J Neurophysiol 122: 2259–2271, 2019.
First published October 2, 2019; doi:10.1152/jn.00017.2019.

RESEARCH ARTICLE | *Society for the Neural Control of Movement*

Effects of visuomotor delays on the control of movement and on perceptual localization in the presence and absence of visual targets

Guy Avraham,[1,2,3,4]* Erez Sulimani,[1,2]* Ferdinando A. Mussa-Ivaldi,[5,6] and Ilana Nisky[1,2]
[1]*Department of Biomedical Engineering, Ben-Gurion University of the Negev, Be'er-Sheva, Israel;* [2]*Zlotowski Center for Neuroscience, Ben-Gurion University of the Negev, Be'er-Sheva, Israel;* [3]*Department of Psychology, University of California, Berkeley, Berkeley, California;* [4]*Helen Wills Neuroscience Institute, University of California, Berkeley, California;* [5]*Shirley Ryan AbilityLab, Chicago, Illinois; and* [6]*Department of Biomedical Engineering, Northwestern University, Evanston, Illinois*

Submitted 11 January 2019; accepted in final form 28 September 2019

Avraham G, Sulimani E, Mussa-Ivaldi FA, Nisky I. Effects of visuomotor delays on the control of movement and on perceptual localization in the presence and absence of visual targets. *J Neurophysiol* 122: 2259–2271, 2019. First published October 2, 2019; doi:10.1152/jn.00017.2019.—The sensory system constantly deals with delayed feedback. Recent studies showed that playing a virtual game of pong with delayed feedback caused hypermetric reaching movements. We investigated whether this effect is associated with a perceptual bias. In addition, we examined the importance of the target in causing hypermetric movements. In a first experiment, participants played a delayed pong game and blindly reached to presented targets. Following each reaching movement, they assessed the position of the invisible cursor. We found that participants performed hypermetric movements but reported that the invisible cursor reached the target, suggesting that they were unaware of the hypermetria and that their perception was biased toward the target rather than toward their hand position. In a second experiment, we removed the visual target, and strikingly, the hypermetria vanished. Moreover, participants reported that the invisible cursor was located with their hand. Taking these results together, we conclude that the adaptation to the visuomotor delay during the pong game selectively affected the execution of goal directed movements, resulting in hypermetria and perceptual bias when movements are directed toward visual targets but not when such targets are absent.

NEW & NOTEWORTHY Recent studies showed that adaptation to visuomotor delays causes hypermetric movements in the absence of visual feedback, suggesting that visuomotor delay is represented using current state information. We report that this adaptation also affects perception. Importantly, both the motor and perceptual effects are selective to the representations that are used in the execution of goal-directed movements toward visual targets.

action; delay; perception; proprioceptive space; reaching

INTRODUCTION

When we interact with the environment, e.g., playing a game of tennis, our sensory system receives inputs from different modalities. We feel the stretch of our arm muscles as they control the racket movement; as the racket hits the ball, we see the collision and hear its thud, and a haptic sensation is delivered to the hand. These different sensory inputs originate from a single event, but they arrive at different times to the brain (Murray and Wallace 2012), and active reconstruction must remove the time differences to perceive these inputs as a single event (Rohde and Ernst 2016; Vroomen and Keetels 2010). The saliency of such a process can be understood by examining how breaking the simultaneity between sensory stimuli that are derived from a common cause would affect our motor behavior and our perception (Fujisaki et al. 2004; Vogels 2004; Vroomen and Keetels 2010).

Previous studies investigated the dissociation between sensory processing for perception and for action. A dissociation between vision for perception and vision for action was suggested in grasping (Aglioti et al. 1995; Ganel and Goodale 2003) and lifting (Flanagan and Beltzner 2000) of objects. Others showed that during interaction with elastic objects with delayed force feedback, there is a dissociation between the estimation of stiffness for perception and for grip force adjustment (Leib et al. 2015, 2018). However, alternative explanations to the apparent differences between sensory processing for perception and action exist that highlight the importance of tight matching between the tasks that are used to assess perception and action (Brenner and Smeets 1996; de Grave et al. 2005). Furthermore, several studies reported that motor adaptation drives changes in proprioceptive perception and suggested that perception and action are coupled (Bernardi et al. 2013; Cressman and Henriques 2009; Mattar et al. 2013; Salomonczyk et al. 2012).

Delayed sensory feedback can affect both perception and action. Introducing a delay between movement and force feedback during interaction with virtual objects biases the perception of their mechanical impedance (Di Luca et al. 2011; Kuling et al. 2015; Leib et al. 2015, 2016; Nisky et al. 2008, 2010; Pressman et al. 2007). Also, the sensorimotor system can adapt to delayed visual or force feedback by modifying kinematic and dynamic properties of the movements (Avraham et al. 2017a, 2017b, 2018; Botzer and Karniel 2013; Levy et al. 2010; Miall and Jackson 2006; Witney et al. 1999). Recently, we used a virtual game of pong to investigate adaptation to a delayed visual feedback, in which the paddle movement is delayed with respect to the movement of the hand. We chose

* G. Avraham and E. Sulimani contributed equally to this work.
Address for reprint requests and other correspondence: I. Nisky, Dept. of Biomedical Engineering, Ben-Gurion Univ. of the Negev, Be'er-Sheva, Israel (e-mail: nisky@bgu.ac.il).

the pong game because it is an ecological interception task in which participants receive both visual and haptic feedback at the time of the paddle-ball interception (Avraham et al. 2017a; Farshchian et al. 2018). To evaluate how the sensorimotor system represents the delay, we examined the transfer of adaptation to reaching and tracking tasks and found that participants' movements become hypermetric due to the experience with the delay. These results suggest that we use current state variables (Avraham et al. 2017a) and modified inertia estimation (Farshchian et al. 2018) to represent the delay. Although this representation has a clear influence on action, it is currently unknown whether it also affects perception.

The first question we set out to address in this study is whether the hypermetria observed following adaptation to delayed visual feedback is a result of an altered representation of space that also affects perception. Participants played a game of delayed pong and performed a subsequent transfer task of blind reaching movements toward a target. After they completed the reaching, the target disappeared and they were presented with a psychophysical forced-choice location assessment task. We entertained two possible hypotheses: *1*) the effects of the delay are limited to action and do not affect perception, resulting in colocation of the reported imagined cursor with the hand of the participants, or *2*) the delay affects both perception and action, resulting in a perceptual bias in the location assessment task, i.e., a mismatch between the actual location of the hand and the reports regarding the location of the cursor. The results were consistent with the latter hypothesis.

In all the previous pong game studies, the movements during the blind transfer tasks were carried out toward a stationary or a moving visual target (Avraham et al. 2017a; Farshchian et al. 2018). In our new experiment, even though the target was removed before the perceptual task, the remembered target location could bias the reports of the participants. Therefore, in a second experiment, we removed the visual target from the blind reaching task and asked the participants to perform movements toward a location freely chosen within the workspace. This design aimed to minimize a possible target recall effect on the perceptual localization task. We expected that even without the presence of the target, the distributions of the participants' reaching amplitudes after playing the pong game with delay would have a larger mean than those following pong without delay. Surprisingly, we found that even though the participants' movements during the delayed pong game were hypermetric, the transfer of hypermetria to the blind reach movements vanished, together with the perceptual bias. Thus they were both contingent on the existence of a visible target.

METHODS

Notation

We use lowercase letters for scalars, lowercase bold letters for vectors, and uppercase bold letters for matrices. $\boldsymbol{x}$ is the Cartesian space position vector, with x and y the position coordinates for the right-left and forward-backward dimensions, respectively. $\boldsymbol{f}$ is the force vector, with f_x and f_y force coordinates. N indicates the number of participants in a group.

Participants

Forty healthy right-handed volunteers (aged 19–29 yr, 21 women) participated in two experiments: 10 participated in *Experiment 1* and 30 participated in *Experiment 2*. *Experiment 1* included one group, GT100 (group target, 100-ms delay). The participants of *Experiment 2* were divided into two groups: 20 participants in GNT100 (group no target, 100-ms delay) and 10 participants in GNT200 (group no target, 200-ms delay). No statistical methods were used to predetermine sample sizes, but the sample sizes that we used were similar to the sample sizes reported in a previous study (Avraham et al. 2017a), and the effects in our study were expected to be of similar size. All participants did the experiment after signing the informed consent form, and both the protocol and the form were approved by the Ben-Gurion University of the Negev Human Subjects Research Committee (Beer-Sheva, Israel).

Experimental Setup

The experiments were administered in a virtual reality environment in which seated participants controlled the handle of a robotic device, a 6 degrees-of-freedom Phantom Premium 1.5 haptic device (Geomagic), with their right hand (Fig. 1*A*). A projector that was suspended from the ceiling projected the experimental scene onto a horizontal white screen that was placed ~10 cm above the participant's hand and ~10 cm below the chin. The hand was hidden from sight by the screen, and a dark sheet covered the upper body of the participants to remove all visual cues about the arm configuration. The participant's arm was placed on an armrest that was connected to a pressurized air system and placed on a smooth surface; this allowed them to move their arm in a horizontal (transverse) plane with minimal friction and without effort against gravity. When visual feedback of the hand location was provided, the movement of the device was mapped to the movement of a cursor. Because of the refresh rate of the display (100 Hz), the cursor was always delayed with respect to the movement of the hand. However, during baseline (no delay condition), this delay did not exceed 10 ms, and thus the cursor movement was considered consistent with the hand movement. The experimentally manipulated delay in the delay condition (100/200-ms delay) was added on top of this video delay.

Tasks

Each experiment consisted of three tasks: a pong game task, a "blind" reaching task, and a "blind" reporting task. During both the reaching and reporting tasks, no visual feedback about the hand location was provided.

Pong game. In the pong game, participants observed the scene illustrated in Fig. 1*B*. The rectangle delineated by the dark gray walls (right-left × forward-backward dimensions: 26 cm × 18 cm) indicates the pong arena. The black horizontal bar (2.4 cm × 0.5 cm) marks the location of the paddle and corresponds to the hand location. Each experiment included two types of pong sessions: Pong No Delay and Pong Delay. During Pong No Delay, the paddle moved synchronously with the hand. During Pong Delay, the paddle movement was delayed with respect to the hand movement. To apply the delay, we saved the location of the hand in a buffer that was updated at the same rate as the control loop (1,000 Hz) and displayed the paddle at the location of the hand τ seconds before it. τ was set to either 0, 100, or 200 ms depending on the protocol and the stage within the experiment. The duration of each Pong trial was 60 s. Information about the elapsed time from the beginning of the trial was provided to the participants by a magenta-colored timer bar. Feedback on performance in each trial was also provided using a blue hit bar that incremented in proportion of the recorded paddle-ball hits from trial initiation. The total number of hits required to fill the bar completely was set to 60 in all Pong trials.

