Distinct optimization of motor control and learning:
Self-paced motor learning achieves different motor patterns from overtrained

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Author contributions

T.H. and K.T. designed the experiments. T.H. performed the experiments. T.H. analyzed the data. T.H. and K.T. wrote the paper.

Competing interests

The authors declare no competing interests.

Abstract

Self-paced movement, resulting from extensive training and optimization, serves as an ideal model for investigating internal objectives without external constraints within the sensorimotor system. Previous studies have shown that the self-paced movement is consistent within individuals but inconsistent across individuals, highlighting a robust, unique optimization in motor control. Although motor learning is similarly an optimization process, it is unknown whether the internal objectives are shared with motor control and learning, i.e., whether it replicates the motor patterns identified by self-paced motor control. As the optimality principles typically address redundancy, a human behavioral experiment was designed to equate movement distance for motor control and learning, comparing redundant motion parameters, movement velocity, and duration, through detailed analysis that accommodates their nonlinear interaction and significant inter-individual baseline differences. Participants, instructed to use their preferred velocities and duration, exhibited minimal intra-individual variability in motion parameters. Notably, visuomotor shift perturbations exclusively affected velocity, while changes in target distances affected both velocity and duration. These findings suggest that the sensorimotor system employs distinct optimization mechanisms for motor control and learning to resolve redundancy.

Significance statement

Our natural behaviors are thought to be well-optimized. Self-paced movements, a major form of the behaviors, demonstrate significant stability within individuals but vary across individuals, suggesting that the sensorimotor system in the central nervous system operates a unique and robust optimization involved in self-paced motor control. Self-paced motor control is further refined during the motor learning process. However, it is unknown whether motor control and learning share a common objective function. We demonstrated that laboratory-based motor learning never resulted in identical motor patterns from the overtrained movements with natural instruction. Thus, the sensorimotor system would employ distinct optimization mechanisms for motor control and learning, suggesting that these processes are not contiguous.

INTRODUCTION

In guiding movements, the sensorimotor system in the central nervous system employs visuomotor mapping to convert visual information into motor commands (1, 2). For instance, golfers learn to adjust their club-head motion to control ball distance based on the hole's proximity. Conditions on the green, such as an unexpected, steep slope, may cause the ball to travel farther, prompting adjustments in subsequent putts. This error between the expected and actual ball positions can lead golfers to modify their club-head motion, potentially standardizing the motion for longer putts on steep slopes to that of shorter ones. However, it remains uncertain whether motor commands aimed at the visual target and those adapted from visual errors result in identical motor patterns.

The sensorimotor system aims to minimize costs and maximize rewards when executing movements (3). Self-paced movements, devoid of external constraints, serve as an ideal model for investigating these internal objectives. The optimality principle often resolves redundancy (3, 4), which is evident in their velocity and duration of the movements. Despite constant movement distances, kinematic adjustments in either velocity, duration, or both are necessary. Previous studies have demonstrated that both velocity and duration significantly vary based on the distance to the movement target (5). Self-paced movements are consistent within individuals but inconsistent across individuals (6, 7). These long-term, overtrained movements indicate that the robust optimization in motor control is effectively identified by self-paced movements targeting different distances. When internal objectives align with motor control and learning, the learned motion parameters mirror those generated in motor control across varying distances.

This study investigates the impact of motor learning in spatial tasks on movement velocity and duration, compared to self-paced motor control targeting visual cues. Participants executed self-paced reaching movements to balance individual velocity and duration. The experiment induced sensorimotor adaptation using a visuomotor shift (8, 9) that modified the visual cursor's distance representing hand position, either increasing or decreasing it. We introduced a refined analysis to manage substantial baseline inter-individual differences and the nonlinear interactions between velocity and duration. Notably, our results reveal that visuomotor perturbations uniquely influence velocity, whereas changes in target distance affect both parameters. These findings suggest that the sensorimotor system utilizes distinct optimization strategies for motor control and learning, resolving the inherent redundancy.

RESULTS

A refined analysis for movement velocity and duration

Understanding movement velocity and duration in self-paced movements poses significant challenges. One is redundancy, multiple combinations of velocity and duration can result in the same movement distance. For example, in contrast to 100-mm reaching movement, 120-mm reaching movement can be accomplished with a 1.2-fold increase in velocity, duration, or multiplication of the two. Thus, there are multiple solutions for each distance. Additionally, if only velocity is modified, 1 mm/ms at baseline has to increase by 0.2 mm/ms, while 3 mm/ms at baseline has to increase by 0.6 mm/ms, i.e., triple the velocity modulation. Thus, the baseline motor

patterns, which vary widely among individuals (6, 7), determine the required adjustments. Furthermore, while the relationship between distance, velocity, and duration in constant-speed movements can be described by a simple equation (distance = velocity × duration), the actual trajectory of reaching movements exhibits a smooth, bell-shaped profile in the velocity domain (10, 11). The height and width of this bell-shaped curve, representing preferred velocity and duration, systematically vary with target distance (6, 7). However, previous theoretical studies that successfully captured the bell-shaped curves explicitly fixed duration at first (4, 12–14), an approach that proves inadequate for variable durations. To date, no analysis has resolved these issues comprehensively.

