position, a target (1.4 cm in diameter), and a virtual stick (length: 40 cm, width: 0.5 cm). A circular cursor (1 cm diameter) was displayed on the right tip of the stick. The participants held the left tip of the stick with their left hand (left handle) and the stick 15 cm away from the left hand with their right hand (right handle). The distance between the handles was fixed using a strong elastic force produced by the manipulandum (spring constant = 2000 N/m). The positions and velocities of the hands were analogue/digitally converted at 1.129 kHz and then recorded at 1 kHz for offline analysis.

Baseline phase

All the experiments (Experiments 1–3) comprised a baseline phase (360 trials) followed by an adaptation phase (240 trials). The baseline phase, which was common to all experiments, was performed to investigate the basic strategy of how the participants moved the stick to reach the targets with a cursor at the right tip. Before each reaching movement, the participants were asked to move the stick to the home position with the help of a manipulandum (Fig. 2c). After maintaining the home position for 0.5−1 s, a gray target was pseudo-randomly chosen from nine possible targets (0°: horizontal direction, ±10°, ±20°, ±30°, ±40°) appearing 10 cm away from the initial right 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 cursor to the target. The participants were instructed to maintain the peak velocities of the cursor as constant as possible across the trials. When the cursor reached the target, a feedback message, “fast” or “slow,” was presented on the monitor if the movement speed was higher or lower than the range of 300−450 mm/s, respectively. After maintaining the cursor at the target for 0.5 s, the visual feedback of the stick disappeared. Then, the handles automatically returned to their home position, and the next trial began. During the subsequent 240 trials in the adaptation phase, the target appeared only in the 0° direction, and distinct visual perturbations were introduced in Experiments 1–3 as described below. The home positions, size of the visual feedback and the target, inter-trial interval, and criteria for the cursor velocity feedback for the adaptation phase were the same as those in the baseline phase.

Experiment 1

Experiments 1A (N = 13) and 1B (N = 19) were performed to investigate how participants moved the stick when adapting to task-relevant perturbations (cursor position perturbations). In Experiment 1A, the cursor-movement direction (CMD) on the monitor suddenly rotated counterclockwise (CCW) direction by 30° about the starting point. However, the stick tilting angle (STA) remained unchanged (i.e., the stick-tilting angle was identical to the angle of the line connecting both handles). In Exp. 1A, the participants noticed the presence of CMD rotation, which enabled them to use an explicit strategy during the adaptation. Experiment 1B was conducted to exclude the influence of the explicit strategy by gradually increasing the CMD rotation in 1° increments per trial up to 30°.

Experiment 2

Experiment 2 examined whether the motor system was indifferent to task-irrelevant perturbations (stick-tilt perturbations). The STA on the monitor was rotated

about the cursor in the clockwise (CW) direction (E2CW-group, N = 10) or in the CCW direction (E2CCW-group, N = 10). Notably, this perturbation did not affect the cursor position. During each reaching trial, the STA perturbation increased from 0° to 6° in proportion to the distance between the cursor and starting point (0.6°/cm) (Fig. 5a). The participants did not notice perturbations during the experiment.

Experiment 3

In Experiment 3 (N = 20), to examine how task-irrelevant STA perturbations influenced adaptation to task-relevant CMD perturbations, both CMD rotation (same as in Experiment 1 B) and STA rotation (same as in Experiment 2) were simultaneously imposed. Ten participants participated in a task in which CCW CMD and CCW STA rotations were imposed (the E3CCW-group). The remaining ten participants participated in a task in which CCW CMD and CW STA rotations were imposed (the E3CW-group). The application of CMD and STA perturbations was the same as in Experiments 1B and 2, respectively. The participants did not notice perturbations during the experiment. We assumed that adaptation to the CMD perturbation is facilitated if the CMD and STA perturbations are aligned with the inherent stereotypical movement pattern or, conversely, interfered if the combination of the CMD and STA perturbations is orthogonal to the inherent stereotypical movement pattern.

Data analysis

Data analyses were performed using MATLAB R2021a (MathWorks, Natick, Massachusetts, USA). The behavioral data were low-pass filtered (10 Hz, fourth-order Butterworth filter). The CMD was calculated as the movement direction of the cursor relative to the horizontal direction. The STA was calculated as the tilting angle of the stick from the horizontal line. Positive values for both parameters were defined as the degree to the CCW direction.

Minimum distance of hand movement

The total movement distance of both hands in Fig. 2i was estimated by summing the Euclidean distances between the initial and final positions of the hands. The distance is represented as a function of the stick-tilting angle at the movement offset (θ).

$$\begin{aligned} f(\phi,\theta) = &\sqrt{(d\cos\phi - L\cos\theta + L)^2 + (d\sin\phi - L\sin\theta)} \\ &+ \sqrt{(d\cos\phi - R\cos\theta + R)^2 + (d\sin\phi - R\sin\theta)} \end{aligned} \tag{1}$$

The first term on the right side represents the distance of the left-hand movement, whereas the second term represents the distance of the right-hand movement. ϕ, d, L,

and *R* represent a target direction (0°, ±10°, ±20°, ±30°, and ±40°), a target distance (10 cm), a distance between the left hand and the cursor (40 cm), and a distance between the right hand and the cursor (25 cm), respectively. The minimum distance (Fig. 2i, a red line) was derived by solving the following equation:

$$\frac{\partial f}{\partial \theta} = 0 \qquad (2)$$

Statistical analysis

To statistically evaluate the behavioral data, we conducted *t*-tests, correlation analyses, two-way repeated-measures ANOVA, and MANOVA using MATLAB, the software package JASP (http://jasp-stats. org), and R studio.

Data Availability

Data collected in Experiments 1–3 and the code are uploaded in zenodo and are available at https://zenodo.org/record/8033232.

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Competing Interest Statement

Authors declare that they have no competing interests.