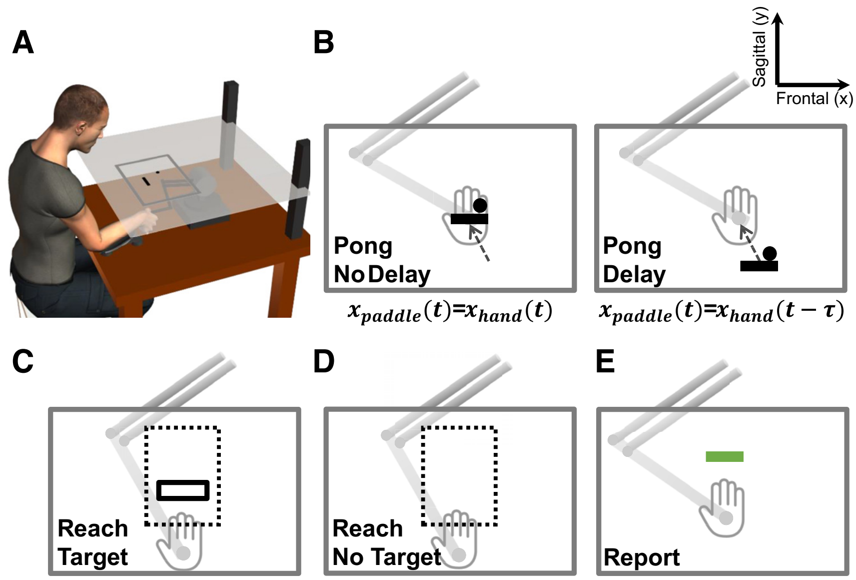

Fig. 1. Experimental setup and tasks. *A*: an illustration of the experimental setup: participants held the handle of a robotic arm with their right hand and observed the experimental scene on an opaque screen. *B*: during the pong game, participants controlled the movement of the paddle (black bar) in two dimensions (*inset*), attempting to hit a moving ball (black circle) toward the upper wall of the pong arena (delineated by solid gray borders). Paddle movement was either concurrent (*left*; No Delay) or delayed (*right*; Delay) with respect to the hand movement (black arrow indicates paddle movement direction). $\boldsymbol{x}_{hand}(t)$, hand movement; $\boldsymbol{x}_{paddle}(t)$, paddle movement; τ, delay. *C* and *D*: during blind reaching tasks, participants were not provided with visual feedback and were asked to imagine that they control a cursor. When they were presented with a target (*C*; open black rectangle), they were requested to reach to it and to place the imagined cursor at the target. When the target was not presented (*D*), they were requested to reach to a desired location in front of the starting point. In both conditions (*C* and *D*), movement end points were restricted within an invisible allowed area in the workspace (designated by dotted black frame). *E*: during the reporting task, the participant's hand was held at the reaching stop location by the robotic device, and they were asked to report whether a comparison marker (green bar) was closer or farther than the imagined cursor with respect to their body.

The ball was not displayed between trials. The initiation of a trial was associated with the appearance of the ball in the arena. We did not display the paddle between trials, and participants were instructed to initiate a trial by moving the handle of the robotic device backward (toward their body). When the hand crossed a distance of 2 cm from the bottom (proximal) border of the arena, the trial was initiated. The initial velocity of the ball in the first Pong trial was 20 cm/s, and in every other Pong trial, it was the same as the velocity at the end of the previous trial.

The participants were instructed to bounce the ball toward the upper (distal) wall as many times as possible. When the ball hit a wall, its movement direction was changed to the reflected arrival direction, keeping the same absolute velocity (consistent with the laws of elastic collision). To prevent the participants from adopting a strategy of repeatable movements, the reflection of the upper wall (but not the other walls) included a jitter. This jitter effectively created the variability in ball paths that could be a result of playing against an opponent instead of against the wall. The jitter (j) was added to the horizontal component of the ball velocity before the collision with the upper wall ($\dot{x}_b^{preUB}$) such that

$$\dot{x}_b^{postUB} = \dot{x}_b^{preUB} + j, \quad (1)$$

where $\dot{x}_b^{postUB}$ is the horizontal component of the ball's velocity following the collision with the upper wall. j was set as $j = -\dot{y}_b^{preUB} \cdot \tan(\alpha_j)$, where $\dot{y}_b^{preUB}$ is the vertical component of the ball's velocity before the collision with the upper wall and $\alpha_j \sim N(0, 0.05\pi)$.

The velocity of the ball after a paddle hit ($\dot{x}_b^{postP}$) was determined by the velocity of the ball before the hit ($\dot{x}_b^{preP}$) and the velocity of the paddle ($\dot{x}_p$) at the time of a hit as

$$\dot{x}_b^{postP} = 0.7 \cdot \dot{x}_b^{preP} + 0.42 \cdot \dot{x}_p \quad (2)$$

$$\dot{y}_b^{postP} = -0.7 \cdot \dot{y}_b^{preP} + 0.42 \cdot \dot{y}_p. \quad (3)$$

For the forward-backward dimension, we let a hit occur only when the paddle was moving forward and the ball was moving backward, and after a hit occurred, the ball's movement direction was always reversed and it moved toward the upper wall. In all other cases, the ball passed through the paddle as if they were moving over different planes. The choice of the absolute values of the coefficients of $\dot{y}_b^{preP}$ and $\dot{y}_p$ in *Eqs. 2* and *3* was made to ensure that the participants did not adopt a strategy of coping with the delay by slowing down or even stopping (Avraham et al. 2017b; Ferrell 1965). With these values, to maintain the ball speed after the hit as it was before the hit, or to make it faster, $\dot{y}_p$ needed to be at least $\left|\sim 0.71 \cdot \dot{y}_b^{preP}\right|$. The instructions to the participants were that they could hit the ball only when it was moving backward and their paddle was moving forward, and that they should move the paddle fast enough at the moment of a hit; otherwise, the ball would slow down and reduce the number of opportunities to hit it.

Following a hit, a haptic pulse was delivered by the device simultaneously with the displayed collision, emulating a physical collision. The pulse $\boldsymbol{f}^{postP}$ was applied according to

$$\boldsymbol{f}^{postP} = \frac{m_b \cdot \left(\dot{\boldsymbol{x}}_b^{postP} - \dot{\boldsymbol{x}}_b^{preP}\right)}{\Delta t}, \quad (4)$$

where $m_b = 0.21$ kg is the ball's mass and $\Delta t = 0.025$ s is the duration of the collision. To prevent instability due to an abrupt pulse, the haptic pulse was applied for 0.05 s, in which it gradually and linearly increased from zero to $\boldsymbol{f}^{postP}$ for the first 0.025 s (equivalent to 25 sample intervals at 1,000 Hz) and then decreased back to zero in a similar manner for the remaining 0.025 s.

Blind reaching task with a target. The purpose of this task was to capture the participants' representation of the hand-cursor dynamics, and to examine its transfer to a simple task, following exposure to either the nondelayed or delayed pong game. At the beginning of a reaching trial, the entire display was turned off, and the device applied a springlike force that brought the hand to a start location at the center of the bottom wall of the pong arena (that was displayed only during the Pong trials) and 1 cm backward from it. Throughout this task, the position of the start location in the forward-backward dimension was indicated on the screen by a green line (48 cm × 0.125 cm).

In this task, participants observed the scene illustrated in Fig. 1*C*. The black open rectangle indicates a target (2.4 cm × 0.5 cm inner area, same as the size of the paddle from the pong game) that appeared at the center of the screen in the right-left dimension and at a distance *d* from the start location in the forward-backward dimension. The distance *d* was different from trial to trial and was drawn from a normal distribution such that d ~ N(10, 2). Throughout the reaching task, targets appeared in a random sequence. The appearance of the target was the cue for the participants to reach fast and to stop at the target. During each reaching trial in the experiment, movement stop was defined at 0.3 s after $\dot{y}_h$ went below 10 cm/s. We defined an allowed and invisible stop area (4 cm × 10 cm) at the center of the screen in the right-left dimension and 5 cm from the start location in the forward-backward dimension. After identifying that a reaching movement had been completed and the participants stopped inside the stop area, the robot applied forces in both the right-left and forward-backward dimensions, to prevent participants from moving their hand after they stopped. However, if the participants stopped outside the stop area (this occurred in 12.8% of the trials), the device returned the hand to the start location to give participants another try to reach toward the target. Also, a message appeared on the screen informing participants that they stopped either too close or too far from the start location, or to the right or left of the stop area. After a reaching movement had been completed in the stop area, the entire display was turned off for 1 s and the reporting task was initiated (see below).

Depending on the experimental session, participants were either provided or not with visual feedback about their performance. During the beginning of the Reach Training session, we familiarized participants with the task, and they received full visual feedback of the hand location using a cursor (solid rectangle, 2.4 cm × 0.5 cm) on the screen throughout the entire movement. They were instructed to put the cursor inside the hollow target. In the rest of the Reach Training session, the cursor was not presented during the movement. Participants were requested to imagine there was a cursor and to stop when the invisible cursor was within the target. When they stopped, we displayed the cursor, providing the participants with feedback about their movement end point with respect to the location of the target. This way, we aimed to train participants to reach accurately to the targets when they did not have any visual indication of their hand location throughout the movement and to improve their baseline performance. During Blind Reach sessions that followed Pong sessions, participants were instructed to imagine that there was a cursor on screen and to bring the imagined cursor to the target. During these sessions, they were not provided with visual feedback at any point during or after the movement.

Blind reaching task with no target. This task is similar to the blind reaching task with a target, but here the participants were not presented with a target (Fig. 1*D*). Instead, they were asked to make a reaching movement and stop at a desired location within an invisible allowed stop area (delineated schematically by the dotted borders in Fig. 1*D*). The purpose of this task was to capture the change in participants' representation of the hand-cursor dynamics due to the delay when no target is presented on screen.

