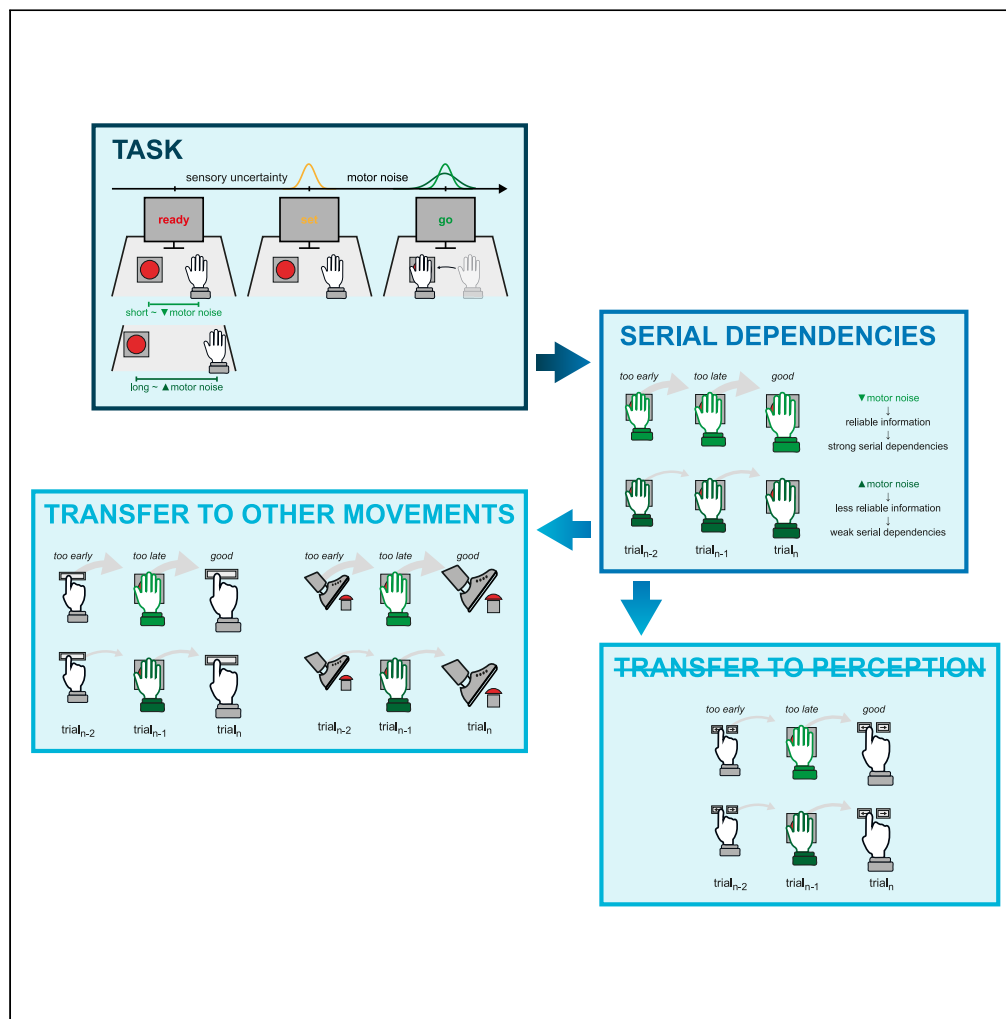


Article

Motor variability modulates calibration of precisely timed movements



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Highlights
Serial dependencies recalibrate timed actions

Motor uncertainty modulate serial dependencies

Movement and vision are recalibrated separately by the sensorimotor system

Serial dependencies generalize across different effectors



Article

Motor variability modulates calibration of precisely timed movements

Nadine Schlichting,^{1,2,*} Clara Fritz,¹ and Eckart Zimmermann¹

SUMMARY

Interacting with the environment often requires precisely timed movements, challenging the brain to minimize the detrimental impact of neural noise. Recent research demonstrates that the brain exploits the variability of its temporal estimates and recalibrates perception accordingly. Time-critical movements, however, contain a sensory measurement and a motor stage. The brain must have knowledge of both in order to avoid maladapted behavior. By manipulating sensory and motor variability, we show that the sensorimotor system recalibrates sensory and motor uncertainty separately. Serial dependencies between observed interval durations in the previous and motor reproductions in the current trial were weighted by the variability of movements. These serial dependencies generalized across different effectors, but not to a visual discrimination task. Our results suggest that the brain has accurate knowledge about contributions of motor uncertainty to errors in temporal movements. This knowledge about motor uncertainty seems to be processed separately from knowledge about sensory uncertainty.

INTRODUCTION

In order to catch a prey, a predator must move to a certain place at a certain time. A successful attack requires measuring the timing of the prey's actions and to plan a precisely timed movement to its future position. In real life, the predator receives feedback about the success of its timed movements. If the movement was too early or too late, the prey will escape. An unsuccessful attack may result from a lack of temporal accuracy at either the measurement (e.g., how long does the prey pause between steps) or the movement stage (e.g., how long does it take to reach the prey). In order to increase accuracy at one or both of these stages, they must adapt to the environment such that future actions minimize the error experienced after the previous movement. In the laboratory, this process can be observed by analyzing the relationship between previous motor errors and current temporal estimates. Typically, these analyses show that judgments and reproductions are biased toward previous trials,^{1–7} a phenomenon widely applicable to other modalities^{8–11} and known as serial dependencies. The functional role of serial dependencies has been discussed to be perceptual stability (i.e., a way to smooth out noisy percepts^{8,11–15}), and shows the brain's surprising ability to tell and use the reliability of its own temporal measurements.^{16,17} Like all neural signals, sensory estimates are subject to uncertainty and a recalibration process is necessary to minimize the impact of noise and to adapt to external statistics. Indeed, there are theoretical claims^{18,19} and empirical evidence^{12,20,21} that serial dependencies are stronger if the current stimulus is noisy, uncertain or less reliable in its visual features.