To address these challenges, we developed an analysis comprising the following 3 steps. First, we modeled the bell-shaped velocity curve using a Gaussian function, $V(t) = v \exp\left(-(T-t)^2/2\tau^2\right)$, where velocity ($V$) is described as a function of time (t) with parameters representing height (v), width (τ), and center (T). These parameters correspond to velocity and duration, respectively. Second, we calculated the movement distance by integrating the Gaussian function, $D = \sqrt{2\pi}v\tau$ (D is distance), yielding the same structure analogous to the constant speed case, i.e., multiplication of the two. Finally, we performed a log transformation on the Gaussian integral, $\log(D) = \log\left(\sqrt{2\pi}\right) + \log(v) + \log(\tau)$. This linearization of the nonlinear interaction facilitates the evaluation of adjustments in velocity and duration across varying motor patterns. Overall, this analysis provides a robust framework for examining velocity and duration in distance-based sensorimotor adaptation, effectively addressing the identified challenges.

Both movement velocity and duration changed along with target distances

We examined the efficacy of the proposed analysis to self-paced movements across various target distances. Right-handed participants (n = 24, 13 males and 11 females, ages between 20 and 46) performed forward-reaching movements with their preferred velocity and duration without altering pace throughout the experiment (Fig. 1a and b). The target was located at [60, 70, 80, 90, 100, 110, 120, 130, and 140] mm away from the start position at pseudo-random (Fig. 1c). Participants aimed to align the visual cursor, representing hand position, with these targets, despite cursor occlusion during movements. This procedure was tested at three phases, the beginning, middle, and end of the experiment interspersed with other motor tasks, including the sensorimotor adaptation task. Figure 1d and e reveal the time course of endpoint position and velocity for 3 target distances, [70, 100, and 130] mm, of a representative participant. The endpoints showed consistent, smooth trajectories without online visual feedback (Fig. 1d). The velocities were bell-shaped and scaled as target distances increased (Fig. 1e). The trajectory scaling implied that both movement velocity and duration varied with the distances.

Utilizing the Gaussian function with the bell-shaped curves revealed significant fitting accuracy; 97.8 ± 0.2% (mean ± SEM) of variances were explained (Figs. 1f and S1a). Notably, predicted distances from the Gaussian integral were consistent with measured distances (slope: 0.9812 ± 0.0034, intercept: −0.0012 ± 0.0004, Fig. S1b). Given an identical target distance, there are possible multiple combinations of movement velocity and duration. Overall data points from all participants were scattered on the solution manifolds (Fig. 1g and h). The raw fitting parameters, v and τ, are nonlinear interactions (Fig. 1g), whereas log

transformation, $\log(v)$ and $\log(\tau)$, makes them linear (Fig. 1h). The linearization with log transformation evaluates velocity and duration because the transformation resolves the nonlinear dependency and the weights of velocity and duration are equal on this plane (i.e., $\log(D) = \log(\sqrt{2\pi}) + \log(v) + \log(\tau)$). Thus, we used $\log(v)$ and $\log(\tau)$ as measures of subjective preferred velocity and duration.

We found that, in the self-paced reaching movements, the movement distances altered along with target distances (Fig. 2a), but the resultant movement distances were slightly overshot for the 70-mm target (73.7 ± 0.1 mm) and undershot for the 130-mm target (12.98 ± 0.1 mm). The small shifts towards the mean of overall movements would be induced by movement history (15); and the subsequent movement was altered to be similar to the previous one, that is, because the target distances were frequently larger than 70 mm just before the 70-mm target, movements towards the 70-mm target became slightly farther. We also found that the log velocity (Fig. 2b) and log duration (Fig. 2c) changed with the target distance. The log velocity changed 0.40 ± 0.01 from 70-mm to 130-mm target distance, while the log duration changed 0.16 ± 0.01, indicating that movement velocity is heavily weighted than the duration on the log plane ($t(23) = 15.07$ and $p = 2.08 \times 10^{-13}$). To examine the stability of self-paced movement within individuals, we computed two representative values: preference, indicating which velocity and duration were preferred (Fig. 2d), and slope, indicating the ratio of how much velocity and duration changed more (Fig. 2e). We found that the preference was significantly biased into velocity preference (Fig. 2d, $t(23) = 6.77$ and $p = 6.60 \times 10^{-7}$) and was highly consistent within individuals (Fig. 2f, intra-individual standard deviation vs inter-individual standard deviation: 0.14 ± 0.02 vs 0.38, $t(23) = 14.03$ and $p = 9.22 \times 10^{-13}$), while the slope was over 45 degrees for all individuals (Fig. 2e, $t(23) = 20.05$ and $p = 4.58 \times 10^{-16}$) and was highly consistent within individuals (Fig. 2g, intra-individual standard deviation vs inter-individual standard deviation: 3.90 ± 0.53 vs 5.25, $t(23) = 2.53$ and $p = 0.019$). There was no correlation between the preference and slope (Fig. 2h, $r = 0.12$, and $p = 0.57$). Participants who preferred faster movement did not necessarily change the velocity, suggesting that individual preferences of velocity and duration are independent of how the two are adjusted due to target distances. The results demonstrate that our analysis effectively captured self-paced movements and that movement velocity and duration were consistent within individuals but varied across individuals.