Reporting task. The purpose of this task was to capture how participants' representation of the hand-cursor dynamics affects their perception following exposure to either the nondelayed or delayed pong game. At the beginning of the task, the participant's hand was located at the end of the reaching movement's stop location, and the robot applied forces in both the right-left and forward-backward dimensions to prevent participants from moving their hand. Participants observed the scene illustrated in Fig. 1*E*. The green rectangle indicates a marker (denoted comparison marker) that was similar in shape and size to the paddle's shape and size. This marker appeared on the screen in the same position as the hand's position in the right-left dimension but shifted with respect to the hand's location in the forward-backward dimension. The shift magnitude was in one of eight different magnitudes (±0.8, ±2.4, ±4, and ± 5.6 cm; positive/negative magnitudes indicate shifts in the forward/backward dimension, respectively). The participants were asked to answer the question "Is the green marker farther from you or closer to you, in the forward-backward dimension, than the imagined cursor?" After they answered the question, the answer was recorded and the device returned the hand to the start location in preparation for the next reaching task. To acquaint the participants with the reporting task, and to train them to be accurate in answering the question regarding the location of the comparison marker and the invisible imagined cursor, during Report Training, the comparison marker appeared on screen together with the target and the controlled cursor. During the Report sessions that were presented after each of the Pong sessions, participants did not receive any visual or verbal feedback about their performance, during or after the trial.

Experimental Protocols

We conducted two experiments. Both *Experiment 1* (Fig. 2*A*) and *Experiment 2* (Fig. 2*B*) had a similar protocol. The main sessions alternated a pong game and a reaching and reporting session. Each trial in the reaching and reporting session consisted of either a blind reaching with a target or blind reaching with no target task (*Experiment 1* or *2*, respectively) that was followed by a reporting task.

An experiment started with a training session consisting of 32 trials that familiarized participants with the reaching and reporting tasks and with the system. During the first 4 Reach Training trials, the stop area and the cursor were presented on screen, and they were removed for the remaining 38 trials of the session. When the training was completed, participants were presented with a Pong No Delay session consisting of 10 trials (total of 10 min). This was followed by a Blind Reach and Report session with 32 trials (8 shift magnitudes × 4 repetitions for each magnitude; Post No Delay I). The shift magnitudes appeared in a pseudorandom and predetermined order. Next, participants were presented with another Pong No Delay session (II) consisting of 5 trials (total of 5 min), which was followed by another Blind Reach and Report session (Post No Delay II) with 32 trials. Next, participants experienced a Pong Delay session consisting of 10 trials. In this session, we introduced a delay of either τ = 100 ms (*Experiment 1*, GT100; *Experiment 2*, GNT100) or τ = 200 ms (*Experiment 2*, GNT200) between hand and paddle movements that remained constant throughout the entire session. This was followed by a Blind Reach and Report session (Post Delay I) with 32 trials. Participants then experienced another Pong Delay session (II) consisting of 5 trials, and another Blind Reach and Report session (Post Delay II) of 32 trials. The purpose of dividing the Pong Delay session (and the Pong No Delay session, as well) into two separate sessions was intended to prevent, or at least reduce, a possible decay that might occur during the reaching and reporting session, which may lead to the disappearance of the effects of the exposure to the delayed pong.

We always presented the delayed pong session after the nondelayed session, and we did not counterbalance the order across participants. This is because we were concerned that presenting the delayed pong session first would have a prolonged effect on both the reaching and perceptual tasks that follow the subsequent nondelayed pong session. Importantly, our previous work verified that the movement hypermetria is specific to the delay given that it was not observed when participants were only presented with a nondelayed pong game throughout the entire experiment (Avraham et al. 2017a).

Data Analysis

Metrics. Device position, velocity, and the forces applied were recorded throughout the experiments at 200 Hz. They were analyzed off-line using custom-written MATLAB code (The MathWorks, Natick, MA).

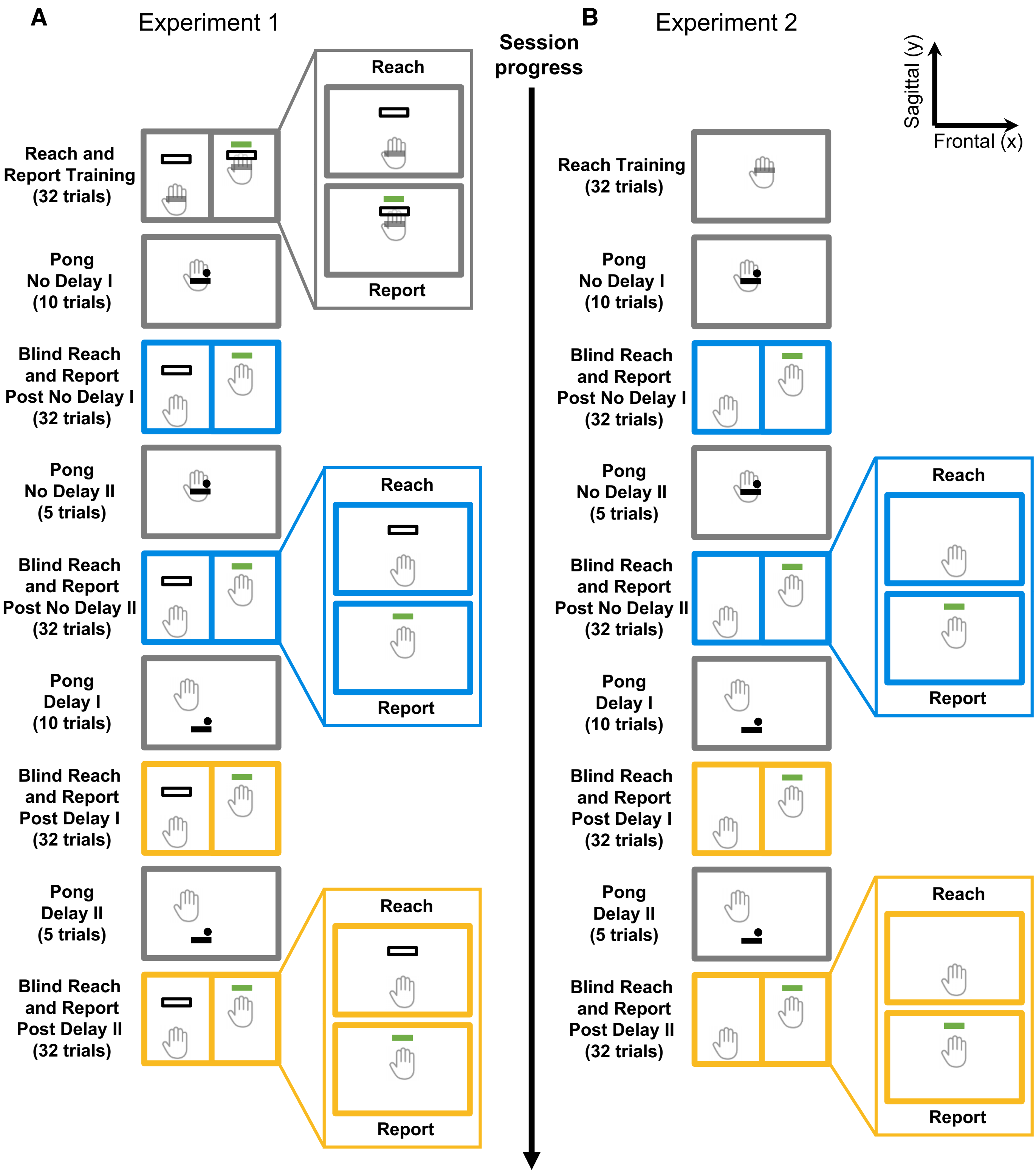

Fig. 2. Experimental protocols. *A*: *Experiment 1*. *B*: *Experiment 2*. In all sessions, the participant's hand (light gray) was hidden from sight the entire time. Experiment started with a Training session of either Reach and Report tasks (*Experiment 1*) or only a Reach task (*Experiment 2*), in which participants received feedback using a cursor (closed gray rectangle). During Reach and Report, each trial consisted of a reaching task that was followed by a reporting task. After training, sessions alternated between a pong game and Blind Reach and Report tasks. During Pong No Delay I and II, the paddle (black bar) moved instantaneously with hand movement, and during Pong Delay I and II, the paddle was delayed with respect to hand movement. Blind Reach and Report sessions followed each of the nondelayed (Post No Delay I and II; blue frames) and delayed pong sessions (Post Delay I and II; yellow frames). Whereas in *Experiment 1* (*A*), reaching movements were performed to a visible target (open black rectangle), in *Experiment 2* (*B*), a target was not presented. Green bar, comparison marker. *Inset* shows movement dimensions.

For data analysis of both experiments, we combined the two Post No Delay sessions into one session consisting of 64 trials, and similarly for both Post Delay sessions.

BLIND REACHING: REACHING AMPLITUDE. For analysis purposes, we defined movement end time as 0.1 s after the first time the velocity dropped below 5% of its maximum value; the reaching end point was thus defined as the hand location ($\boldsymbol{x}_h$) at that time point. Reaching amplitude was calculated as the Euclidean distance between $\boldsymbol{x}_h$ at movement end point and the start location.

BLIND REACHING: TARGET OVERSHOOT. We defined target overshoots in *Experiment 1* as the difference between the reaching amplitude and the target distance from the initial location. This metric is positive/negative if the reaching amplitude is greater/smaller than the target distance. This metric allowed us to examine the difference between the magnitude of motion execution (reaching amplitude) and motion planning (target distance from initial location), and it was chosen to isolate the effect on movement extent (under the assumption that movement direction and movement extent are controlled separately; Sainburg et al. 2003).