Much of the work on serial dependencies in the temporal domain has focused on the sensory component of interval reproduction tasks—that is, how does noise or uncertainty in the perception of an interval affect behavior.^{7,22,23} However, not only the sensory component is subject to noise: The motor component (i.e., the production of precisely timed behavior) comes with its own sources of variability—from noise in movement planning to noise during movement execution.²⁴ Confusion between sensory and motor uncertainty will lead to recalibration of the wrong source and therefore to maladapted behavior. In the present study, we asked whether the brain has separate knowledge of its sensory and of its motor variability.

In two sets of experiments, participants were asked to predict the timing of the last stimulus in a series of three stimuli (akin to a ready-set-go paradigm) either by performing arm movements with a shorter or longer amplitude to push a button (button task), by pressing the space bar on a keyboard (space task),

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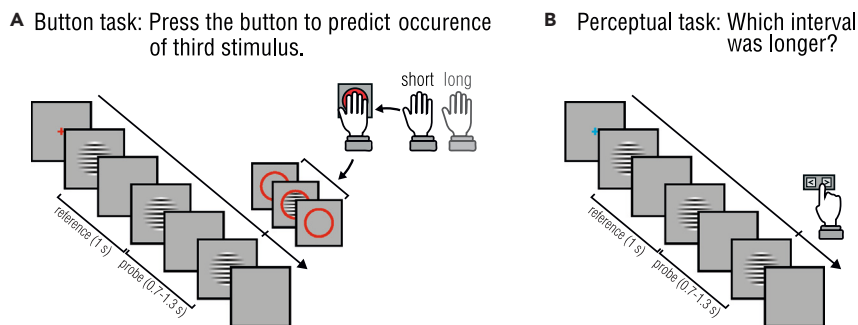


Figure 1. Overview of experimental tasks

Participants ($N = 24$) performed two tasks, a temporal reproduction task (button task, panel A) and a perceptual decision task (perceptual task, panel B) in alternating trials. Visual stimuli consisted of isotropic Gaussian patches. (A) In the button task, participants were asked to predict the occurrence of the third stimulus, while instructing them that the interval between the first and second stimulus was predictive of the occurrence of the third stimulus. The probe interval, however, varied between 0.7 and 1.3 s (in steps of 0.1 s). Upon button press, a red circle was presented on the screen, indicating whether the button press was earlier than, in time with, or later than the third stimulus. We thus created artificial errors with respect to participants' predictions, while the predicted occurrence of the third stimulus should be 1 s in each and every trial (B) In the perceptual task participants were asked to judge which interval of the two intervals (reference or probe) was longer.

or by pressing a foot pedal (foot task). In another task, participants were asked to judge whether the first (ready-set) or second interval (set-go) was longer (perception task). Across trials, we varied the timing of the third stimulus, thus on many trials a discrepancy occurred between the predicted and observed occurrence of the third stimulus. Trials of one version of the button task (short or long amplitude) were interleaved with trials of one of the other tasks (space, foot, or perception task) to test strength of serial dependencies between different effectors and between sensorimotor- and sensory-systems. Movement amplitude was varied to manipulate motor noise or variability: According to Fitt's law the difficulty of a reaching or pointing task is a function of movement amplitude and target size—the larger the movement amplitude, the more difficult the task given a fixed target size.²⁵ The typical finding is that participants compensate for task difficulty (e.g., a larger movement amplitude) by taking more time—to maintain accuracy, participants take more time. In our study, participants could not adopt this compensation strategy because being on time was task critical. We argue that instead task difficulty (movement amplitude) will affect temporal accuracy. The distance manipulation thus allowed us to test the effect of movement variability on the strength of serial dependencies.

We show that serial dependencies act on the sensory- and motor-component separately. While we found serial dependencies between all tasks, effects of motor variance—less reliable previous trials exert weaker serial dependencies—were only transferred between sensorimotor tasks. This finding indicates that (1) in addition to serial dependencies within the sensory component, there are serial dependencies within the motor component that act globally for different motor actions, and that (2) the brain has a robust estimate of the motor noise contribution to the discrepancy between the observed and the reproduced interval.

RESULTS

Increased variability for long versus short arm movements

In a first baseline experiment, we tested whether variability of time critical movements can be reliably manipulated by movement distance. Thirty-six participants were asked to predict the occurrence of the last stimulus in a series of three stimuli by pressing a button with an extended hand movement (button task, Figure 1A). Participants were told that the interval between the first two stimuli was predictive of the interval between the second and third stimulus. The distance between starting position and button varied (short = 40 cm, long = 50 cm), and to only test the effect of movement length on reproduction performance the third stimulus was fully predictable and always occurred after 1 s. Participants' accuracy in predicting the probe interval did not differ between button distance conditions ($M_{\text{short}} = 0.99$ s, 95% CI = 0.01 s; $M_{\text{long}} = 1.00$ s, 95% CI = 0.01 s, $t(35) = 1.16$, $p = 0.254$, $d = 0.19$), meaning that, in general, participants were able to do the task. Further, there was no difference in movement duration (i.e., the time

between the initiation of the movement and the button press; $M_{\text{short}} = 0.71$ s, 95% CI = 0.02 s; $M_{\text{long}} = 0.72$ s, 95% CI = 0.02 s, $t(35) = 0.37$, $p = 0.714$, $d = -0.06$). In order to cover the longer distance, participants must have either adjusted their movement speed or the movement trajectory in order to arrive at the button in time. We have previously shown that compensation strategies are highly individual.³ Finally, precision, measured as the standard deviation, was higher in the short compared to the long button distance condition ($M_{\text{SD short}} = 0.09$ s, 95% CI = 0.01 s, $M_{\text{SD long}} = 0.10$, 95% CI = 0.01 s, $t(35) = 2.07$, $p = 0.046$, $d = 0.35$), meaning that arm movements covering a longer distance are afflicted with more variability than arm movements covering a shorter distance. This pattern is in line with predictions made by Fitt's law (see above).

