Delayed Visual Feedback Affects Both Manual Tracking and Grip Force Control When Transporting a Handheld Object

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2Laboratoire Neurobiologie de la Cognition, Centre National de la Recherche Scientifique and Université de Provence, Marseille, France; and 3Vita-Salute San Raffaele University and Italian Institute of Technology Network Research Unit of Molecular Neuroscience, San Raffaele Foundation, Milan, Italy

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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. First published June 10, 2010; doi:10.1152/jn.00174.2010. When we manipulate an object, grip force is adjusted in anticipation of the mechanical consequences of hand motion (i.e., load force) to prevent the object from slipping. This predictive behavior is assumed to rely on an internal representation of the object dynamic properties, which would be elaborated via visual information before the object is grasped and via somatosensory feedback once the object is grasped. Here we examined this view by investigating the effect of delayed visual feedback during dextrous object manipulation. Adult participants manually tracked a sinusoidal target by oscillating a handheld object whose current position was displayed as a cursor on a screen along with the visual target. A delay was introduced between actual object displacement and cursor motion. This delay was linearly increased (from 0 to 300 ms) and decreased within 2-min trials. As previously reported, delayed visual feedback altered performance in manual tracking. Importantly, although the physical properties of the object remained unchanged, delayed visual feedback altered the timing of grip force relative to load force by about 50 ms. Additional experiments showed that this effect was not due to task complexity nor to manual tracking. A model inspired by the behavior of mass-spring systems suggests that delayed visual feedback may have biased the representation of object dynamics. Overall, our findings support the idea that visual feedback of object motion can influence the predictive control of grip force even when the object is grasped.

I N T R O D U C T I O N

Efficient motor control relies on the brain learning to specify motor commands but also to predict the consequences of these motor commands (Wolpert and Flanagan 2001). Predictive mechanisms are necessary because of the delays associated with visual and proprioceptive feedback pathways and the instability that those delays can induce in feedback controllers (Desmurget and Grafton 2000; Houk and Rymer 1981; Miall et al. 1993). Predictive mechanisms have been demonstrated in motor behaviors as diverse as object manipulation, locomotion, gaze orientation, or manual tracking (Bastian 2006; Flanagan et al. 2003; Miall and Jackson 2006; Vaziri et al. 2006). For instance, when we manipulate a handheld object, grip force is largely determined by predictive mechanisms, as evidenced by its modulation preceding or being in synchrony with the destabilizing load force resulting from the hand movement (i.e., tangential load at the object–finger interface; Danion and Sarlegna 2007; Davare et al. 2007; Johansson and Westling 1988a; White et al. 2005; Zatsiorsky et al. 2005). Moreover, such anticipatory adjustments are observed irrespectively of the number of hands or fingers used to hold the object (de Freitas and Jarić 2009; Flanagan and Tresilian 1994). The leading hypothesis is that the nervous system anticipates the load force using internal representations of the body and the object in conjunction with a copy of the motor commands (Flanagan and Wing 1997; Kawato 1999). How the nervous system develops and updates internal representations of the body and its environment is a central issue in research on motor control (Shadmehr and Wise 2005).

Object manipulation critically relies on the updating of the internal representation of object dynamics based on sensory feedback. Prior to picking up an object, vision provides critical information (e.g., size or shape) to infer its dynamic properties and specify grip force (Cole 2008; Jenmalm et al. 2000; Lukos et al. 2008). Once the object is actually grasped and lifted, visual feedback seems less critical, as suggested by the lack of difference in grip force control between vision and no-vision conditions (Johansson and Westling 1988b; Nowak 2004). In contrast, somatosensory feedback (i.e., tactile and proprioceptive feedback) is essential to quickly adjust grip force (Hermsdörf er and Nowak 2009; Hermsdörfer et al. 2008; Johansson and Flanagan 2009; Witney et al. 2004), notably when lifting objects lighter (or heavier) than expected from their visual appearance (Buckingham et al. 2009; Flanagan and Beltzner 2000; Gordon et al. 1991). Therefore once the object is grasped, somatosensory feedback appears more crucial than visual feedback for dextrous manipulation.