REPORTING: PSYCHOMETRIC CURVE AND POINT OF SUBJECTIVE EQUALITY. To test the effects of exposure to delayed pong on perception, for each type of the pong sessions (Post No Delay and Post Delay), we fitted a psychometric curve to each participant's reports regarding the location of the comparison marker with respect to the imagined cursor. The psychometric curve is a commonly used method to quantify perceptual effects in a psychophysical task. The psychometric function describes a dependence of the performance of an observer on some physical aspect of a stimulus (Wichmann and Hill 2001). The general form of the psychometric function is given by

$$\Psi(x;\alpha,\beta,\gamma,\lambda) = \gamma + (1-\gamma-\lambda)F(x;\alpha,\beta), \tag{5}$$

where x is the physical aspect of the stimulus (in our case, the shift between the comparison marker and the hand). The parameters [α, β, γ, λ] determine the shape of the curve, along with the choice of the function F, which is usually a sigmoid. To derive the psychometric function, we estimated the participant's probability to answer "the comparison marker is farther" as a function of the actual shift $\Delta Pos = Pos_{marker} - Pos_{hand}$, where Pos_{marker} is the position of the comparison marker and Pos_{hand} is the position of the hand at the end of the reaching movement. To estimate this probability, we used the following equation:

$$P(\Delta Pos) = \frac{\sum_{n=1}^{N(\Delta Pos)} A[n]}{N(\Delta Pos)},\ A[n] = \begin{cases} 1, & \text{marker is farther} \\ 0, & \text{marker is closer} \end{cases}, \tag{6}$$

where $A[n]$ is a binary representation of the subject's answers and $N(\Delta Pos)$ is the number of trials that a specific shift magnitude was presented (which is 8 for every shift magnitude). We then used the psignifit toolbox version 2.5.6 for MATLAB (Wichmann and Hill 2001) to calculate the psychometric function, fit the psychometric curve, and extract the point of subjective equality (PSE) and the just noticeable difference (JND). The PSE is extracted by using the 0.5 probability threshold value for which the participants cannot discriminate between the two stimuli (comparison marker and imagined cursor). Thus the probability of the participants to answer "the comparison marker is farther" is 0.5, and this is taken to signify that they perceive the shift between the two cursors to be zero. The JND was calculated using the 0.75 and 0.25 threshold values as follows (Krukowski and Stone 2005):

$$JND = \frac{F^{-1}(0.75) - F^{-1}(0.25)}{2}. \tag{7}$$

PONG: AMPLITUDE. To analyze participants' performance during the pong game, we filtered the hand's velocity in the forward-backward dimension, $\dot{y}$, using a second-order Butterworth filter with a normalized cutoff frequency of 0.05 Hz. We then found the velocity peaks of the filtered velocity, each corresponding to a ball hit try. The start of the hit try was defined as the hand's position at the time in which the velocity rose above 2% of the maximum velocity. Concurrently, the end of the hit try was defined as the hand's position at the time in which the velocity went below 2% of the maximum velocity. We defined movement amplitude as the Euclidean distance between the end of the hit try and the start of the hit try. After finding all movement amplitudes, we removed the amplitudes that were smaller than 1 cm, because we assumed these were not hit tries, but erratic aimless movements in the pong arena.

Statistical analysis. Statistical analyses were performed using custom-written MATLAB functions and MATLAB Statistics Toolbox. After extracting each metric, and before we used statistical tests, we used the Lilliefors test to determine whether our metrics were normally distributed (Lilliefors 1967). Statistical significance was determined at the $P < 0.05$ threshold.

To analyze the effect of exposure to delayed feedback on action, for each participant we calculated the mean target overshoot (*Experiment 1*) or the mean reaching amplitude (*Experiment 2*) of the 64 trials in each of the Post No Delay and Post Delay sessions. We then used a two-sided, paired-sample t test. In addition, we calculated the proportion of participants in each group that show a significant hypermetria [P(hypermetria)] by submitting the individual movement amplitudes of each participant into a one-tailed, unpaired-sample t test that compares between the two sessions. For this analysis, significant effects were determined following Holm–Bonferroni correction for multiple comparison.

For *Experiment 2*, we also calculated the variance of the reaching amplitudes of the 64 trials in each of the Post No Delay and Post Delay sessions. We then used a two-sided, paired-sample t test.

To analyze the effect of exposure to delayed feedback on perception, for each participant we extracted the PSE of the Post No Delay session and the PSE of the Post Delay session and used a two-sided, paired-sample t test. To understand the relationship between the effects of delay on action and perception, we plotted for each participant the PSE difference as a function of target overshoot difference between the Post Delay and Post No Delay conditions and fitted a linear regression line to the data (Fig. 3*E*).

To analyze the effects of the delay on the reaching amplitude and the perceptual bias (the PSE) across experiments using a single model, for each of these measures, we fitted a two-way mixed-effect ANOVA model, with the amplitude/PSE as dependent variables, one between-participants independent factor [experiment: 2 levels, target (GT100 group, *Experiment 1*) and no target (combining both GNT100 and GNT200 groups from *Experiment 2*)], and one within-participants independent factor (session: 2 levels, Post No Delay and Post Delay).

To analyze participants' performance during the pong game, for each participant, we calculated the mean movement amplitude for each of the two pong session types (No Delay and Delay). We then fitted a two-way mixed-effect ANOVA model, with the movement amplitude as the dependent variable, one between-participants independent factor (group: 2 levels, GNT100 and GNT200), and one within-participant independent factor (session: 2 levels, Pong No Delay and Pong Delay).

Throughout this work, we used Cohen's d to calculate effect size. We use *pow* to indicate the observed power.

RESULTS

Experiment 1: Following a Delayed Pong Game, Humans Exhibit Hypermetric Blind Reaching Movements to a Visible Target and Report That the Imagined Invisible Cursor Reached the Target

In *Experiment 1*, participants (N = 10) performed sessions of both a blind reaching task with target and a blind reporting task after the two types of Pong sessions, No Delay and Delay

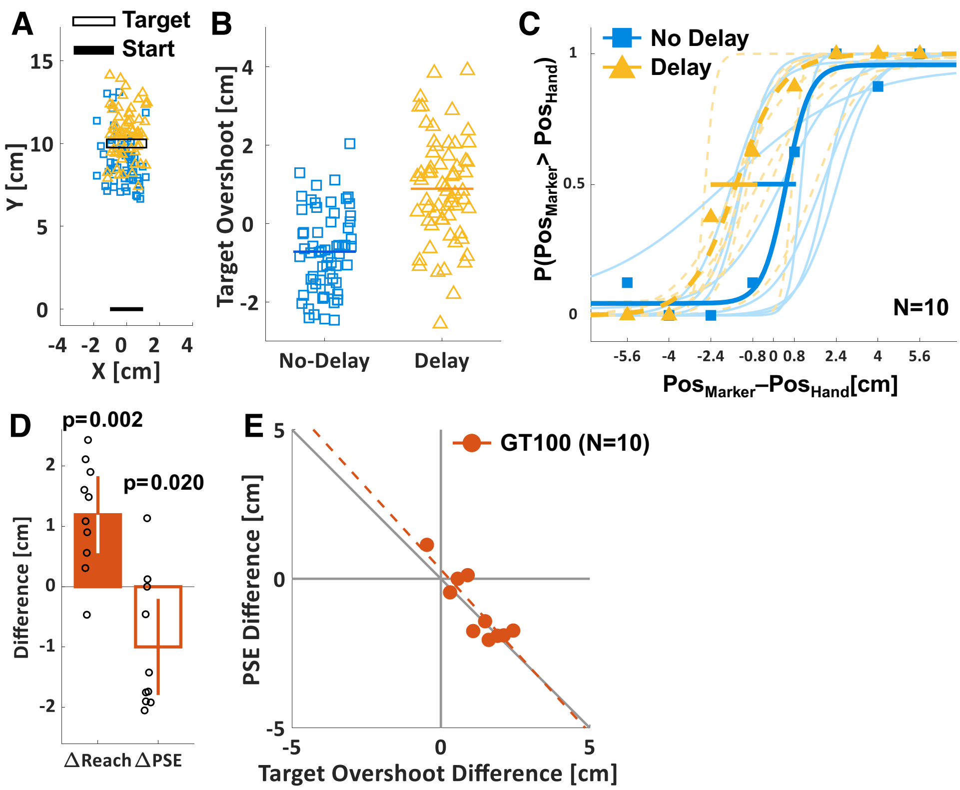

Fig. 3. *Experiment 1*: experimental results. *A*: representative participant's experimental results for the reaching with target task. Movements were performed from a start location (black bar) toward a visual target (open black rectangle). Target position is the mean target position across all trials. Markers represent the end-point locations of the hand at movement terminations during the Post No Delay (blue squares) and Post Delay (yellow triangles) Blind Reach sessions. *B*: target overshoots extracted from the end-point locations (markers) and their means (horizontal lines) for the same representative participant from both Blind Reach sessions. *C*: reporting task results for all participants (shaded colors), including the same representative participant (highlighted by thick lines). Curves represent the probability (P) of participant answering that the comparison marker is farther as a function of the positional difference between the comparison marker (Pos_{marker}) and the hand's position (Pos_{hand}). Data (markers) and fitted psychometric functions (lines) are presented for both the Post No Delay (blue squares and solid blue lines) and Post Delay (yellow triangles and dashed yellow lines) Blind Report sessions. Estimated points of subjective equality (PSE) values and their 95% confidence intervals (CI) are presented by horizontal lines at the probability of 0.5. *D*: group analysis of experimental results. Data are mean target overshoot difference (ΔReach; closed bar) and mean PSE difference (ΔPSE; open bar), averaged over all the participants. Error bars represent the 95% CI. Circles are individuals' data points. *E*: PSE difference between the Post Delay and Post No Delay conditions as a function of target overshoot difference. Orange circles are individuals' data points (N = 10 participants; group GT100: group target, 100-ms delay), and the dashed orange line indicates the fitted linear regression for the data. Gray horizontal line represents a hypothesized regression line for which the delay causes hypermetric movements that are not associated with a change in PSE. By contrast, the gray vertical line represents a hypothesized regression line for which the delay does not yield hypermetric movements but does change the PSE. Diagonal gray line, with a slope of −1, represents a hypothesized regression line for which both hypermetria and PSE change are affected by the same magnitude.

(Fig. 2*A*). The blind reaching task allowed us to capture the representation of hand-paddle dynamics following exposure to either the nondelayed or the delayed pong game. Since participants were not provided with visual feedback of their hand location, they could rely solely on a feedforward mechanism and proprioceptive feedback. Consistent with previous reports (Avraham et al. 2017a; Farshchian et al. 2018), we found that participants made longer (hypermetric) reaching movements during the Post Delay session compared with the Post No Delay session. Figure 3*A* presents the reaching end points (the positions of movement terminations) during the Post No Delay and Post Delay blind reaching sessions for a representative participant. It is evident that Post Delay movement end points are farther from the start location than the Post No Delay movement end points. We also extracted the target overshoots from all movements in each session. Figure 3*B* presents the target overshoots during the Post No Delay and Post Delay blind reaching sessions for the same participant. Although the target position changed throughout the session in a pseudorandom and predetermined order, the target positions and the order of their appearance, for both Post No Delay and Post Delay sessions, were identical. Thus, if there was no effect on reaching movements, we expected that the reaching end points, and thus the target overshoots, would have the same mean. Both Fig. 3, *A* and *B*, and statistical group analysis show that playing pong in the presence of delay significantly affected target overshoots in the subsequent blind reaching task {Post Delay − Post No Delay, mean difference [95% confidence interval (CI)]: 1.193 cm [0.555, 1.830], d = 1.34, $t(9)$ = 4.23, P = 0.002, *pow* = 0.80; Fig. 3*D*, closed bar}, with 8 of 10 participants exhibiting a significant increase in movement amplitude from the Post No Delay to the Post Delay sessions [P(hypermetria) = 0.8; Table 1]. Overall, these analyses suggest that the experience with the delayed pong caused the participants to perform larger blind reaching movements and to overshoot the presented targets.