Motor variability modulates serial dependencies within the motor, but not the visual component

To investigate the effect of movement variability on serial dependencies, we asked 24 participants to perform the button task as described previously, but with the twist that the occurrence of the third stimulus was varied between 0.7 and 1.3 s (Figure 1A). This created artificial errors with respect to participants' occurrence-predictions that drive behavioral adaptation causing the effect of serial dependencies. The button task was performed in the short and long button distance condition in separate sessions. In yet another session, the button task was interleaved with a perceptual interval comparison task (Figure 1B). Alternating these two tasks on a trial-by-trial basis enabled us to analyze both the effect of a perception-task trial (trial n-1) on a current button-task trial (trial n), as well as the effect of a button-task trial (trial n-1) on a current perception-task trial (trial n). This interleaved task-order condition was again performed in the short and long button distance condition in separate sessions. In total, we created three task order conditions (buttonn-1-buttonn, perceptionn-1-buttonn, buttonn-1-perceptionn) that were each performed in the short and long button distance condition. Results are summarized in Figure 2A. We extracted slope and intercept values of linear regressions between the predicted occurrence (button task) or PSE values (perception task) and the previous probe duration for each participant, task order and button distance condition. Slope values indicate the magnitude of serial dependencies. If, for example, the previous probe duration was very short, participants' button press was likely too late. This error-information drives the subsequent button press to be slightly earlier, or, in other words, underestimate the probe duration. The same rationale holds for when the previous trial was very long: Responses were likely too early, thus, in the following trial, participants tend to overestimate the probe duration. Together, these effects are manifested in a positive slope when predictions are plotted against the probe duration of the previous trial (Figure 2A). Note that we discarded all button-task trials in which the probe in the current trial was shorter than 1 s, since those responses likely reflect reaction times instead of predicted occurrences. Details on general performance, statistical analyses and single subject data can be found in the Supporting Information.

The effect of the previously encountered probe duration on current performance is depicted in Figure 2A. Results of Bonferroni-Holm corrected one-tailed t -tests against zero revealed significant serial dependencies in all conditions ($p_s < 0.033$, see Table S1). A two-way repeated measures ANOVA revealed a significant interaction effect between the effects of task order and button distance on slope values (Figure 2B, $F[1.41, 32.32] = 9.22$, $p = 0.002$, $\eta^2_p = 0.29$). Post-hoc t -test showed that the effect of button distance was present only in the buttonn-1-buttonn condition ($p < 0.001$), and that slope values were larger in the buttonn-1-buttonn condition compared to the other task-order conditions ($p_s \leq 0.027$). Two main conclusions can be drawn from these results. First, the differential effect of button distance shows that, if task relevant, the variability of the previous (n-1) trial affects the magnitude of its effect on the current trial: If the previous trial is more variable (or less reliable), its effect on the current trial is less pronounced compared to less variable (or more reliable) previous trials. The absence of the button distance effect in condition perceptionn-1-buttonn indicates that this effect of variability on serial dependencies depends on variability in previous trials, not in the current trial. Second, while we found serial dependencies in each task-order condition, they were strongest when only the button task was performed (buttonn-1-buttonn). This finding reveals that in the temporal prediction task, recalibration takes place at both the sensory measurement and the motor response stage. Stronger serial dependencies within the button task likely reflect higher temporal variability in motor responses compared to visual discrimination.

These conclusions are further supported by the effects of trials further in the past on the current trial (Figures 2D–2F). Statistical analyses on the effect of the pre-previous trial (n-2) revealed a main effect of task order ($F[1.39, 31.87] = 9.78$, $p = 0.002$, $\eta^2_p = 0.30$) and button distance ($F[1, 23] = 7.05$, $p = 0.014$, $\eta^2_p = 0.24$), visually depicted in Figures 2D and 2E. Post-hoc t -test showed that the effect of serial

dependencies is smallest for the effect of an $n-2$ perceptual trial on a current perceptual trial ($p_s < 0.001$). Crucially, whether the previous trial was of sensorimotor or perceptual nature does not affect the strength of $n-2$ serial dependencies between trials of the motor task (Figure 2E, yellow and blue bars, $p = 0.99$). Again, we find that motor-variability of past trials modulates in how far they affect current motor performance. Serial dependencies persisted up to $n-4$ in the buttonn-x-buttonn conditions (Figure S2 and Table S2). As a control analysis, we also looked at the effect of the $n+1$ trial, which should have no effect on the current prediction, reflected in slope values around zero. Indeed, slope values did not differ from zero in any of the tested conditions ($p_s > 0.999$, Figure S2 and Table S1).

Movement amplitude biases the motor and visual component

While slope values larger than zero reflect serial dependencies, differences in intercept values between conditions reflect a general bias of temporal estimates. In the data, this would manifest in either a dilation or compression of time independent of (previous) probe durations. Results of Bonferroni-Holm corrected two-tailed t -tests against one revealed that intercept values did not differ from one in any condition ($p_s > 0.19$, see Table S1). However, analyzing the effect of the previous trial on intercept values revealed a main effect of button distance (Figure 2C, $F [1, 23] = 9.51$, $p = 0.005$, $\eta^2p = 0.29$). This effect persisted for the $n-2$ (Figure 2F, $F [1, 23] = 10.44$, $p = 0.004$, $\eta^2p = 0.31$) and up to the $n-5$ trial (Figure S2 and Table S3). We find a general underestimation of the probe interval in the long compared to the short button distance condition, most pronounced in the perception task (purple bars in Figures 2C and 2F) and in the buttonn-1-buttonn condition (yellow/orange bars).