Not movement duration but velocity change in sensorimotor adaptation

In Experiment 1, we investigated how the sensorimotor system resolved the redundancy of movement velocity and duration during sensorimotor adaptation. We introduced a 30-mm shift-up (Fig. 3a) or 30-mm shift-down perturbation (Fig. 3b) to 12 participants (seven males and five females, aged between 21 and 37). The target was always located at 100 mm; thus, ideal learning led to movement distances of 70 mm (down modulation) and 130 mm (up modulation). Participants performed 200 learning trials with either visuomotor shifts before or after the null trials (20-trial baseline and the 50-trial washout) (Fig. 3c). Each participant experienced both shift-up and shift-down perturbations in a counterbalanced order between the random phases.

No perfect learning occurs in sensorimotor adaptation in the distance domain (16), with movement deviations averaging 74.1 ± 0.8 mm for down-modulation and 129.9 ± 0.8 mm for up-modulation in the final 30 trials of the learning phase (Fig. 3c). These results were not statistically different from the movements toward 70-mm and 130-mm targets in the random phases (Fig. 2a, interaction of [random vs. learning phases] × [70-

vs. 130-mm target distances], $F(1,11) = 0.09$, $p = 0.78$). Log movement velocity adjusted due to sensorimotor adaptation (Fig. 3d-f; −1.58 ± 0.06 for down-modulation, −1.07 ± 0.08 for up-modulation, $t(11) = 11.33$, $p = 2.10 \times 10^{-7}$). Contrarily, log movement durations did not differ significantly between down-modulation (−1.90 ± 0.05) and up-modulation (−1.85 ± 0.08) (Fig. 3d, g, h, $t(11) = 1.25$, $p = 0.24$). The results suggest that sensorimotor adaptation to visuomotor shifts affects velocity more than duration, suggesting different optimization strategies in motor control and learning.

Changes in target distances to match movement volatility

We found that both movement velocity and duration changed with the target distance (Fig. 2b and c), whereas only velocity changed with sensorimotor adaptation (Fig. 3e-h). In addition to motor control and learning, an additional methodological difference is the volatility of movement distances. Target distances that varied in every trial always altered the movement distances in the random phase, whereas sensorimotor adaptation in the learning phase maintained a constant movement distance.

To test the possibility that movement volatility causes an imbalance in velocity and duration adjustments, we used the mean movement distances in Experiment 1 for the target sequence in Experiment 2 for the remaining 12 participants (Fig. 4a; six males and six females, aged between 20 and 46). This enabled us to investigate whether target distances alter both movement velocity and duration under the same movement volatility observed in sensorimotor adaptation. The movement distances completely followed the target sequences (Fig. 4b, 76.1 ± 0.9 for down-modulation, 131.8 ± 1.0 for up-modulation, $t(11) = 96.95$ and $p = 1.76 \times 10^{-17}$). Additionally, we found both log movement velocity (Fig. 4c-e, −1.58 ± 0.06 for down-modulation, −1.12 ± 0.06 for up-modulation, $t(11) = 23.41$ and $p = 9.82 \times 10^{-11}$) and log movement duration changed (Fig. 4c, f, g, −1.88 ± 0.05 for down-modulation, −1.79 ± 0.05 for up-modulation, $t(11) = 4.71$ and $p = 6.38 \times 10^{-4}$). The results demonstrate that movement volatility, influenced by target distances, does not disrupt the balance between updates in movement velocity and duration. This underscores the distinct optimization processes in motor control and learning.

DISCUSSIONS

The sensorimotor system generates natural behavior autonomously without external constraints, which is a fundamental model to elucidate the internal objective function. This optimality principle often helps resolve a redundancy inherent in the sensorimotor system. Interestingly, movement velocity and duration, although redundant in a self-paced movement, are consistent within individuals but vary across individuals (Fig. 2) (6, 7), suggesting unique and robust optimization. However, it is largely unknown whether motor control and learning share common objectives, i.e., whether motor learning replicates motor patterns identified by self-paced motor control.

The human behavioral experiment was designed to assess two redundant motion parameters in motor control and learning. Participants performed self-paced reaching movements toward targets set at 70-mm or 130-mm distances and adapted to 30-mm shifts up or down for a 100-mm target. Although the required movement amplitudes were consistent, allowing for identical motion parameters if optimized similarly, our

results found that motor learning, induced by the visuomotor shifts perturbations, exclusively changed the movement velocity (Fig. 3). In contrast, motor control adjustments for different target distances changed both (Figs. 2 and 4). The discrepancy in motion parameters between motor control and learning indicates a distinct optimization process.