To examine if the change in the representation, which was evidenced by the hypermetric movements during the transfer reaching task, also had a perceptual effect, we analyzed the answers of the reporting task. Figure 3*C* presents the psycho-

Table 1. *Statistical analysis results for the effect of delayed pong on individuals' movement hypermetria during blind reaching*

GT100			GNT100			GNT200		
Participant	$t(126)$	P	Participant	$t(126)$	P	Participant	$t(126)$	P
1	**9.10**	**<0.001**	***1***	**14.31**	**<0.001**	***1***	**12.03**	**<0.001**
2	**7.63**	**<0.001**	***2***	**4.35**	**<0.001**	***2***	**5.03**	**<0.001**
3	**6.96**	**<0.001**	***3***	**3.75**	**<0.001**	*3*	1.49	0.070
4	**6.79**	**<0.001**	***4***	**3.22**	**<0.001**	*4*	0.73	0.234
5	**6.42**	**<0.001**	*5*	0.97	0.167	*5*	−0.56	0.712
6	**2.77**	**0.003**	*6*	0.76	0.223	*6*	−1.25	0.894
7	**2.45**	**0.008**	*7*	0.72	0.236	*7*	−1.32	0.906
8	**2.17**	**0.016**	*8*	0.43	0.334	*8*	−1.96	0.974
9	1.52	0.065	*9*	−0.08	0.530	*9*	−2.93	0.998
10	−1.30	0.902	*10*	−0.46	0.676	*10*	−4.27	1.000
			11	−0.76	0.776			
			12	−0.79	0.786			
			13	−1.20	0.885			
			14	−1.44	0.924			
			15	−2.07	0.980			
			16	−2.65	0.995			
			17	−5.10	1.000			
			18	−7.41	1.000			
			19	−9.579	1.000			
P(hypermetria) = 0.80			P(hypermetria) = 0.21			P(hypermetria) = 0.20		

For each participant in each of the GT100 (group target, 100-ms delay), GNT100 (group no target, 100-ms delay), and GNT200 (group no target, 200-ms delay) groups, we performed a one-tailed unpaired-sample t test to examine whether there was a significant increase in movement amplitude from the Post No Delay to the Post Delay blind reaching sessions. Reported values for each participant are the t statistics with the degrees of freedom (in parentheses) and the corresponding P values. P(hypermetria) presents the proportion of participants in each group that exhibited a significant hypermetria following Holm–Bonferroni correction; data for these participants are highlighted in bold.

metric curves that we fitted for all participants in both the Post No Delay and Post Delay blind reporting sessions, highlighting the same representative participant. It is evident that the psychometric curves fitted for the Post Delay session were shifted to the left compared with the psychometric curves fitted for the Post No Delay session (for the highlighted participant, PSE = −0.143 cm and PSE = 0.048 cm, respectively). A leftward shift of the psychometric curve indicates that the participant reported the imagined cursor as being closer to the body, relative to the location of the hand. Statistical group analysis showed that playing pong in the presence of delay led to a significant shift of the curve (i.e., a change in the PSE) to the left {Post Delay − Post No Delay: mean difference [95% CI], −0.997 cm [−1.793, −0.201], $d = -0.90$, $t(9) = -2.83$, $P = 0.020$, $pow = 0.72$; Fig. 3*D*, open bar}. The perceptual change was not associated with a significant change in the JND {mean difference [95% CI], −0.117 cm [−0.304, 0.539], $d = -0.20$, $t(9) = 0.63$, $P = 0.545$, $pow = 0.09$}. Overall, the statistical analysis suggests that the delayed pong caused a perceptual bias in the location assessment of the imagined cursor such that it is perceived as closer to the body than the hand.

The reaching and reporting tasks were administered consecutively, and both are affected by the experience during the pong game with nondelayed or delayed feedback. Therefore, to better understand the altered representations following the pong game experience, we plotted for each participant the PSE difference as a function of target overshoot difference between the Post Delay and Post No Delay conditions and fitted a regression line to the data (Fig. 3*E*). The fitted regression line has a slope that is close to −1 and significantly different from 0 (coefficient [95% CI], −1.095 [−1.583, −0.607], $R^2 = 0.77$) and an intercept that is not significantly different from 0 (coefficient [95% CI], 0.309 [−0.404, 1.023]). This means that the perceptual bias was similar in magnitude to the target overshoot on a subject-by-subject basis; essentially, the participants reported the location of the imagined cursor as being close to the target.

Experiment 2: In the Absence of a Visual Target, Reaching Hypermetria Does Not Occur, and Participants Report the Imagined Invisible Cursor at the Location of the Hand

In *Experiment 1*, we found that the movement hypermetria following the delayed pong game was associated with a perceptual bias, in which participants reported the imagined cursor being closer to the body than the hand. However, we could not rule out the possibility that even though the target was removed 1 s before the onset of the reporting task, participants reported the remembered location of the target. This is also supported by the finding that the perceptual bias is similar in magnitude to the target overshoot. Therefore, in *Experiment 2*, we attempted to minimize a possible influence of recalling a target position, and thus also evaluate the effect of the visual target on both the hypermetria and the perceptual bias. A group of participants, GNT100 ($N = 20$), performed sessions of a blind reaching task with no target after the two Pong sessions (Fig. 2*B*), with the same delay value (100 ms) for the Pong Delay sessions as in *Experiment 1*. One participant did not understand the instructions of the experiment, and therefore, the acquired data of this participant were excluded from data analyses.

Figure 4*A* presents the reaching end points (the positions of movement terminations) during the Post No Delay and Post Delay blind reaching sessions for a representative participant. This participant's end points were scattered around the same workspace area during both session types. In addition, the reaching amplitudes (the Euclidean distance of the end points from the start location) during the Post Delay session were

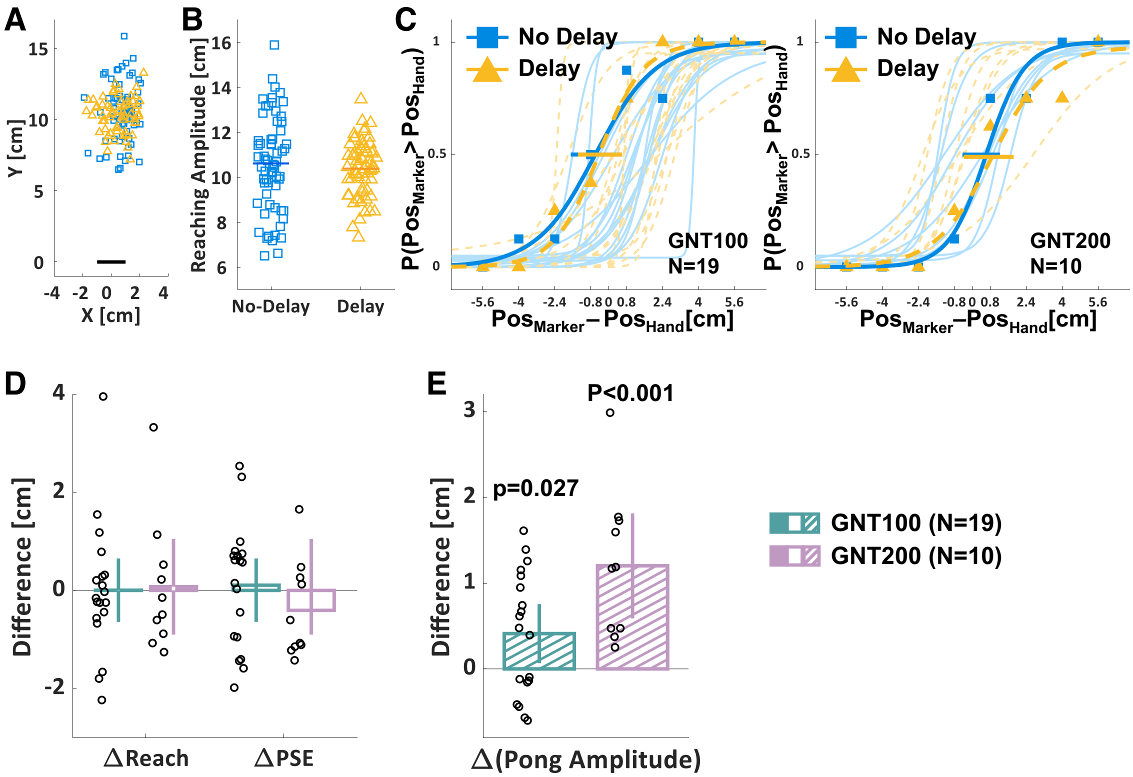

Fig. 4. *Experiment 2*: experimental results. *A*: representative participant's experimental results for the reaching with no target task. This participant is from GNT100 (group no target, 100-ms delay), but results are similar in both GNT100 and GNT200 (group no target, 200-ms delay). Movements were performed from a start location (black bar). Markers represent the end-point locations of the hand at movement terminations during the Post No Delay (blue squares) and Post Delay (yellow triangles) Blind Reach sessions. *B*: reaching amplitudes (markers) and their means (horizontal lines) for the same representative participant from both Blind Reach sessions. *C*: reporting task results for all participants (shaded colors) in GNT100 (*left*) and in GNT200 (*right*), with representative participant highlighted (thick lines). Curves represent the probability (P) of participant answering that the comparison marker is farther as a function of the positional difference between the comparison marker (Pos_{marker}) and the hand's position (Pos_{hand}). Data (markers) and fitted psychometric functions (lines) are presented for both the Post No Delay (blue squares and solid blue lines) and Post Delay (yellow triangles and dashed yellow lines) Blind Report sessions. Estimated points of subjective equality (PSE) values and their 95% confidence intervals (CI) are presented by horizontal lines at the probability of 0.5. *D*: group analysis of experimental results. Data are mean target overshoot difference (ΔReach; closed bars) and mean PSE difference (ΔPSE; open bars), averaged over all the participants, for both groups. Error bars represent the 95% CI. Circles are individuals' data points (GNT100: turquoise bars, $N = 19$ participants; GNT200: purple bars, $N = 10$ participants). *E*: group analyses for movement amplitudes during the pong game, for both groups. Striped bars represent the mean movement amplitude difference, averaged over all participants in each group. Error bars represent the 95% CI. Circles are individuals' data points.

similar to the reaching amplitudes during the Post No Delay session (Fig. 4*B*). Statistical group analysis showed that the reaching amplitudes of GNT100 did not significantly increase from the Post No Delay to the Post Delay session {Post Delay − Post No Delay: mean difference [95% CI], 0.005 cm [−0.642, 0.652], $d = 3 \times 10^{-3}$, $t(18) = 0.01$, $P = 0.988$, $pow = 0.05$; Fig. 4*D*, closed turquoise bar}, with only 4 of 19 [P(hypermetria) = 0.21] participants exhibiting a significant increase in movement amplitude from the Post No Delay to the Post Delay sessions (Table 1). These results indicate that the removal of the target eliminated the effect of the delayed pong game on the blind reaching movements. Note that the sample size was larger here than in *Experiment 1*, reensuring that the result is not due to an underpowered test. The results presented in Fig. 4*B* may suggest that the variance of the reaching amplitudes during the Post Delay session was lower compared with the variance of the reaching amplitudes during the Post No Delay session. However, statistical group analysis showed that the variance of the reaching amplitudes of GNT100 did not significantly change between the sessions {Post Delay – Post No Delay: mean difference [95% CI], −0.148, [−0.714, 0.419], $d = -0.13$, $t(18) = -0.55$, $P = 0.591$, $pow = 0.08$}.