Motor variability effects generalize across different motor responses

Results of the button-perception experiments suggest that, in addition to serial dependencies within the sensory component, there are separate serial dependencies within the motor component. We have previously shown that adapting one response action to a temporal perturbation generalizes across other response actions, a finding that is special to the temporal domain.³ In a set of three additional experiments, we tested whether there are serial dependencies between time critical motor actions involving different effectors. First, we repeated the button experiment as described previously, including the manipulation of button distance. In a second and third experiment, we asked participants to do the same task as in the button task, but give their response either with their right foot (i.e., pressing a foot pedal) or with a space bar press. The foot and space bar tasks were again interleaved with the button task, leading to five task order conditions (buttonn-1-buttonn, footn-1-buttonn, buttonn-1-footn, spacen-1-buttonn, buttonn-1-spacen) performed in the short and long button distance condition. If, as we previously found, the planning of time critical movements is effector unspecific, we expect serial dependencies to be equally strong across all conditions, and, crucially, we expect a transfer of the button distance effect to the foot and space bar tasks.

Results of Bonferroni-Holm corrected one-tailed t -tests against zero revealed significant serial dependencies in all conditions ($p_s < 0.03$, see Table S4) except in conditions spacen-1-buttonn and buttonn-1-footn ($p_s > 0.1$). A two-way repeated measures ANOVA analyzing the effect of the previous trial on temporal predictions given with different effectors revealed a main effect of task order ($F [2.49, 54.78] = 6.76$, $p = 0.001$, $\eta^2p = 0.24$) and button distance ($F [1, 22] = 8.78$, $p = 0.007$, $\eta^2p = 0.29$), visually depicted in Figures 3A–3C. There was no interaction, meaning that the effect of motor variability caused by the movement distance did not affect different task-order conditions differentially ($F [2.58, 56.75] = 0.55$, $p = 0.625$). Post-hoc t -test showed that the effect of serial dependencies is strongest in the button only condition compared to all other task-order conditions ($p_s < 0.01$). We were able to replicate our findings that motor variability of the previous trial modulates the influence of serial dependencies: If the previous trial was more reliable (i.e., less variable), it is taken more into account than when it was less reliable. This effect seems strongest when performing the same task, but generalizes to other motor responses used in interleaved trials (see Figure 3B).

While there were effects of serial dependencies observable when looking at the effect of the pre-previous ($n-2$) trial, strength of serial dependencies was not modulated by button distance anymore ($F [1, 22] = 0.17$, $p = 0.684$), and there were no differences between conditions ($F [2.31, 50.91] = 1.97$, $p = 0.144$). Serial dependencies persisted up to $n-5$ in the buttonn-x-buttonn conditions (Figure S3 and Table S5). As a control analysis, we again looked at the effect of the $n+1$ trial, which should have no effect on the current prediction. With one exception, slope values did not differ from zero in any of the tested conditions ($p_s > 0.193$,

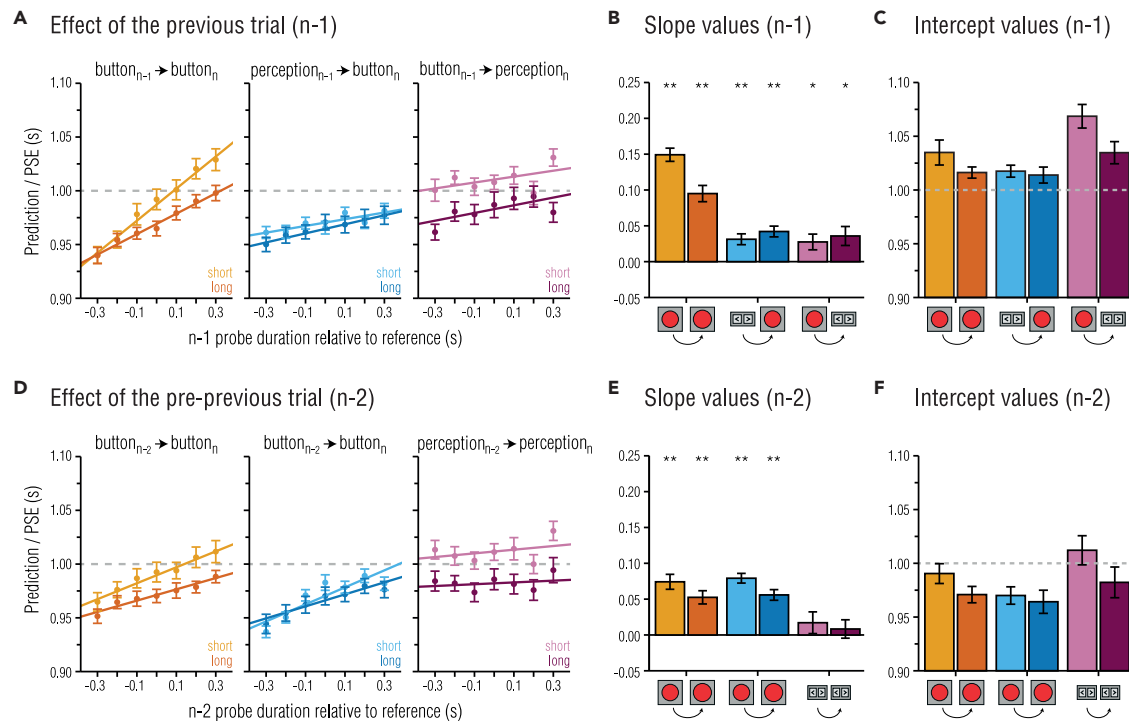


Figure 2. Results for the button-perception experiment

(A) Prediction and comparison performance as a function of the previous probe duration (trial n-1) relative to the reference duration of 1 s in different task order conditions (yellow/orange: button_{n-1}-button_n, blue: perception_{n-1}-button_n, purples: button_{n-1}-perception_n) and button distance conditions (light: short, dark: long). Slope and intercept values were extracted from linear regressions for each participant and condition.

(B) Group-level summary of slope values reflecting serial dependencies of the n-1 trial.

(C) Group-level summary of intercept values reflecting more general biases.

(D) Prediction and comparison performance as a function of the pre-previous probe duration (trial n-2). Note that in task-order conditions with alternating tasks the n-2 trial is of the same task.