Previous studies did not distinguish movement velocity and duration, combining them into one index, a movement vigor (17). Several objectives that determine movement vigor have been proposed, such as expectation of reward (18–20), metabolic energy expenditure (21, 22), mechanical smoothness (12, 13, 23), sensorimotor noise (14), and environmental uncertainty (24). These studies constrained movement vigor by explicitly setting movement velocity or duration, thus, overlooking biologically natural behavior in a self-paced manner, rendering direct observation of internal objectives problematic. Notably, Huh and Sejnowski (2016) proposed a potential objective that mediates a self-paced movement, called “drive,” which refers to the internal motivational level (25). This drive maintains individual movement vigor throughout the trajectory curvatures and sizes, aligning with our results demonstrating low intra-individual variability in preferences and slopes in self-paced motor control (Fig. 2d-g). Future research should aim to identify unique objectives for motor learning.

The “as quickly as possible” instruction has been extensively used to investigate human motor control and its computational model (5, 22, 26–29) as well as the “comfortable-speed” instruction (6, 7, 10, 11, 23, 25, 30–33). Al-Fawakhiri and McDougle (2024) found that sensorimotor adaptation changes both movement velocity and duration with the “as-quickly-as-possible” instruction (16), which contrasts this study where no change in movement duration was found with the comfortable-speed instruction. An additional external constraint on movement vigor could significantly modulate motion parameters, superseding internal objectives.

Motor commands are modulated by visuomotor mismatches, as demonstrated by numerous studies (34–36). The visual distortion at movement midpoint does not affect the success of the target acquisition, they prompt corrective adjustments in hand motion to align with visual cues, suggesting that visual information predominates over motor and proprioceptive information. Sensorimotor adaptation is often driven implicitly (37) thus, in Experiment 1, the modulation of movement distances, attributed not to movement duration but by velocity, primarily reflects an implicit motor learning process. A computational theory proposed that movement duration is determined by the task's accuracy or success rate at movement completion (38). Our results corroborate that movement velocity is flexible but movement duration is fixed to the visual target distances, underscoring that the sensorimotor system optimizes internal objectives in motor planning based on visual information during both motor control and learning.

MATERIAL and METHODS

Participants

Twenty-four right-handed participants (13 males, 11 females, aged 20 - 46) engaged in two experiments after providing informed consents. The experiments were evaluated by UTokyo ethical committees.

General task settings

Participants performed point-to-point reaching movements while holding a robot manipulandum (KINARM) with their right hand. Seated and facing a monitor via a mirror (Fig. 1a), which occludes their direct hand view, they experienced reduced awareness of the visual-motor mismatch. A visual target was presented 200 ms after the visual cursor that represented the hand position was at the start position, prompting participants to perform point-to-point reaching movement without the visual cursor (Fig. 1b). At the end of the movement with threshold, <0.03 mm/ms for 250 ms, after which the cursor reappeared, with or without visuomotor shift perturbations. During backward movements, driven by KINARM-generated force, the cursor remained visible without additional feedback from participants' movements. We recorded handle positions with a 1000 hz sampling rate.

In the experiment, participants engaged in three consecutive "random" sessions, interspersed with either "up-modulation" or "down-modulation" sessions (e.g., random, up-modulation, random, down-modulation, and random phases). We provided a one-minute break every 5 minutes, in which there were 137.9 ± 4.2 trials (mean ± SEM). Participants were instructed to perform movements at their preferred velocity/duration, focusing on accuracy rather than altering their preferred pace. These instructions ensured that their movements remained consistent within individuals but diverse across individuals throughout the experiments (Fig. 2).

Self-paced movements towards a target distance changing trial-by-trial

In the random phases, the target location varied trial-by-trial among nine possible distances, [60, 70, 80, 90, 100, 110, 120, 130, and 140] mm, in pseudo-random orders (Fig. 1c). Participants iterated a block of nine trials 15 times, totaling 135 trials in each of the three random phases. Prior to the experiment, participants practiced these movement distances.

Experiment 1: Movement distances modulated by visuomotor shift perturbation

Twelve participants (seven males and five females, aged between 21 and 37) performed adaptation tasks. The target consistently remained at 100 mm. Initially, no visual shift occurred, but at the movement's end, the visual cursor shifted 30 mm forward or backward along the longitudinal axis from the actual hand positions, resulting in an ideal movement distance of either 70 mm (down-modulation) or 130 mm (up-modulation). Each participant experienced both types of visuomotor shift perturbations, with the sequence counterbalanced. Participants performed 20-trial no shift (baseline), 200-trial perturbation, and 50-trial no-shift again (washout).

Experiment 2: Movement distances modulated by adaptive target shift

The other twelve participants (six males and six females, aged 20 and 46) performed different target sequences without the visuomotor shift perturbations. To match movement volatility from Experiment 1, we used the mean movement distances of Experiment 1 as the target distances in Experiment 2. Additionally, we counterbalanced the order of the up- and down-modulation for these 12 participants.