The present study aimed at testing whether vision of the object still contributes to the predictive control of grip force once the object is grasped. For this purpose, we delayed the visual feedback of object motion while participants manually tracked a target on a screen by moving a handheld object. Although the effects of delayed visual feedback on manual tracking are well established (Foulkes and Miall 2000; Vercher and Gauthier 1992), its effects on grip force control have never been examined. In fact, it is important to note that delaying the visual feedback does not require a priori any adaptation in grip force control since it does not change the dynamic properties of the object nor the relationship between the hand movement and the load force. In this respect, this study differs from a study of Witney and colleagues (1999) in which all sensory conse-
quences (i.e., visual and somatosensory ones) of the action were delayed.

We chose to continuously vary the visual delay within trials to assess whether grip force control is tuned on-line by visual feedback. Although we were mainly interested in the immediate effects of delayed visual feedback on grip force control and manual tracking, a secondary goal was to assess the presence of adaptation to this perturbation. To achieve this goal, we used a protocol with pretest, exposure, and posttest trials (Held and Freedman 1963; Sarlegna et al. 2007; Witney et al. 1999). Assuming that the internal representation of a handheld object is mainly influenced by somatosensory feedback when moving this object, we hypothesized that the predictive control of grip force should not be influenced by delayed visual feedback. Surprisingly, the results of our first experiment revealed a significant effect of vision on grip force control. This finding was further investigated in a second experiment.

Considering that delaying the visual feedback might have increased the task complexity as reflected by increased tracking errors (Foulkes and Miall 2000; Smith 1972) and that task complexity per se can influence grip force control (Serrien and Wiesendanger 2001), the second experiment included two novel conditions that aimed at teasing apart the effects of task complexity and delayed visual feedback. In the first condition, the effect of task complexity was examined in the absence of visual delay, whereas in the second condition, the effect of visual delay was examined in the absence of tracking task (which was suppressed in an attempt to decrease task complexity).

METHODS

Subjects

Twenty self-proclaimed right-handed subjects participated in this study. Participants were split in two groups of eight males and two females (Group 1 mean age = 29 yr, Group 2 mean age = 29 yr), each group performing a different experiment. All participants were healthy and gave informed consent prior to the study, according to University regulations and the 1964 Declaration of Helsinki.

Apparatus

In a fully illuminated room, participants had to move an object held between the thumb and the index finger of their right hand (Fig. 1A).

For each participant, two experimenters were present to ensure that task requirements were respected. In particular, we made sure that the object was grasped with the fingertips at the center of the contact surfaces throughout the experiment. The handheld object was a force sensor (ELPM-T1M-50N; Entran, Fairfield, NJ measuring the force perpendicular to its surface (i.e., grip force, GF). The cylindrical object (4 cm large, 2 cm in diameter) was covered with sandpaper, resulting in a mean (±SD) friction coefficient of 0.97 ± 0.13 for Group 1 and 0.99 ± 0.17 for Group 2. The equipped object (mass = 0.056 kg) was attached to an elastic cord (stiffness = 33 N/m) to create a load force (LF) that varied as a function of hand movements (linearity between hand position and elastic tension in the workspace: $R > 0.99$) and remained substantial even for slow movements. LF was measured with another force sensor (ELPM-T1M-25N; Entran) attached to the elastic cord (see Fig. 1B). Both LF and GF were collected at 1,000 Hz. As in other studies (Danion and Sarlegna 2007; Danion et al. 2009; Hersmsdörfer et al. 2008; Uygur et al. 2010; Witney et al. 1999), this methodology assumes that GF and LF are shared symmetrically between the thumb and the other finger(s). We also ensured that the object was grasped such that the center of gravity of the object was between the contact points and that torques about the grip axis were minimized.

Each participant had to hold the object with a precision grip during all trials. Participants were seated about 65 cm in front of a 20-in. computer monitor (1,600 × 1,200 pixel resolution; 75 Hz refresh rate). The computer monitor displayed the target (white circle, 6 mm in diameter) and a cursor (red rectangular cursor, 2 × 4 mm) that provided visual feedback about the object position (see Fig. 1B). The horizontal position of the cursor was displayed according to the current LF, using customized software and a real-time acquisition system (ADwin-Pro; Jäger, Lorsch, Germany). The gain between object and cursor displacement was 0.92. The time needed to translate the data recorded by the force transducer into the visual feedback was 27 ms. For the sake of clarity, this delay between object and cursor motion was used as baseline (i.e., 0). Target and cursor positions were recorded (in N) at 1,000 Hz.