Group-level summary of (E) slope and (F) intercept values with regard to the n-2 trial. Error bars represent standard errors. Asterisks reflect results of Bonferroni-Holms corrected t-tests (tested against zero for slope values and against one for intercept values, see also Table S1), **p < 0.001, *p < 0.05.

Figure S3 and Table S4). In the button_n-foot_{n+1} long button distance condition, slope values were significantly larger than zero (p = 0.036).

General intercept bias dependent on movement type

Consistently throughout the different n-back analyses, the temporal predictions of the occurrence of the third stimulus made with foot pedal or space bar presses were underestimated compared to button press responses (Figures 3A and 3D). Indeed, results of Bonferroni-Holm corrected two-tailed t-tests against one revealed significantly lower intercept values (i.e., underestimation) in condition button_n-1-space_n (ps < 0.04, see Table S4). A two-way repeated measures ANOVA analyzing differences in intercept values revealed a main effect of task order condition for n-1 (Figure 3C, F[2.3, 51.6] = 17.10, p < 0.001, η²p = 0.44), n-2 (Figure 3F, F[2.4, 52.6] = 17.73, p < 0.001, η²p = 0.45), and up to the n-5 trial (Figure S3 and Table S6). Post-hoc tests confirm the previously described bias, such that space bar and foot pedal responses were systematically given earlier compared to button responses (striped versus solid bars in Figures 3C and 3F, ps < 0.001).

DISCUSSION

Precisely timed interactions with the environment require measuring and predicting the duration of external events as well as predicting the temporal characteristics of one's own motor actions. Both the measurement and the movement production stage contain neural variability that the brain must overcome. In the current study, we asked whether the brain tracks and recalibrates sensory and motor uncertainty separately. We manipulated sensory uncertainty by presenting the to-be-predicted target at varying time points

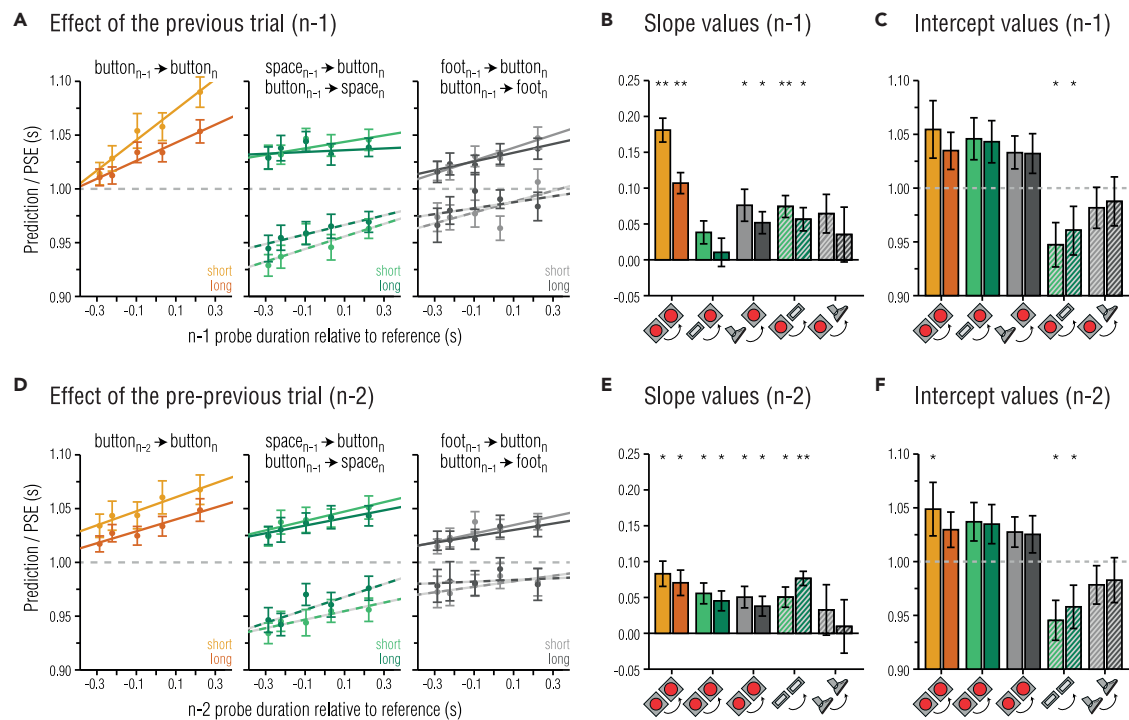


Figure 3. Results for the second set of experiments

Participants ($N = 23$) performed the same temporal reproduction task as the button task (Figure 1A) giving their responses predicting the occurrence of the third stimulus in different ways. Response options were the button (button task), pressing the space bar on the keyboard (space task), or pressing a foot pedal (foot task). (A) Prediction performance as a function of the previous probe duration (trial n-1) relative to the reference duration of 1 s in different task order conditions (yellow/orange: buttonn-1-buttonn, green: footn-1-buttonn, green-striped: buttonn-1-footn, gray: spacen-1-buttonn, gray-striped: buttonn-1-spacen) and button distance conditions (light: short, dark: long). Slope and intercept values were extracted from linear regressions for each participant and condition.

(B) Group-level summary of slope values reflecting serial dependencies of the n-1 trial.