To further confirm that the absence of hypermetria is indeed a result of the removal of the target and not a statistical nuisance of a weak effect size, an additional group of participants, GNT200 ($N = 10$), performed the same experiment but was introduced with a larger delay (200 ms), which was previously shown to increase the delay-induced hypermetric movements even further (Avraham 2016). Statistical group analysis showed that despite the larger delay, the hypermetric movements were still absent {Post Delay – Post No Delay: mean difference [95% CI], 0.075 cm [−0.901, 1.052], $d = 0.06$, $t(9) = 0.17$, $P = 0.866$, $pow = 0.05$; P(hypermetria) = 0.2; Fig. 4*D*, closed purple bar; Table 1}. Again, statistical group analysis showed that the variance of the reaching amplitudes did not significantly decrease from the Post No Delay to the Post Delay session {Post Delay – Post No Delay: mean difference [95% CI], −0.250, [−0.944, 0.444], $d = -0.26$, $t(9) = -0.82$, $P = 0.436$, $pow = 0.11$}.

Figure 4*C* presents the psychometric curves that we fitted for the Post No Delay and Post Delay blind reporting sessions for all participants, highlighting a representative participant from each of the GNT100 and GNT200 groups. It is evident that the highlighted psychometric curves fitted for the Post Delay session were not shifted compared with the psychometric curve fitted for the Post No Delay session (for the representative participant from GNT100: PSE = −0.439 cm and PSE = −0.588 cm, and from GNT200: PSE = 0.868 and PSE = 0.616, respectively). This suggests that these participants did not change their reports regarding the imagined invisible cursor, relative to the location of the hand. Statistical group analyses showed that playing pong in the presence of delay, regardless of its magnitude, did not lead to significant shifts of the curves (i.e., changes in the PSE) {Post Delay – Post No Delay: mean difference [95% CI], 0.107 cm [−0.498, 0.711], $d = 0.09$, $t(18) = 0.37$, $P = 0.715$, $pow = 0.06$ for GNT100, and −0.407 cm [−1.121, 0.308], $d = -0.41$, $t(9) = -1.29$, $P = 0.230$, $pow = 0.21$ for GNT200; Fig. 4*D*, open bars} and did not significantly influence the JND {mean difference [95% CI], −0.082 cm [−0.196, 0.359], $d = -0.14$, $t(18) = 0.62$, $P = 0.545$, $pow = 0.09$ for GNT100, and −0.022 cm [−0.466, 0.509], $d = -0.03$, $t(9) = 0.10$, $P = 0.922$, $pow = 0.05$ for GNT200}.

We also validated the influence of the target on action and perception following adaptation to delay by submitting the reaching amplitude and the perceptual bias (PSE) from both experiments to a single ANOVA model for each measure. Consistent with the separate analyses reported above, we found a significant interaction effect for both measures [amplitude: $F(1,37) = 6.61$, $P = 0.014$; PSE: $F(1,37) = 4.71$, $P = 0.036$]. Pairwise comparisons for the Target group revealed a significant increase in the reaching amplitude from the Post No Delay to the Post Delay conditions ($P = 0.004$) and a significant decrease in the PSE ($P = 0.010$). For the No Target group, pairwise comparisons resulted in no change in both the reaching amplitude ($P = 0.900$) and the PSE ($P = 0.747$) between the sessions. Overall, these results indicate that in the absence of a target, the experience with the delayed pong did not cause participants to perform larger (hypermetric) blind reaching movements, nor did it affect participants' reports, regardless of the magnitude of the delay.

A possible explanation of these results is that the changed experimental design eliminated any effect of the recalibration due to delayed feedback in the pong game. To verify that this is not the case, we analyzed the participants' performance during the pong game by extracting the mean pong amplitude for every participant during each of the two pong sessions (Pong No Delay and Pong Delay). Indeed, prior observations showed that the hypermetric movements were not limited to the reaching movements but were also present during the pong game (Avraham et al. 2017a). We found that both groups increased their mean movement amplitude from the Pong No Delay session to the Pong Delay session {session main effect: $F(1,27) = 29.125$, $P < 0.001$, $pow = 0.99$; Pong Delay – Pong No Delay: mean difference [95% CI], 0.806 cm [0.499, 1.112]}. Furthermore, this increase in amplitude was significantly different between the groups [group-session interaction effect: $F(1,27) = 7.001$, $P = 0.013$, $pow = 0.72$], with a larger increase in GNT200 (1.200 cm [0.705, 1.696], $P < 0.001$) than in GNT100 (0.411 cm [0.051, 0.770], $P = 0.027$). This strengthens the claim that the hypermetria is directly related to the delay. Overall, these results confirm that the absence of the effects in *Experiment 2* was not due to an absence of a recalibration of the cursor-hand dynamics during the delayed pong game, but rather a result of the absence of a target in the subsequent reaching task.

DISCUSSION

To explore how delayed feedback affects our action and perception, we exposed participants to a virtual pong game in which the movements of the controlled paddle were delayed with respect to the movements of the hand, and we examined the transfer of the delay representation to blind reaching and reporting tasks. We reproduced our previous results (Avraham et al. 2017a) showing that when participants blindly reached toward visible targets after playing the delayed pong game, their movements became hypermetric. Furthermore, we revealed that this hypermetria was associated with a perceptual bias: participants reported at the end of the reaching movement that the imagined cursor they were controlling was behind their hand and closer to their body. We also found that these effects of adaptation to delayed feedback on action and perception are contingent on the existence of a visual target in the blind reaching task. Taking these results together, we conclude that the adaptation to the delay during the pong game selectively affects the representation of space subserving the execution of goal-directed movements, resulting in hypermetria and perceptual bias when movements are directed toward visual targets, but not when such targets are absent.

In this study, we used a perceptual location assessment task to probe the effects of adaptation to delayed feedback on perception. Successful interaction with and perception of the environment requires an integration of multiple sensory inputs. Previous studies showed that such a process is based on the integration of the different sensory cues according to their reliability (Ernst and Banks 2002; van Beers et al. 2002), in such a way that more reliable cues are given larger weights than less reliable ones (Jacobs 1999; Knill and Richards 1996; Landy and Kojima 2001). In our perceptual task in *Experiment 1*, participants could utilize remembered visual information about the target location, a mental (visual) representation of the imagined cursor, and proprioceptive information about the hand location to a different extent. With this, participants' perception of the location of the imagined cursor was biased toward the visual target. However, in *Experiment 2*, when they had no visual information of the target, their perception was biased toward the proprioceptive cue—the location of the hand—and not toward the location of the imagined cursor. Therefore, one possible explanation for our results is that following the recalibration during the pong game, the visual information was much more reliable than the proprioceptive feedback, and thus it had a much larger weight that completely dominated the integration process. This is also consistent with previous studies that suggested that vision is typically the dominant sensory modality (Colavita 1974; Colavita and Weisberg 1979; Cooper 1998; Posner et al. 1976; Rock and Victor 1964; Sinnett et al. 2007; Spence 2009).

The results of *Experiment 2* show that when there was no target in the reaching movements, neither hypermetric reaches nor changes in perception in the reporting task were observed. It is well established that the target is important for the planning of reaching and pointing movements, specifically, for computing a difference vector between the target and the hand (Shadmehr and Wise 2005; Vindras and Viviani 1998). This in turn serves to compute a movement plan (Krakauer et al. 2000; Sarlegna and Sainburg 2007; Sober and Sabes 2003) before the execution of the movement using feedforward and feedback mechanisms (Kawato 1999; Wolpert and Ghahramani 2000). Possibly, our two experiments imposed a dissociation between different control processes. When the visual target is present, the task space is in the visual domain, and therefore participants control an imagined visual cursor and exhibit motor and perceptual biases. In the absence of a visual target, the task space is in the proprioceptive domain; participants could have imagined a proprioceptive target that would elicit the use of a different planning mechanism (Sarlegna and Sainburg 2007; Sober and Sabes 2005) by which they control their hand rather than the cursor, and thus it is not associated with any recalibration. Overall, this explanation is based on the idea that following the adaptation during the pong game, the motor and perceptual biases depend on utilizing visual information, a process that is driven by the presence of the visual target.

The differential effect of the presence of the target on the participants' change in reaching amplitude could also be attributed to differences in the processing of externally and internally triggered movements. Previous studies showed that those types of movements are controlled by different brain areas and can influence performance (Lau et al. 2004; Thaler et al. 1995). The visual target in *Experiment 1* is a salient external cue that defines the movement goal; its absence in *Experiment 2*, together with the instructions to move to a freely chosen location, naturally engage a self-triggered process. It is not clear though what is the mechanism that eliminates the hypermetria in the latter case. The uncertainty about the movement goal is likely higher in the absence of the target, and thus could elicit the preparation of multiple movement plans that eventually result in movements that represent an averaged behavior (Gallivan et al. 2016, 2017). This can explain the comparable reaching amplitudes between the Post No Delay and Post Delay conditions in the absence of the target.