Data analysis

For movement distances, we used the location at movement completion. We developed an analysis to estimate movement velocity and duration independently. To achieve this, we fit a Gaussian function to the velocity profiles over time (Fig. 1f). The Gaussian function can obtain the parameters of the movement velocity (v) and duration (τ) independently. We performed the Gaussian fitting into the velocity profiles from cue presentation to target acquisition in each trial with the Matlab function, "*fminsearch*," minimizing mean squared error. To validate the analysis, we examined the differences between the measured and predicted movement distances from the Gaussian integral as well as the fitting accuracy using the explained variance (R^2). We identified several trials with poor fitting accuracies, leading to the exclusion of outliers based on an R^2 threshold; trials with less than 90% R^2 were discarded, amounting to 15.1 ± 1.6 trials (1.6 ± 0.2 % of the total) (Fig. S1).

For the random phases, we performed the outlier rejection of trials where the movement distance, velocity, or duration were away from the threshold, median ± 3IQRs, in each target distance within participants. We then computed the representative values, preferences, and slopes. To determine the preferred velocity and duration, we computed the differences in mean velocity and duration. For the slope, revealing how much these two change with different target distances, we compared the changes in mean velocity and mean duration with the target distances. We computed them from data points separately for the beginning, middle, and end phases in the log space and then compared the standard deviation across the phases (intra-individual variance) and across the participants (inter-individual variance) to examine the consistency of the motor patterns within individuals. Furthermore, we computed the correlation coefficients between preference and slope to examine whether individuals favoring faster movements change their velocity in response to variations in target distances.

For the learning phases, we discarded the outlier data points across participants with the threshold, median ± 3IQRs. Furthermore, we discarded the outlier data points within participants in the last 30 trials of the learning phases and then computed the mean to evaluate the asymptotic motor patterns of sensorimotor adaptation. Hypothetical testing was performed between the up- and down-modulation or across the random and learning phases with a paired sample t-test or two-way repeated ANOVA. Statistical significance was set at $p < 0.05$.