Procedure

The participants were instructed to continuously move the handheld object in the frontoparallel plane to track the target with the cursor as accurately as possible (Fig. 1). Object motion was seen through a computer monitor and, as in similar studies (Dingwell et al. 2002; Flanagan et al. 2003), subjects were able to complete the task. Each experiment was preceded by a 1-min trial with normal visual feedback to familiarize the participant with the task.

FIG. 1. Experimental setup. Participants had to track a visual target oscillating horizontally with a cursor representing the position of a handheld object. A delay could be introduced between hand motion and cursor motion.
EXPERIMENT 1. Participants (Group 1) had to track a target oscillating sinusoidally (period = 1.8 s, frequency = 0.556 Hz) on a 12 cm horizontal line. The target motion was sinusoidal and thus highly predictable to facilitate the tracking task (Weir et al. 1989). Target oscillation required the LF varying between 3 and 7 N.

Participants performed 12 trials of 130 s each. The first three NORMAL trials served as PRE-test trials to assess baseline performance with normal visual feedback (i.e., with no delay). During the subsequent six trials (DELAY trials), the delay between object and cursor motion was manipulated while participants tracked the target. After the first 5 s of each trial, the delay increased linearly from 0 to 300 ms in 60 s, then decreased linearly back to 0 ms in 60 s and then remained null for the last 5 s. Right after the six DELAY trials, participants performed three NORMAL trials (similar to the first three trials). Despite the fact that any residuals of motor adaptation were potentially washed off (the visual delay being reset to 0 at the end of each DELAY trial), comparisons between POST-test and PRE-test trials were investigated to assess the presence of aftereffects (Held and Freedman 1963; Sarlegna et al. 2010; Shadmehr and Wise 2005). For each participant, breaks were given between trials to avoid fatigue. The experiment lasted about an hour.

EXPERIMENT 2. Using the same setup, we asked a new group of subjects (Group 2) to participate in a second experiment that included 13 trials of 130 s. The first three NORMAL trials (as previously defined) served as PRE-test trials. In the next three trials (so-called COMPLEX trials), we increased the task complexity without delaying visual feedback by making target motion less predictable. In COMPLEX trials, target motion represented the weighted sum of two signals. The first signal corresponded to the initial sinusoid (F = 0.556 Hz), whereas the second signal was generated using five nonharmonic sinusoids (F = 0.101, 0.185, 0.219, 0.420, and 0.556 Hz) whose relative phases were randomized (for a similar procedure, see Miall and Jackson 2006). During the first and last 5 s of the COMPLEX trials, the weight of the sinusoidal signal was set to 1, whereas the weight of the second signal was set to 0 such that the target moved like that in the NORMAL trials. Between 5 and 65 s, target motion became increasingly random and difficult to predict because both weights varied linearly in opposite directions such that at t = 65 s, the weight of the sinusoidal signal was 0 whereas the weight of the second signal was 1. The unpredictability of target motion was then symmetrically decreased, so that target motion returned to a pure sinusoid for the last 5 s. The parameters of target motion were selected based on pilot experiments to obtain similar evolutions of tracking errors and cursor–target lag in DELAY and COMPLEX trials. To preserve the unpredictability of target motion, the relative phases of the five nonharmonic sinusoids were randomized across the three COMPLEX trials. After these trials, participants performed three NORMAL, POST-test trials that enabled participants to restore baseline performance (washout).

Then, participants performed three trials similar to DELAY trials (experiment 1), except that no target ("noT") was displayed on the screen. In these so-called DELAY-noT trials, participants were instructed to attend to the screen and to keep the cursor moving so that its displacement on the screen was identical in terms of frequency and amplitude to the preceding NORMAL trials. Occasionally, participants received verbal feedback to ensure adequate frequency and amplitude. Finally, participants performed a NORMAL, posttest trial (labeled POST2 trial). The experiment lasted approximately an hour.