We set out to examine the effects of adaptation to delay on perception and action and their possible dissociation following the pong game with delay. In the context of adaptation, the dissociation between perception and action may also be related to explicit and implicit adaptation processes. Explicit and implicit processes (Taylor et al. 2014; Taylor and Ivry 2011) and the effects of adaptation on perception and action (Darainy et al. 2013; Mattar et al. 2013; Ostry et al. 2010) have gained recent attention as two separate topics. However, they may be connected; the high-level cognitive mechanisms that are involved in perception may be linked to explicit mechanisms of motor adaptation, and the automatic mechanisms that are involved in the control of action may be linked to implicit mechanisms of motor adaptation. A large body of evidence for a dissociation between perception and action exists in the processing of properties of objects based on visual information (Goodale and Milner 1992). Prominent examples are the size-weight illusion in lifting that does not affect grip force adjustments after several lifts (Flanagan and Beltzner 2000) or visual illusions about the size of objects that do not affect the aperture of the fingers in grasping (Aglioti et al. 1995; Ganel and Goodale 2003). It could be that this observed dissociation between perception and action may be related to a dissociation between the cognitive explicit strategy (i.e., the perceptual assessment of the object, before the action to grasp it) and the implicit movement planning that occurs when participants plan to act (i.e., to grasp the object). The hypermetria observed in *Experiment 1* is an example of such a dissociation, although unlike all the examples reported to date (except from Nisky et al. 2011), the action is affected. This effect is implicit and without awareness, and hence the bias in perception with respect to the actual hand position. A similar view can generally describe other examples of motor adaptation; for example, in adaptation to force fields, participants report that by the end of training, they can no longer feel the force field, and when it is suddenly removed, they report that they begin to feel a sensation of an opposite force even though the robotic device is not applying any forces (Shadmehr and Mussa-Ivaldi 1994).

Our results of hypermetric movements are consistent with a state-based representation of the delay, i.e., approximation of the delayed location of the cursor using current state variables (e.g., position and velocity) (Avraham et al. 2017a, 2017b, 2019; Farshchian et al. 2018; Leib et al. 2017; Sarlegna et al. 2010; Takamuku and Gomi 2015). Interestingly, this state-based behavior was not dependent on the pong task: hypermetria in delay adaptation also appeared during transfer from simple reaching movements to slicing (Botzer and Karniel 2013) and a circle drawing task (Avraham et al. 2018; Conditt and Mussa-Ivaldi 1999). However, other works that studied adaptation to visuomotor delay suggested a time-based representation of visuomotor delay that estimates the actual time lag (Farshchiansadegh et al. 2015; Rohde et al. 2014). Therefore, it is not yet clear under which circumstances the sensorimotor system utilizes each type of representation. The state-based representation of the delay in our experiment may be related to the fact that the adaptation process was implicit, and it raises the speculation that a time-based representation would be associated with an explicit learning. For example, maybe a larger delay would elicit an explicit time representation, as described in Witney et al. (1999). This view is consistent with the idea that brain areas that are proposed to have an internal timing system, i.e., the basal ganglia and the cerebellum (Breska and Ivry 2018; Ivry 1996), also have a substantial role in cognitive processes that can support explicit computation (King et al. 2019; Stocco et al. 2010). Further studies are required to examine how explicit awareness about delayed feedback influences its representation.

Importantly, this study does not directly deal with the question of whether the sensorimotor system uses a time-based or a state-based representation of visuomotor delay. In this context, the results of *Experiment 1* replicate previous findings that are consistent with a state-based representation (Avraham et al. 2017a; Farshchian et al. 2018). In *Experiment 2*, participants exhibited hypermetric movements during the delayed pong game, which is also consistent with a state-based representation. However, this hypermetria did not transfer to the subsequent blind reaching task without visual targets. This result suggests that the presence of a visual target in the space engages the state-based behavior; possibly, when the target is absent, the system fails to recall the state-based representation, employs a different planning and execution mechanism that is completely isolated from the information that is acquired during goal-directed interception movements, or uses a time-based representation of the visuomotor delay.

Understanding the way delay is represented in the motor system and the way it influences our perception and action may help in understanding pathological conditions that are characterized by delayed information transmission, such as multiple sclerosis. In addition, it can help in designing or controlling systems that contain inherent delays and are used by humans, such as teleoperation, surgical robotics, and virtual or augmented reality systems.

ACKNOWLEDGMENTS

We thank Raz Leib, Amit Milstein, and Eli Peretz for technical assistance and Ran Weiss for contributions to the early experiments that eventually led to this work.

GRANTS

This study was supported by National Science Foundation Grant 1632259, Binational United-States Israel Science Foundation Grants 2011066 and 2016850, Israel Science Foundation Grant 823/15, and the Helmsley Charitable Trust through the Agricultural, Biological and Cognitive Robotics Initiative of Ben-Gurion University of the Negev, Israel. E. Sulimani was supported by the Kreitman Fellowship.

DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

G.A., E.S., F.A.M.-I., and I.N. conceived and designed research; E.S. performed experiments; G.A. and E.S. analyzed data; G.A., E.S., F.A.M.-I., and I.N. interpreted results of experiments; G.A. and E.S. prepared figures; E.S. and G.A. drafted manuscript. G.A., E.S., F.A.M.-I., and I.N. edited and revised manuscript; G.A., E.S., F.A.M.-I., and I.N. approved final version of manuscript.

REFERENCES

Aglioti S, DeSouza JF, Goodale MA. Size-contrast illusions deceive the eye but not the hand. *Curr Biol* 5: 679–685, 1995. doi:10.1016/S0960-9822(95)00133-3.

Avraham C, Avraham G, Mussa-Ivaldi FA, Nisky I. Neglect-like effects on drawing symmetry induced by adaptation to a laterally asymmetric visuomotor delay. *Front Hum Neurosci* 12: 335, 2018. doi:10.3389/fnhum.2018.00335.

Avraham C, Dominitz M, Khait H, Avraham G, Mussa-Ivaldi FA, Nisky I. Adaptation to laterally asymmetrical visuomotor delay has an effect on action but not on perception. *Front Hum Neurosci* 13: 312, 2019. doi:10.3389/fnhum.2019.00312.

Avraham G. *Delay Representation in the Sensorimotor System* (PhD thesis). Be'er-Sheva, Israel: Ben-Gurion University of the Negev, 2016.

Avraham G, Leib R, Pressman A, Simo LS, Karniel A, Shmuelof L, Mussa-Ivaldi FA, Nisky I. State-based delay representation and its transfer from a game of pong to reaching and tracking. *eNeuro* 4: ENEURO.0179-17.2017, 2017a. doi:10.1523/ENEURO.0179-17.2017.

Avraham G, Mawase F, Karniel A, Shmuelof L, Donchin O, Mussa-Ivaldi FA, Nisky I. Representing delayed force feedback as a combination of current and delayed states. *J Neurophysiol* 118: 2110–2131, 2017b. doi:10.1152/jn.00347.2017.

Bernardi NF, Darainy M, Bricolo E, Ostry DJ. Observing motor learning produces somatosensory change. *J Neurophysiol* 110: 1804–1810, 2013. doi:10.1152/jn.01061.2012.

Botzer L, Karniel A. Feedback and feedforward adaptation to visuomotor delay during reaching and slicing movements. *Eur J Neurosci* 38: 2108–2123, 2013. doi:10.1111/ejn.12211.

Brenner E, Smeets JB. Size illusion influences how we lift but not how we grasp an object. *Exp Brain Res* 111: 473–476, 1996. doi:10.1007/BF00228737.

Breska A, Ivry RB. Double dissociation of single-interval and rhythmic temporal prediction in cerebellar degeneration and Parkinson's disease. *Proc Natl Acad Sci USA* 115: 12283–12288, 2018. doi:10.1073/pnas.1810596115.

Colavita FB. Human sensory dominance. *Percept Psychophys* 16: 409–412, 1974. doi:10.3758/BF03203962.

Colavita FB, Weisberg D. A further investigation of visual dominance. *Percept Psychophys* 25: 345–347, 1979. doi:10.3758/BF03198814.

Conditt MA, Mussa-Ivaldi FA. Central representation of time during motor learning. *Proc Natl Acad Sci USA* 96: 11625–11630, 1999. doi:10.1073/pnas.96.20.11625.

Cooper R. Visual dominance and the control of action. In: *Proceedings of the 20th Annual Conference of the Cognitive Science Society*, edited by Gernsbacher MA, Derry SJ. Mahwah, NJ: Erlbaum, 1998, p. 250–255.

Cressman EK, Henriques DY. Sensory recalibration of hand position following visuomotor adaptation. *J Neurophysiol* 102: 3505–3518, 2009. doi:10.1152/jn.00514.2009.

Darainy M, Vahdat S, Ostry DJ. Perceptual learning in sensorimotor adaptation. *J Neurophysiol* 110: 2152–2162, 2013. doi:10.1152/jn.00439.2013.

de Grave DD, Biegstraaten M, Smeets JB, Brenner E. Effects of the Ebbinghaus figure on grasping are not only due to misjudged size. *Exp Brain Res* 163: 58–64, 2005. doi:10.1007/s00221-004-2138-0.

Di Luca M, Knörlein B, Ernst MO, Harders M. Effects of visual-haptic asynchronies and loading-unloading movements on compliance perception. *Brain Res Bull* 85: 245–259, 2011. doi:10.1016/j.brainresbull.2010.02.009.

Ernst MO, Banks MS. Humans integrate visual and haptic information in a statistically optimal fashion. *Nature* 415: 429–433, 2002. doi:10.1038/415429a.

Farshchian A, Sciutti A, Pressman A, Nisky I, Mussa-Ivaldi FA. Energy exchanges at contact events guide sensorimotor integration. *eLife* 7: e32587, 2018. doi:10.7554/eLife.32587.

Farshchiansadegh A, Ranganathan R, Casadio M, Mussa-Ivaldi FA. Adaptation to visual feedback delay in a redundant motor task. *J Neurophysiol* 113: 426–433, 2015. doi:10.1152/jn.00249.2014.

Ferrell WR. Remote manipulation with transmission delay. NASA TN D-2665. *NASA Contract Rep NASA CR* HFE-6: 1–119, 1965.

Flanagan JR, Beltzner MA. Independence of perceptual and sensorimotor predictions in the size-weight illusion. *Nat Neurosci* 3: 737–741, 2000. doi:10.1038/76701.

Fujisaki W, Shimojo S, Kashino M, Nishida S. Recalibration of audiovisual simultaneity. *Nat Neurosci* 7: 773–778, 2004. doi:10.1038/nn1268.

Gallivan JP, Logan L, Wolpert DM, Flanagan JR. Parallel specification of competing sensorimotor control policies for alternative action options. *Nat Neurosci* 19: 320–326, 2016. doi:10.1038/nn.4214.

Gallivan JP, Stewart BM, Baugh LA, Wolpert DM, Flanagan JR. Rapid automatic motor encoding of competing reach options. *Cell Rep* 18: 1619–1626, 2017. [Erratum in *Cell Rep* 19: 890–893, 2017.] doi:10.1016/j.celrep.2017.01.049.

Ganel T, Goodale MA. Visual control of action but not perception requires analytical processing of object shape. *Nature* 426: 664–667, 2003. doi:10.1038/nature02156.

Goodale MA, Milner AD. Separate visual pathways for perception and action. *Trends Neurosci* 15: 20–25, 1992. doi:10.1016/0166-2236(92)90344-8.