Figure 1

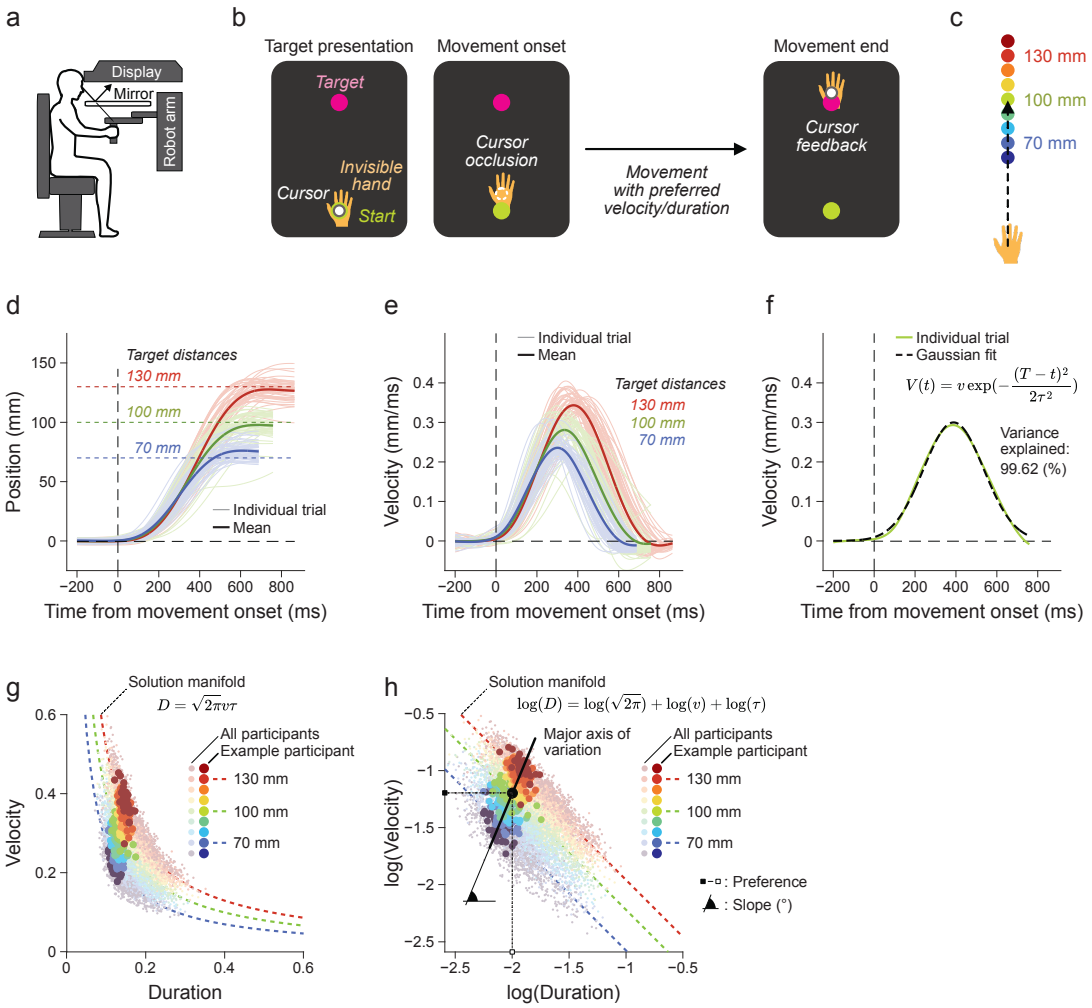

a
Display
Mirror
Robot arm
b
Target presentation
Movement onset
Movement end
Target
Invisible hand
Cursor
Start
Cursor occlusion
Movement with preferred velocity/duration
Cursor feedback
c
130 mm
100 mm
70 mm
d
Target distances
130 mm
100 mm
70 mm
Individual trial
Mean
Position (mm)
Time from movement onset (ms)
e
Individual trial
Mean
Target distances
130 mm
100 mm
70 mm
Velocity (mm/ms)
Time from movement onset (ms)
f
Individual trial
Gaussian fit
$V(t) = v\exp(-\frac{(T-t)^2}{2\tau^2})$
Variance explained: 99.62 (%)
Velocity (mm/ms)
Time from movement onset (ms)
g
Solution manifold
$D = \sqrt{2\pi}v\tau$
All participants
Example participant
130 mm
100 mm
70 mm
Velocity
Duration
h
Solution manifold
$\log(D) = \log(\sqrt{2\pi}) + \log(v) + \log(\tau)$
Major axis of variation
All participants
Example participant
130 mm
100 mm
70 mm
: Preference
: Slope (°)
log(Velocity)
log(Duration)

Figure 2

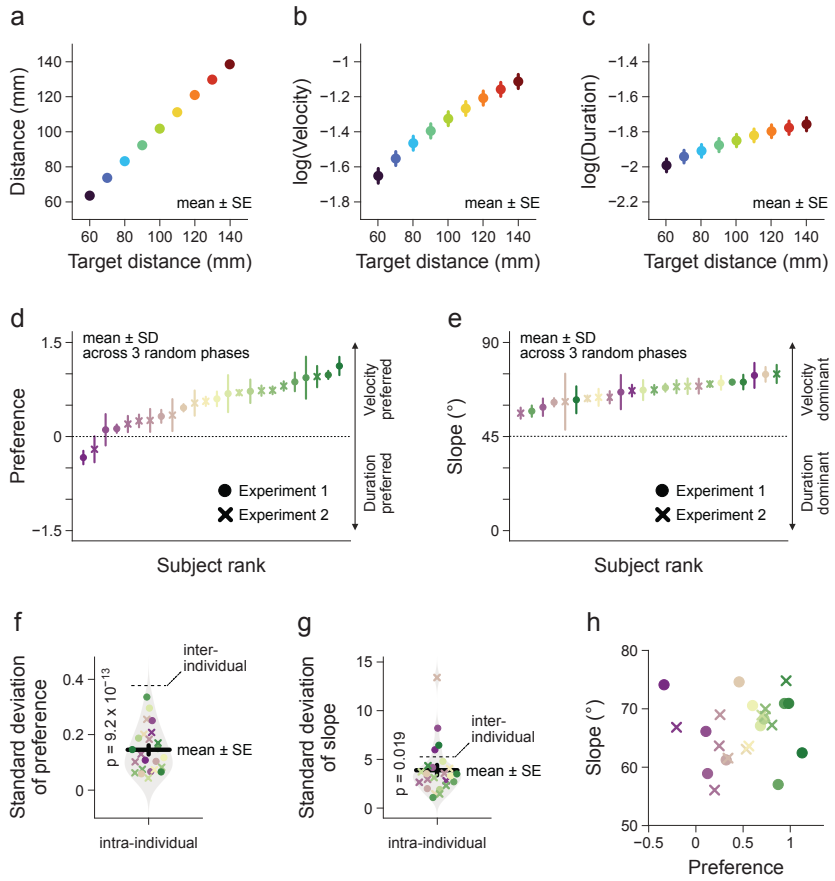

a
Distance (mm)
140
120
100
80
60
mean ± SE
60 80 100 120 140
Target distance (mm)
b
log(Velocity)
−1
−1.2
−1.4
−1.6
−1.8
mean ± SE
60 80 100 120 140
Target distance (mm)
c
log(Duration)
−1.4
−1.6
−1.8
−2
−2.2
mean ± SE
60 80 100 120 140
Target distance (mm)
d
Preference
1.5
0
−1.5
mean ± SD
across 3 random phases
Experiment 1
Experiment 2
Velocity preferred
Duration preferred
Subject rank
e
Slope (°)
90
45
0
mean ± SD
across 3 random phases
Experiment 1
Experiment 2
Velocity dominant
Duration dominant
Subject rank
f
Standard deviation of preference
0.4
0.2
0
p = 9.2 x 10−13
inter-individual
mean ± SE
intra-individual
g
Standard deviation of slope
15
10
5
0
p = 0.019
inter-individual
mean ± SE
intra-individual
h
Slope (°)
80
70
60
50
−0.5 0 0.5 1
Preference