Data analysis

All signals were low-pass filtered at 5 Hz (fourth-order, no-lag, dual-pass Butterworth). Because of the lightness of the object and slowness of the movement, the resulting inertial load force (<0.1 N) was small compared with the elastic load force (3 < LF < 7 N) and thus was neglected (Danion and Sarlegna 2007). Figure 2 shows representative time windows of LF and GF signals in each experimental condition, but also target and cursor signals. For each panel, it should be noted that the cursor and load force signals are the same (although they are shifted in time in Fig. 2, B and D due to the visual

![Figure 2](http://jn.physiology.org/)

**FIG. 2.** Representative cursor–target and grip–load force signals. A and B: data collected during NORMAL (no visual delay) and DELAY trials (visual delay close to its maximum) from the same participant. C and D: data collected during COMPLEX (target motion complexity close to its maximum) and DELAY-noT trials (visual delay close to 300 ms, no tracking task) from another participant. For all panels, the time window within the trial was 62.5 to 67.5 s.
Each trial was segmented into 26 bins of 5 s except for the first bin that did not include the first second of the trial because the participants needed some time to start moving the cursor (see Miall 1996). Tracking performance was assessed by computing the root mean squared error (RMSE) and the time lag between target and cursor motions (using cross-correlations; Weir et al. 1989), to determine whether tracking errors stemmed from the cursor preceding or following the target. To analyze movement kinematics, hand position (estimated from LF) was differentiated to obtain velocity and acceleration signals. The absolute values of peak velocity, mean velocity, and peak acceleration were used as dependent variables. The grip–load force coupling was assessed using cross-correlation between GF and LF, which provides a correlation coefficient (R) as well as the temporal relationship (lag) between the two signals (Flanagan and Wing 1997). Negative values of cursor–target lag indicate that cursor motion precedes target motion. Negative values of grip–load lag indicate that GF precedes LF. Mean GF was also investigated.

The main statistical analyses used in this study were ANOVAs. To analyze the effect of delayed visual feedback in experiment 1, we report the results of a two-way repeated-measures ANOVA with Delay (13 levels: 0, 25, 50, . . ., 300 ms) and Trial (6 levels) as within-subject factors. This analysis pools together the two 5-s bins with the same visual delay in the ascending and descending phases of each trial. Similar procedures were used in experiment 2 to analyze the effect of Complexity (13 levels: 0, 0.08, 0.16, . . ., 1 arbitrary units) and Delay (13 levels: 0, 25, 50, . . ., 300 ms). When significant effects were found, trend analyses were performed using polynomial contrasts. Greenhouse–Geisser correction was used to correct for nonsphericity. The normality of data sets was verified using the Kolmogorov–Smirnov method. Newman–Keuls technique was used for post hoc analyses. Since correlation coefficients do not follow a normal distribution, z scores (Fisher transformation) were used for statistical analysis. A 0.05 significance threshold was used for all analyses.

**RESULTS**

**Experiment 1**

**MANUAL TRACKING WITH DELAYED VISUAL FEEDBACK.** The effect of delayed visual feedback on tracking performance is presented in Fig. 3, which shows the average behavior during all 12 experimental trials. The three initial NORMAL, PRE-test trials were used to assess baseline performance. RMSE is presented in Fig. 3A, GF and LF appear in Fig. 3B, and the temporal lag between cursor and target motion is shown in Fig. 3C. The thin line in Fig. 3C represents the visual delay. The instant at which the maximal delay is reached is indicated by vertical dash-dotted lines on all panels. In the first DELAY trial, it can be seen that the cursor–target lag increased when the visual delay increased. However, the cursor–target lag varied less than the visual delay, indicating that participants actively compensated for the presence of the visual delay. For instance, when the visual delay was 300 ms, the cursor lagged behind the target by 100 ms, meaning that participants partly compensated for the visual delay by having their hand motion preceding target motion by 200 ms. When the visual delay...
significant delay in the visual delay and the cursor–target lag. There was no significant effect from 0.12 to 0.13 m/s; similar findings, i.e., a significant increase of errors with the task. Performance improved across trials. Analysis of RMSE revealed an observation consistent with the view that tracking performance improved across trials. Analysis of RMSE revealed similar findings, i.e., a significant increase of errors with the visual delay and a significant improvement across trials.

Figure 3C shows that in POST trials, the cursor preceded the target. To assess the significance of this anticipatory behavior, the (entire) first POST trial was compared with the last PRE trial using a repeated-measures ANOVA with Trial (PRE, POST) and Time bin (26 levels) as within-subject factors. Although signs of adaptation in the posttest trials were potentially washed off (due to the fact that the visual delay was reset to 0 at the end of DELAY trials), significant main and interaction effects on the cursor–target lag were revealed (all values of $F > 2.5$; all values of $P < 0.01$). Post hoc analysis of the interaction effect $[F_{(25,225)} = 2.6; P < 0.001]$ showed that the lag significantly differed for the first three 5-s bins between PRE and POST trials.