Ivry RB. The representation of temporal information in perception and motor control. *Curr Opin Neurobiol* 6: 851–857, 1996. doi:10.1016/S0959-4388(96)80037-7.

Jacobs RA. Optimal integration of texture and motion cues to depth. *Vision Res* 39: 3621–3629, 1999. doi:10.1016/S0042-6989(99)00088-7.

Kawato M. Internal models for motor control and trajectory planning. *Curr Opin Neurobiol* 9: 718–727, 1999. doi:10.1016/S0959-4388(99)00028-8.

King M, Hernandez-Castillo CR, Poldrack RA, Ivry RB, Diedrichsen J. Functional boundaries in the human cerebellum revealed by a multi-domain task battery. *Nat Neurosci* 22: 1371–1378, 2019. doi:10.1038/s41593-019-0436-x.

Knill DC, Richards W (Editors). *Perception as Bayesian Inference*. Cambridge, UK: Cambridge University Press, 1996.

Krakauer JW, Pine ZM, Ghilardi MF, Ghez C. Learning of visuomotor transformations for vectorial planning of reaching trajectories. *J Neurosci* 20: 8916–8924, 2000. doi:10.1523/JNEUROSCI.20-23-08916.2000.

Krukowski AE, Stone LS. Expansion of direction space around the cardinal axes revealed by smooth pursuit eye movements. *Neuron* 45: 315–323, 2005. doi:10.1016/j.neuron.2005.01.005.

Kuling IA, Smeets JB, Lammertse P, Onneweer B, Mugge W. Delays in admittance-controlled haptic devices make simulated masses feel heavier. *PLoS One* 10: e0138023, 2015. doi:10.1371/journal.pone.0138023.

Landy MS, Kojima H. Ideal cue combination for localizing texture-defined edges. *J Opt Soc Am A Opt Image Sci Vis* 18: 2307–2320, 2001. doi:10.1364/JOSAA.18.002307.

Lau HC, Rogers RD, Ramnani N, Passingham RE. Willed action and attention to the selection of action. *Neuroimage* 21: 1407–1415, 2004. doi:10.1016/j.neuroimage.2003.10.034.

Leib R, Karniel A, Mussa-Ivaldi FA. The mechanical representation of temporal delays. *Sci Rep* 7: 7669, 2017. doi:10.1038/s41598-017-07289-3.

Leib R, Karniel A, Nisky I. The effect of force feedback delay on stiffness perception and grip force modulation during tool-mediated interaction with elastic force fields. *J Neurophysiol* 113: 3076–3089, 2015. doi:10.1152/jn.00229.2014.

Leib R, Mawase F, Karniel A, Donchin O, Rothwell J, Nisky I, Davare M. Stimulation of PPC affects the mapping between motion and force signals for stiffness perception but not motion control. *J Neurosci* 36: 10545–10559, 2016. doi:10.1523/JNEUROSCI.1178-16.2016.

Leib R, Rubin I, Nisky I. Force feedback delay affects perception of stiffness but not action, and the effect depends on the hand used but not on the handedness. *J Neurophysiol* 120: 781–794, 2018. doi:10.1152/jn.00822.2017.

Levy N, Pressman A, Mussa-Ivaldi FA, Karniel A. Adaptation to delayed force perturbations in reaching movements. *PLoS One* 5: e12128, 2010. doi:10.1371/journal.pone.0012128.

Lilliefors HW. On the Kolmogorov-Smirnov test for normality with mean and variance unknown. *J Am Stat Assoc* 62: 399–402, 1967. doi:10.1080/01621459.1967.10482916.

Mattar AA, Darainy M, Ostry DJ. Motor learning and its sensory effects: time course of perceptual change and its presence with gradual introduction of load. *J Neurophysiol* 109: 782–791, 2013. doi:10.1152/jn.00734.2011.

Miall RC, Jackson JK. Adaptation to visual feedback delays in manual tracking: evidence against the Smith Predictor model of human visually guided action. *Exp Brain Res* 172: 77–84, 2006. doi:10.1007/s00221-005-0306-5.

Murray MM, Wallace MT. *The Neural Bases of Multisensory Processes*. Boca Raton, FL: CRC, 2012.

Nisky I, Baraduc P, Karniel A. Proximodistal gradient in the perception of delayed stiffness. *J Neurophysiol* 103: 3017–3026, 2010. doi:10.1152/jn.00939.2009.

Nisky I, Mussa-Ivaldi FA, Karniel A. A regression and boundary-crossing-based model for the perception of delayed stiffness. *IEEE Trans Haptics* 1: 73–82, 2008. doi:10.1109/TOH.2008.17.

Nisky I, Pressman A, Pugh CM, Mussa-Ivaldi FA, Karniel A. Perception and action in teleoperated needle insertion. *IEEE Trans Haptics* 4: 155–166, 2011. doi:10.1109/TOH.2011.30.

Ostry DJ, Darainy M, Mattar AA, Wong J, Gribble PL. Somatosensory plasticity and motor learning. *J Neurosci* 30: 5384–5393, 2010. doi:10.1523/JNEUROSCI.4571-09.2010.

Posner MI, Nissen MJ, Klein RM. Visual dominance: an information-processing account of its origins and significance. *Psychol Rev* 83: 157–171, 1976. doi:10.1037/0033-295X.83.2.157.

Pressman A, Welty LJ, Karniel A, Mussa-Ivaldi FA. Perception of delayed stiffness. *Int J Robot Res* 26: 1191–1203, 2007. doi:10.1177/0278364907082611.

Rock I, Victor J. Vision and touch: an experimentally created conflict between the two senses. *Science* 143: 594–596, 1964. doi:10.1126/science.143.3606.594.

Rohde M, Ernst MO. Time, agency, and sensory feedback delays during action. *Curr Opin Behav Sci* 8: 193–199, 2016. doi:10.1016/j.cobeha.2016.02.029.

Rohde M, van Dam LC, Ernst MO. Predictability is necessary for closed-loop visual feedback delay adaptation. *J Vis* 14: 4, 2014. doi:10.1167/14.3.4.

Sainburg RL, Lateiner JE, Latash ML, Bagesteiro LB. Effects of altering initial position on movement direction and extent. *J Neurophysiol* 89: 401–415, 2003. doi:10.1152/jn.00243.2002.

Salomonczyk D, Henriques DY, Cressman EK. Proprioceptive recalibration in the right and left hands following abrupt visuomotor adaptation. *Exp Brain Res* 217: 187–196, 2012. doi:10.1007/s00221-011-2985-4.

Sarlegna FR, Baud-Bovy G, Danion F. Delayed visual feedback affects both manual tracking and grip force control when transporting a handheld object. *J Neurophysiol* 104: 641–653, 2010. doi:10.1152/jn.00174.2010.

Sarlegna FR, Sainburg RL. The effect of target modality on visual and proprioceptive contributions to the control of movement distance. *Exp Brain Res* 176: 267–280, 2007. doi:10.1007/s00221-006-0613-5.

Shadmehr R, Mussa-Ivaldi FA. Adaptive representation of dynamics during learning of a motor task. *J Neurosci* 14: 3208–3224, 1994. doi:10.1523/JNEUROSCI.14-05-03208.1994.

Shadmehr R, Wise SP (Editors). *The Computational Neurobiology of Reaching and Pointing: A Foundation for Motor Learning*. Cambridge, MA: MIT Press, 2005.

Sinnett S, Spence C, Soto-Faraco S. Visual dominance and attention: the Colavita effect revisited. *Percept Psychophys* 69: 673–686, 2007. doi:10.3758/BF03193770.

Sober SJ, Sabes PN. Multisensory integration during motor planning. *J Neurosci* 23: 6982–6992, 2003. doi:10.1523/JNEUROSCI.23-18-06982.2003.

Sober SJ, Sabes PN. Flexible strategies for sensory integration during motor planning. *Nat Neurosci* 8: 490–497, 2005. doi:10.1038/nn1427.

Spence C. Explaining the Colavita visual dominance effect. *Prog Brain Res* 176: 245–258, 2009. doi:10.1016/S0079-6123(09)17615-X.

Stocco A, Lebiere C, Anderson JR. Conditional routing of information to the cortex: a model of the basal ganglia's role in cognitive coordination. *Psychol Rev* 117: 541–574, 2010. doi:10.1037/a0019077.

Takamuku S, Gomi H. What you feel is what you see: inverse dynamics estimation underlies the resistive sensation of a delayed cursor. *Proc Biol Sci* 282: 20150864, 2015. doi:10.1098/rspb.2015.0864.

Taylor JA, Ivry RB. Flexible cognitive strategies during motor learning. *PLoS Comput Biol* 7: e1001096, 2011. doi:10.1371/journal.pcbi.1001096.

Taylor JA, Krakauer JW, Ivry RB. Explicit and implicit contributions to learning in a sensorimotor adaptation task. *J Neurosci* 34: 3023–3032, 2014. doi:10.1523/JNEUROSCI.3619-13.2014.

Thaler D, Chen YC, Nixon PD, Stern CE, Passingham RE. The functions of the medial premotor cortex. I. Simple learned movements. *Exp Brain Res* 102: 445–460, 1995. doi:10.1007/BF00230649.

van Beers RJ, Wolpert DM, Haggard P. When feeling is more important than seeing in sensorimotor adaptation. *Curr Biol* 12: 834–837, 2002. doi:10.1016/S0960-9822(02)00836-9.

Vindras P, Viviani P. Frames of reference and control parameters in visuomanual pointing. *J Exp Psychol Hum Percept Perform* 24: 569–591, 1998. doi:10.1037/0096-1523.24.2.569.

Vogels IM. Detection of temporal delays in visual-haptic interfaces. *Hum Factors* 46: 118–134, 2004. doi:10.1518/hfes.46.1.118.30394.

Vroomen J, Keetels M. Perception of intersensory synchrony: a tutorial review. *Atten Percept Psychophys* 72: 871–884, 2010. doi:10.3758/APP.72.4.871.

Wichmann FA, Hill NJ. The psychometric function: I. Fitting, sampling, and goodness of fit. *Percept Psychophys* 63: 1293–1313, 2001. doi:10.3758/BF03194544.

Witney AG, Goodbody SJ, Wolpert DM. Predictive motor learning of temporal delays. *J Neurophysiol* 82: 2039–2048, 1999. doi:10.1152/jn.1999.82.5.2039.

Wolpert DM, Ghahramani Z. Computational principles of movement neuroscience. *Nat Neurosci* 3, *Suppl*: 1212–1217, 2000. doi:10.1038/81497.