(C) Group-level summary of intercept values reflecting more general biases. (D) Prediction and comparison performance as a function of the pre-previous probe duration (trial n-2). Note that in task-order conditions with alternating tasks the n-2 trial is of the same task. Group-level summary of (E) slope and (F) intercept values with regard to the n-2 trial. Error bars represent standard errors. Asterisks reflect results of Bonferroni-Holms corrected t-tests (tested against zero for slope values and against one for intercept values, see also Table S4), $**p < 0.001$, $*p < 0.05$.

and in conflict with the informative interval. This led to an artificial discrepancy between the predicted and observed target occurrence. Motor uncertainty was manipulated by varying the amplitude of the response movement. The strength of recalibration in the button task depended on the movement variability: Serial dependencies were stronger the more reliable the previous trial was. The sensorimotor system recalibrates sensory and motor components separately by taking into account their respective reliabilities. The effect of movement variability was only transferred between sensorimotor tasks, extending the effect of temporal context on interval timing,^{26,27} and shedding light on the locus of serial dependencies.^{14,20}

The magnitudes of slope values revealed two critical implications for the relationship between motor- and sensory-time. First, we observed serial dependencies between all task order conditions, that is, between trials of a sensorimotor task involving different effectors and between trials of a perceptual judgment and sensorimotor task. Crucially, they were more pronounced if the current and previous trial both required time critical motor actions than when the previous or current trial was a perceptual judgment task. However, stronger serial dependencies within sensorimotor tasks cannot be interpreted unambiguously as evidence for a dominance in motor recalibration. Sensory time estimates require a comparison of temporal intervals while the motor production consists in a judgment of an absolute point in time. Our findings could hint at two sources of temporal information which exhibit distinct serial dependencies. Stronger serial dependencies in sensorimotor tasks could be explained by the involvement of two sources of temporal information: the sensory- and motor-component. While there is a debate of the exact locus of serial dependencies (serial dependencies act directly on perception^{17,27–29} versus they affect post-perceptual stages^{30,31–33}),

our findings speak to the existence of both: One that acts early on the sensory level, and one that acts later on other cognitive processes (e.g., the planning of time critical movements). Observed dominance in one of them depends on the exact nature and goal of the task.

Second, variance associated with the time critical movement modulated the strength of serial dependencies: If previous trials were less reliable (associated with a higher variance), they were taken less into account in a current trial compared to more reliable previous trials. However, this observation held only within motor tasks, the effect of variance on strength of serial dependencies was not observed for the perceptual task or if the previous trial was a perceptual trial. Thus, the effect of variance may only occur later during the motor planning phase and affect serial dependencies within the motor component only. The effect of variance generalized to other effectors and movement-types, suggesting that either the temporal estimate is a global ingredient to the motor plan, or that serial dependencies act on early, effector and movement unspecific planning stages upstream of the specific effector control. Previous research has demonstrated that subjects indeed have knowledge of their motor variability and can account for that variability in novel, complex tasks in order to optimize their behavior.^{28,29}

Recalibration of a global movement plan could also be responsible for the observed bias in sessions in which subjects had to switch between response movements. In all sessions in which a movement with a large trajectory (here, a button press) was followed by a movement with a small trajectory (e.g., a space bar press), temporal intervals were systematically underestimated. An underestimation would be the logical consequence if the previous trial recalibrated a global time to start signal. The generalization across effectors would be a maladaptive strategy in real life if the concrete movement parameters of the effectors are ignored by the system. Thus, the observed bias may be caused by the artificial laboratory task. In real life, specific effectors serve specific tasks, such that recalibration will likely not be carried over to different effectors.

When the button task was intermingled with trials of the perceptual task, motor variance affected the intercept of perceptual serial dependencies. When the previous trial required a long movement amplitude, lower intercepts were found than when the amplitude was smaller. Longer movements require an update of movement planning (e.g., a temporal backward shift of the start signal) in order to meet the temporal requirements. If this movement planning update is transferred to perception, temporal underestimation, as indicated by lower intercepts, may be the consequence. An alternative explanation pinpoints the effect to a different origin. Previous studies have shown effects of motor actions on the perception or estimation of time in general. For example, temporal judgments are attracted to concurrent short or long lasting movements,³¹ slow movements due to environmental perturbations compress concurrent temporal judgments,³² and being allowed to freely move one hand during a temporal judgment task improves precision.³³ In this case, movement amplitude could have a systematic effect on perceptual judgments, reflected in intercept differences, and not modulate trial-by-trial calibration, reflected in the absence of slope differences.

Electrophysiological work revealed that temporal intervals are measured prospectively in relation to the desired motor plan to reproduce that interval.^{2,16} Our data suggest that the recalibrated signal is a global movement planning impulse. Consistent with our findings, time measurements in a temporal discrimination task cannot access this signal. This interpretation is in line with results showing that whether or not sensorimotor recalibration occurs likely depends on what the temporal estimate is used for (e.g., a discrimination judgment or a time critical motor action) and how different task contexts are.²³ Within the time perception literature, it is a popular view that motor actions and the perception of time are closely related¹⁸—if not generated within motor areas directly^{16,34–39}—or recalibrate each other.^{18,40}

In conclusion, our data reveal that the brain weighs the contributions of sensory and motor uncertainty separately in order to calibrate interval timing. Recalibration of interval timing most likely occurs upstream of specific motor control, adjusting a signal that determines movement start. The temporal flexibility needed to successfully interact and explore our environments is reflected in the way temporal information is processed and used to generate behavior.

MATERIALS AND METHODS

Participants

For the baseline experiment, 36 participants were recruited (26 female, age range: 19–44 years, $M = 26.25$ years, all right-handed). In the button-perception experiments data of 26 participants (18

female, age range: 18–33 years, $M = 23.16$ years, all right-handed) was obtained. The sample of the second set of experiments (button-foot-space bar) consisted of 23 participants (19 female, age range: 19–32 years, $M = 23.56$ years, all right-handed). Five participants took part in both the button-perception and button-foot-space bar studies. All participants had normal or corrected-to-normal vision and gave informed consent prior to participation. All experiments were approved by the local ethics committee of the psychological department of the Heinrich-Heine-University Düsseldorf (identification number: 757184).