With respect to movement kinematics, participants moved the handheld object at the target frequency. Indeed, a peak-to-peak analysis showed that, for each trial, the average movement frequency was 0.555 Hz. We further analyzed whether delayed visual feedback influenced hand-movement kinematics. Two-way ANOVAs with Delay (13 levels) and Trial (6 levels) as within-subject factors showed that as the visual delay increased, peak hand velocity increased [from 0.25 to 0.31 m/s; $F_{(12,108)} = 24.9; P < 0.001$] as well as mean hand velocity [from 0.12 to 0.13 m/s; $F_{(12,108)} = 10.6; P < 0.001$] and peak hand acceleration [from 1.61 to 1.82 m/s$^2$; $F_{(12,108)} = 6.2; P < 0.001$]. Peak hand velocity decreased across trials [from 0.29 to 0.27 m/s; $F_{(5,45)} = 6.8; P < 0.01$] and so did peak hand acceleration [from 1.78 to 1.58 m/s$^2$; $F_{(5,45)} = 7.5; P < 0.001$]. There were no significant interactions.

**GRIP FORCE CONTROL WITH DELAYED VISUAL FEEDBACK.** The main finding of the present study is illustrated in Fig. 3D, which shows that delayed visual feedback affected the temporal coupling between GF and LF such that the two signals were less synchronized. Indeed, in all DELAY trials, GF was shifted forward and thus preceded more LF as a function of the visual delay. When the visual delay was maximal (300 ms), GF preceded LF by about 80 ms, whereas GF preceded LF by nearly 30 ms at the initiation of DELAY trials (as in PRE trials). A two-way repeated-measures ANOVA with Delay (13 levels) and Trial (6 levels) as within-subject factors confirmed the main effect of Delay $[F_{(12,108)} = 8.4; P < 0.01]$. The trend analysis revealed that the linear component ($P < 0.05$) explained 81% of the variance. Figure 4B illustrates the linear correlation between the visual delay and the grip–load lag, indicating that the observed effect is not a purely default response.

The grip–load lag was not significantly affected by Trial $[F_{(5,45)} = 1.3; P > 0.05]$ and there was no significant interaction effect $[F_{(60,540)} = 1.1; P > 0.05]$. In summary, although the physical properties of the handheld object remained strictly

![Figure 4](http://jn.physiology.org/)

**FIG. 4.** Correlations with visual delay (*experiment 1*). **A:** correlation between the visual delay and the cursor–target lag (data averaged across subjects and DELAY trials). **B:** correlation between the visual delay and the grip–load lag (data averaged across subjects and DELAY trials). Each trial was segmented in 26 bins of 5 s. Solid and empty squares correspond to data points during the first and second halves of the trials (increasing and decreasing delay, respectively). Vertical bars correspond to the 90% confidence interval (CI) of the mean.
identical, the visual delay affected the predictive control of grip force, shifting forward its modulation (up to ~50 ms). This is shown in Fig. 5A, which compares the mean temporal profiles of GF and LF with and without visual delay. Figure 5B shows the related GF–LF phase portraits in which a straight line corresponds to perfect synchrony, whereas an ellipse indicates a phase lag between the two signals. This figure clearly illustrates that the visual delay increased the asynchrony between GF and LF.

Although the grip–load lag was affected by the visual delay, the coefficient of cross-correlation between GF and LF was not. Indeed, a Delay × Trial ANOVA on the R value (transformed in z score) between GF and LF did not reveal any significant main effect or interaction (all values of P > 0.05). The mean R value was 0.93 across DELAY trials and was 0.91 across PRE trials.

Figure 3B shows that although LF was stable, GF decreased within trials and across trials. The decrease in GF was not correlated with the up-and-down variation in visual delay, as supported by a Delay × Trial ANOVA that did not reveal any significant effect (mean GF = 7.7 N; all values of P > 0.05). Similar decreases across trials have been reported elsewhere (Crevecoeur et al. 2009; Gordon et al. 1993) and likely reflect familiarization with the manipulation task. Our data suggest that with longer trials (compared with earlier studies), similar familiarization effects can be observed at the timescale of a single trial.