Figure 3

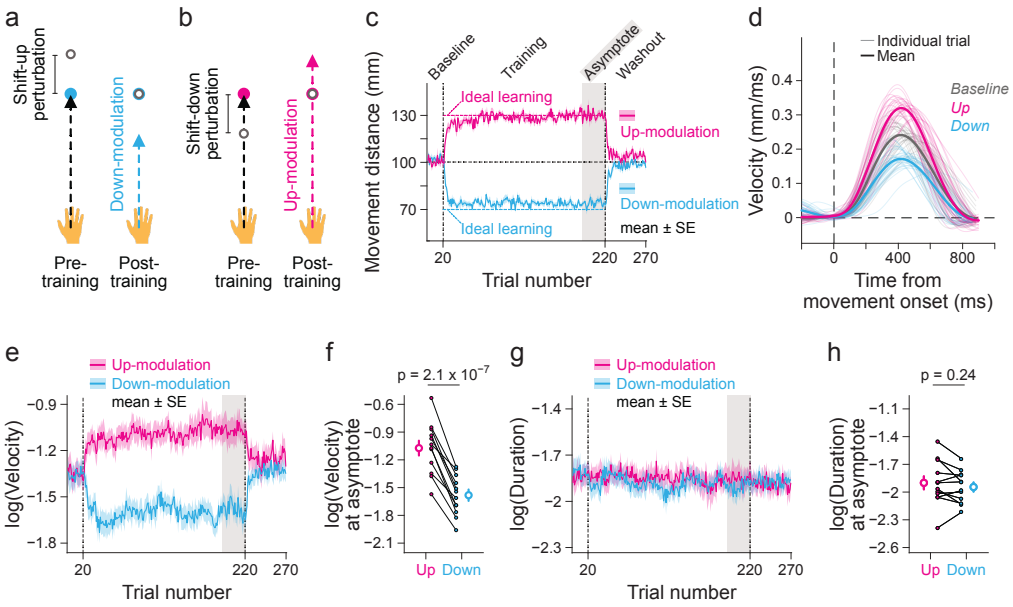

a
Shift-up perturbation
Down-modulation
Pre-training
Post-training
b
Shift-down perturbation
Up-modulation
Pre-training
Post-training
c
Baseline
Training
Asymptote
Washout
Ideal learning
Up-modulation
Down-modulation
Ideal learning
mean ± SE
Movement distance (mm)
130
100
70
20
220
270
Trial number
d
Individual trial
Mean
Baseline
Up
Down
Velocity (mm/ms)
0.4
0.3
0.2
0.1
0
0
400
800
Time from movement onset (ms)
e
Up-modulation
Down-modulation
mean ± SE
log(Velocity)
−0.9
−1.2
−1.5
−1.8
20
220
270
Trial number
f
p = 2.1 x 10−7
log(Velocity) at asymptote
−0.6
−0.9
−1.2
−1.5
−1.8
−2.1
Up
Down
g
Up-modulation
Down-modulation
mean ± SE
log(Duration)
−1.4
−1.7
−2
−2.3
20
220
270
Trial number
h
p = 0.24
log(Duration) at asymptote
−1.1
−1.4
−1.7
−2
−2.3
−2.6
Up
Down

Figure 4

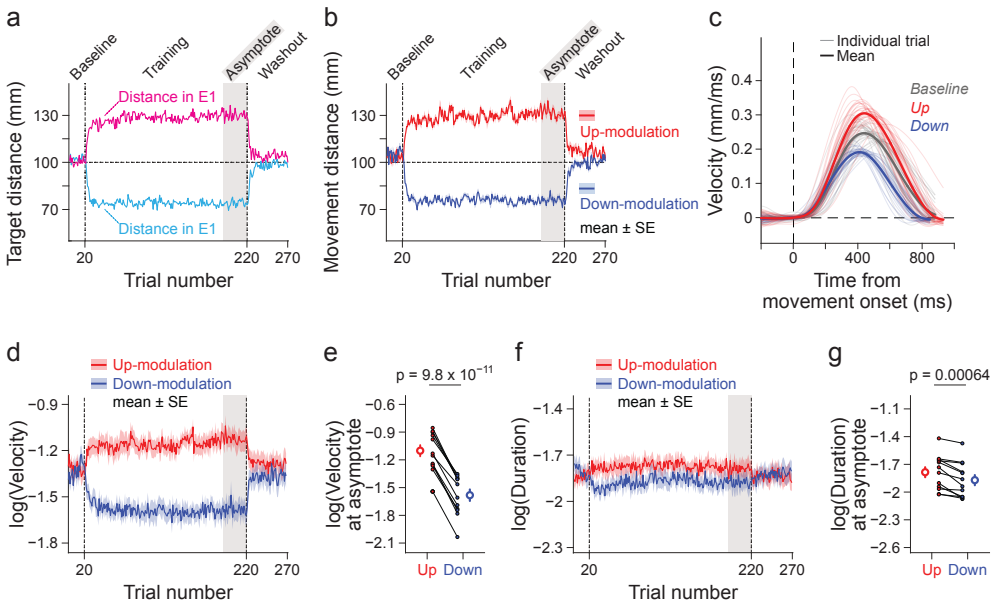
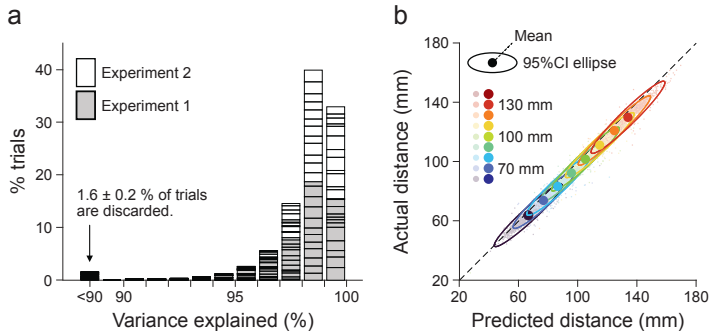