Stimuli and tasks

Participants were asked to perform a temporal target prediction task using different effectors (arm, hand, foot) or a perceptual interval comparison task. Visual appearance and temporal structure were almost identical in all tasks: In each trial participants first saw a centrally positioned fixation cross on a gray background for 1 s, fixation cross color informed participants which task to perform. Next, a Gabor patch (horizontal orientation, 400 x 400 pixels, contrast = 100, spatial frequency = 0.05) was presented centrally for 50 ms (stimulus 1). One second later a second Gabor patch was flashed for 50 ms (stimulus 2). The interval between stimulus 1 and 2 defined the reference duration of 1 s. A third Gabor patch (stimulus 3) was presented after 1 s (baseline experiment) or with a varying delay (all other experiments) with respect to the onset of stimulus 2. (The interval between stimulus 2 and 3 defined the duration of the probe interval. All experiments were built in MATLAB (version 2020b, Mathworks, Natick, MA) using the Psychophysics Toolbox Version 3.^{41–43}

Button task

In the button task, participants were asked to press a buzzer-like button when they thought the third stimulus would occur (Figure 1A). Participants were instructed that the reference interval was predictive of the probe interval. The button was placed at one of two positions on the left side of a keyboard. In the short button distance condition, the distance between keyboard (space bar) and button was 40 cm and 59 cm toward the monitor. In the long button distance the distance between keyboard (space bar) and button was 50 cm and 67 cm toward the monitor. A new trial started with pressing the space bar. To record movement onset, participants were instructed to hold down the space bar until the movement toward the button was initiated. They were further instructed to perform one smooth movement and not, for example, hover above the button until giving their response. A red circle appeared as visual feedback on the screen simultaneously to the button press (i.e., if they pressed the button too early the red circle appeared before the third stimulus, if they pressed too late the circle appeared after the third stimulus, or they appeared simultaneously, see Figure 1A).

In the baseline experiment, the probe always occurred after 1 s, thus, the reference duration was fully predictive. The baseline experiment was used to test the effect of movement length (short vs. long button distance condition) on precision of temporal predictions. Button distance conditions were tested in separate sessions.

In all other button tasks, the probe duration was varied (0.7, 0.8, 0.9, 1, 1.1, 1.2 or 1.3 s in the button-perception experiments; 0.85, 0.9, 1, 1.1 or 1.25 s in the button-foot-space experiments) to create an artificial error with respect to participants' predictions. That is, participants' predictions were more often and more severely too early (third stimulus occurred after 1 s) or too late (third stimulus occurred before 1 s). Button distance conditions were again tested in separate sessions.

Perceptual comparison task

In the perceptual comparison task, participants were asked to indicate which of the two intervals between three Gabor patches was longer by either pressing the right (probe longer) or left (reference longer) arrow key on the keyboard. A new trial started automatically after a response was given.

Space task

In the space task, instead of pressing the button to predict the occurrence of the third stimulus they were asked to press the space bar. A trial was initiated with a single spacebar press, the space bar did not have to be held down. All other details, including the variable probe duration, were identical to the button task.

Foot task

In the foot task, instead of pressing the button to predict the occurrence of the third stimulus they were asked to press a foot pedal (Bewinner B09ZR7FV3R), placed 22cm in front of them on the ground. A trial was initiated with a single foot pedal press. All other details, including the variable probe duration, were identical to the button task.

Procedure

In the baseline experiment participants performed 31 trials of the button task in each button distance condition. The order of button distance conditions was counterbalanced.

In the first set of experiments (button-perception), participants performed the button task (button_{n-1}-button_n) as well as two different task order conditions in which trials from different tasks were interleaved (perception_{n-1}-button_n, button_{n-1}-perception_n). Note that data from the two interleaved conditions can be obtained in one session. All task-order conditions were performed in the short and long button distance in separate sessions. The order of sessions was randomized. Each session consisted of 140 trials in total (10 trials per probe duration and task), participants completed nine sessions per distance condition (three sessions button-button, six sessions button-perception), resulting in a total of 18 sessions.

For the second set of experiments (button-foot-space), participants performed the button task (button_{n-1}-button_n) as well as four different task order conditions in which trials from different tasks were interleaved (foot_{n-1}-button_n, space_{n-1}-button_n, button_{n-1}-foot_n, button_{n-1}-space_n). Note again that data from two conditions can be obtained in one session. All task-order conditions were performed in the short and long button distance in separate sessions. The order of sessions was randomized. Participants completed one session with 376 trials of each task order and button distance condition, resulting in a total of six sessions.

Data analysis

All statistical analyses were conducted in R version 4.0.3.⁴⁴ For prediction trials (button, space or foot task), we removed trials with predicted occurrences of 0.5 or 1.5 times the probe duration (note that these cut-offs were more liberal than removing trials shorter/longer than the average $\pm 2*SD$, which produced the same qualitative results). We additionally removed the subsequent trial to avoid distortions of n-1 effects. This affected 18.1% ($SE = 1.5\%$) of all trials in the first set of experiments, and 44.4% ($SE = 0.9\%$) of all trials in the second set of experiments. Two participants were removed from the analysis of the button-perception experiments because of general poor performance (i.e., comparison performance at chance level for all stimulus intensities and more than 50% of predictions trials were rejected).

Different parameters of the baseline button task (movement duration, measured as the time point of the release of the space bar until the button press; precision measured as the standard deviation of the predictions; and accuracy measured as the target predictions) were compared for the short and long button distance condition by means of paired sample t-tests.

For all other experiments, we extracted slope and intercept values of linear regressions between the predicted occurrence (button/foot/space task) or PSE values (perception task) and the previous probe duration for each participant, task order and button distance condition. Slope values indicate the magnitude of serial dependencies. We discarded all button/foot/space-task trials in which the probe in the current trial was shorter than 1 s, since those responses likely reflect reaction times instead of predicted occurrences. Slope values of each task order and button distance condition were first tested against zero by means of t-test (Bonferroni-corrected for multiple testing), based on the rationale that slope values greater than zero reflect serial dependencies. Likewise, we tested intercept values against one, since 1 s predictions reflect accurate performance. Next, slope and intercept values were analyzed by means of repeated measures ANOVAs, testing the factors button distance and task order. We repeated these analyses for slope and PSE values based on n-2, n-3, n-4, and n-5 values.