a
Baseline
Training
Asymptote
Washout
Distance in E1
Distance in E1
Target distance (mm)
130
100
70
20
220
270
Trial number
b
Baseline
Training
Asymptote
Washout
Movement distance (mm)
Up-modulation
Down-modulation
mean ± SE
Trial number
c
Individual trial
Mean
Baseline
Up
Down
Velocity (mm/ms)
0.4
0.3
0.2
0.1
0
400
800
Time from movement onset (ms)
d
Up-modulation
Down-modulation
mean ± SE
log(Velocity)
−0.9
−1.2
−1.5
−1.8
Trial number
e
p = 9.8 x 10^−11
log(Velocity) at asymptote
−0.6
−2.1
Up
Down
f
Up-modulation
Down-modulation
mean ± SE
log(Duration)
−1.4
−1.7
−2
−2.3
Trial number
g
p = 0.00064
log(Duration) at asymptote
−1.1
−2.6
Up
Down

Figure S1


a
Experiment 2
Experiment 1
% trials
40
30
20
10
0
1.6 ± 0.2 % of trials
are discarded.
<90
90
95
100
Variance explained (%)
b
Mean
95%CI ellipse
130 mm
100 mm
70 mm
Actual distance (mm)
180
140
100
60
20
20
60
100
140
180
Predicted distance (mm)

FIGURES CAPTIONS

Figure 1: Experimental settings and data analysis

a. The participants performed point-to-point reaching movements while holding the robot manipulandum. b. Verbal instructions encouraged the participants to initiate movements with their preferred velocity and duration. Visual feedback was not provided during movements but was observed at the end of the movements. c. The visual target distances were randomly varied trial-by-trial from 60 mm to 140 mm in the random phase. d,e. Position (d) and velocity (e) profiles towards 70 (blue), 100 (green), and 130 mm (red) of a representative participant were shown. The light thin lines indicate individual trials and the thick dark lines indicate the mean. f. The Gaussian fitting (broken black line) of the example velocity profile was highly accurate (99.62% of variance explained). g. Curved solution manifolds (colored broken lines) were used to achieve the target distances on the velocity-duration plane of the Gaussian fitting. Each individual trial (dots are from all participants; solid dots are from the representative participant shown in d and e) was on the manifolds. h. Log transformation, which linearizes the manifolds, can fairly evaluate the motion parameters under large inter-individual differences. From the scatter plot, we computed the preferences and slopes for each participant (Fig. 2).

Figure 2: Target position determines movement velocity and duration

a-c. The nine target distances changed movement distances (a), velocities (b), and durations (c). d,e. We computed two indices; preference (d) is a difference between mean movement velocity and duration, and slop (e) is an angle of the black line as shown in Figure 1h. Color indicates the subject rank sorted by preference (d), which is also used for the slope (e). f,g. Intra-individual standard deviation, which indicates error bars in d and e, was smaller than the inter-individual standard deviation both in the preference (f) and slope (g). h. The preference was not correlated with the slope (the color is identified in d).

Figure 3: Visuomotor shift modulates only movement velocity

a,b. Visuomotor shift perturbations were introduced in the longitudinal direction, which modulates movement distances shorter (a, down-modulation) or farther (b, up-modulation). c. The visuomotor shifts altered movement distances (thick lines) correctly to the ideal levels (thin broken lines). d. In the baseline (gray) and the resultant velocity profiles of a representative participant (magenta and cyan), the height (velocity) seems to change while the width (duration) remains the same. e,f. The movement velocity was modulated along with the movement distance adjustment. g,h. In contrast, no modulation of movement duration was found.

Figure 4: Target position with matched movement volatility modulates both

a. To match movement volatility to sensorimotor adaptation, we used the mean movement distances observed in Experiment 1 (E1) for the target distances in Experiment 2. b. The movement distances obviously changed, similar to the sensorimotor adaptation. c. In the baseline (gray) and resultant velocity profiles of a representative participant (red and blue), the height (velocity) and width (duration) appeared to change. d-g. In

contrast to sensorimotor adaptation, movement velocity (d, e) and duration changed (f, g). These panels are analogous to those in Figure 3.

Supplementary Figure 1: Fitting quality and accuracy

a. For almost all trials, we found >90% of variance explained. Note that the small fraction of trials where <90% of variances explained were discarded as outliers (1.6 ± 0.2%). b. The actual distances from the data and the predicted distances from the Gaussian integral are highly correlated on the unity line (black broken line).

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