We did not detrend or normalize slope and PSE values as is sometimes suggested to control for central tendency effects or probability matching when testing serial dependencies. The design of our experiments eliminates the influence of central tendency effects, however. The prediction should, in principle, be 1 s in each and every prediction-trial. Only the artificial error, generated by the varying occurrence of the third stimulus, was manipulated. Serial dependency effects thus cannot result from central tendency effects.

Limitations of the study

The study presented here has some limitations that open possibilities for future research. The scenario devised in our study is specific, thus limiting generalizability of results for all settings and populations. We did not collect the socioeconomic status, ancestry, or ethnicity of the test subjects. We cannot make any statement as to whether there were differences in the behavior of the test subjects due to these factors. In a follow-up study, it would be important to collect and correlate these criteria accordingly.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at <https://doi.org/10.1016/j.isci.2023.107204>.

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AUTHOR CONTRIBUTIONS

E.Z. designed research, N.S. and C.F. performed research, N.S. and C.F. analyzed data, N.S., C.F. and E.Z. wrote the paper.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Data and code to reproduce analyses have been deposited in OSF available at https://osf.io/nx5g6/ .	This paper	Open Science Framework: https://osf.io/nx5g6/ .
Software and algorithms		
R version 4.0.3	R Core Team	https://www.r-project.org/
MATLAB 2020b, Psychophysics Toolbox Version 3	Mathworks	http://psychtoolbox.org/download

RESOURCE AVAILABILITY

Lead contact

Lead contact: Further information and requests should be directed to and will be fulfilled by the lead contact, Nadine Schlichting (nadine.schlichting@hhu.de). For communication during the production process (copyediting and proofs) please contact Clara Fritz (clara.fritz@hhu.de).

Materials availability

This study did not generate new unique reagents.

Data and code availability

Data and code to reproduce analyses have been deposited in OSF available at <https://osf.io/nx5g6/>. All original code has been deposited and is publicly available as of the date of publication. DOIs are listed in the [key resources table](#). Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

All Experiments were approved by the local ethics committee of the Faculty of Mathematics and Natural Sciences of Heinrich Heine University, Düsseldorf (identification number: 757184). Experiments were in accordance with the Declaration of Helsinki and informed consent was obtained from all participants.

36 (26 female, age range: 19-44 years, $M = 26.25$ years, all right-handed) participants took part in the baseline experiment. In the button-perception experiments the sample consisted of 26 participants (18 female, age range: 18-33 years, $M = 23.16$ years, all right-handed). For the second set of experiments (button-foot-spacebar) we used data of 23 participants (19 female, age range: 19 - 32 years, $M = 23.56$ years, all right-handed). Five participants took part in both the button-perception and button-foot-spacebar studies. We cannot report the race, ancestry, ethnicity or socioeconomic status of subjects since we did not include this query in the demographic data.

METHOD DETAILS

We described Stimuli and Tasks in detail in our Materials and Method section in the main text. Generally, participants task was to predict temporal targets by either pressing a red button, a foot pedal or a keyboard button. Participants were seated in front of a monitor. They first saw a red (Button, Space and Foot task) or blue (Perceptual comparison task) fixation cross on a grey background programed in Psychophysics Toolbox in MATLAB 2020b. To start a new trial the spacebar had to be pressed. Next, the first stimulus (Gabor Patch) was presented for 50 ms in the middle of the screen, followed after one second by another Gabor stimulus presented for 50 ms as well. A third Gabor patch was presented with a varying delay between 0.7 to 1.3 s (probe interval). In the button task experiment participants were asked to press a red button when they were feeling the third stimulus to occur. In the short button distance condition, the distance between keyboard (spacebar) and button was 40 cm and 59 cm towards the monitor whereas in the long button distance keyboard (spacebar) and button were 50 cm apart. In the space task participants were

asked to use the spacebar for giving a response and in the foot task a foot pedal placed 22 cm in front of them was used. When pressing either the foot pedal or the buttons visual feedback appeared in form of a red circle on the screen. If the press occurred too early the red circle appeared before the third stimulus, if the press was too late the circle appeared after the third stimulus, or they appeared simultaneously. In the baseline experiment the probe interval was fixed to one second, thus making the reference fully predictable.

In the perceptual comparison task participants had to indicate which of two intervals between three Gabor patches (again being shown for one second between the first and the second and at varying times between the second and third) appeared to be longer. Answers could be given by either pressing the right (probe appeared to be longer) or left (reference appeared to be longer) arrow key.

QUANTIFICATION AND STATISTICAL ANALYSIS

We conducted statistical analyses in R version 4.0.3.⁴⁶ We initially removed two participants from the button-perception experiment due to overall poor performance (i.e., comparison performance at chance level for all stimulus intensities and more than 50% of predictions trials were rejected). During preprocessing we excluded certain trials. For prediction trials of the button, space and foot tasks trials with predicted occurrences of 0.5 or 1.5 times the probe duration was removed including subsequent trials to avoid influences on n-1 effects. N represents the current trial. We excluded all button/foot/space-task trials in which the probe in the current trial was shorter than one second, as we assumed these trials rather reflect reaction times instead of predicted occurrences.

For the baseline button task, we compared differences between the short and long button distance by means of paired sample t-tests. For all other experiments we performed linear regression between PSE values (perception task) or the predicted occurrence (button/foot/space task) and the previous probe duration for each participant, task order and button distance condition. Slope values of the linear regression were used as a measure of magnitude of serial dependencies and we compared means against zero individually per subject. We Bonferroni-corrected for multiple testing. Intercept values were tested against one, since a prediction of one second reflected accurate performance. Afterwards we analyzed slope and intercept values with a repeated measures ANOVA with button distance and task order as factors. Same analysis was used for slope and PSE values based on n-2, n-3, n-4, and n-5 values.

Further information concerning statistical analysis can be found in the Results section in the main text and in the figure legends of [Figures 2](#) and [3](#). In the graphs error bars represent standard errors. Asterisks reflect results of Bonferroni-Holms corrected t-tests (see also [Table S4](#)).