We also examined whether, when the visual delay varied (i.e., in DELAY trials), variations in grip–load lag were influenced by subjects’ ability to compensate for the visual delay in the manual tracking task. For each subject, the mean grip–load lag obtained across NORMAL trials (at t = 65 s) was subtracted from the mean grip–load lag obtained across DELAY trials observed at t = 65 s, i.e., when the visual delay was maximum. The ability to compensate for the visual delay was assessed by subtracting for each subject the mean cursor–target lag across DELAY trials (at t = 65 s) from the maximum visual delay (300 ms). Across subjects, there was no significant correlation between these two parameters (R = −0.15; P > 0.05).

To assess the presence of changes in grip force control after exposure to delayed visual feedback, we compared the trials immediately preceding and following DELAY trials using a Trial (PRE, POST) × Time bin (26 levels) repeated-measures ANOVA. This analysis did not reveal any significant main or interaction effect on the grip–load lag (all values of P > 0.05).

**Experiment 2**

The first experiment demonstrated the influence of delayed visual feedback on grip force control. Because increasing the visual delay also increased the complexity of the task, we performed two additional conditions to tease apart the effects of task complexity and delayed visual feedback. To achieve this goal, we focused on the comparison between DELAY trials from experiment 1 and COMPLEX or DELAY-noT trials from experiment 2 (rather than on the comparison between COMPLEX and DELAY-noT trials).

**Tracking an Unpredictable Target (Without Visual Delay)**. Figure 6 shows that although the RMSE and the cursor–target lag remained stable throughout the initial NORMAL trials, both RMSE and cursor–target lag varied in COMPLEX trials such that they increased when the complexity of the target motion increased (throughout the first 65 s). Conversely, when the complexity of target motion decreased, both RMSE and cursor–target lag decreased. The influence of target motion complexity was statistically confirmed by an ANOVA with Complexity (13 levels) and Trial (3 levels) as within-subject factors. The ANOVA on the cursor–target lag showed a significant effect of Complexity [F_{12,108} = 128.9; P < 0.001]. The trend analysis of this effect showed that the cursor–target lag increased linearly with the complexity (P < 0.001), the linear trend explained 95.4% of the variance. There was no significant interaction [F_{24,216} = 1.1; P > 0.05] but there was a main effect of Trial [F_{2,18} = 6.0; P < 0.01]. The trend analysis showed that the mean cursor–target lag decreased toward 0 between trial 1 and trial 3 (P < 0.01), supporting the idea that participants performed better with practice.

Concerning hand movement kinematics, two-way ANOVAs with Complexity (13 levels) and Trial (3 levels) as within-subject factors showed that when target motion complexity increased, peak hand velocity [from 0.26 to 0.27 m/s; F_{12,108} = 2.7; P < 0.05] and peak hand acceleration increased [from 1.65 to 2.32 m/s^2; F_{12,108} = 25.2; P < 0.001]. There were no significant Trial effects or interactions.

An important issue was to verify whether task complexity was similar in COMPLEX trials (experiment 2) and DELAY.
trials (experiment 1). To test this, cursor–target lag and RMSE were compared between the two types of trials. For each parameter, we computed the mean value across COMPLEX trials (at \( t = 65 \) s, i.e., when the target motion complexity reached its maximum) and the mean value across DELAY trials (also at \( t = 65 \) s, i.e., when the visual delay reached its maximum). For both the cursor–target lag (\( t = 0.8; P = 0.05 \)) and the RMSE (\( t = 1.7; P > 0.05 \)), \( t \)-tests did not reveal any significant difference between COMPLEX and DELAY trials.

**GRIP FORCE CONTROL WHILE TRACKING AN UNPREDICTABLE TARGET.** Figure 6B shows that, although some variations in the grip–load lag were observed during COMPLEX trials, these variations were not related to target motion complexity (which increased and decreased within each of the three COMPLEX trials). An ANOVA with Complexity (13 levels) and Trial (3 levels) as within-subject factors did not reveal any significant difference between COMPLEX and DELAY trials.

**EXPOSURE TO DELAYED VISUAL FEEDBACK IN A NONTRACKING TASK AFFECTS SUBSEQUENT TRACKING PERFORMANCE.** In DELAY-noT trials, no target was displayed but a peak-to-peak analysis showed that participants moved the handheld object at the requested frequency (mean \( = 0.554 \) Hz). Analyzing hand movement speed and acceleration, two-way ANOVAs with Delay (13 levels) and Trial (3 levels) as within-subject factors showed that when the visual delay increased, peak hand acceleration decreased [from 1.86 to 1.61 m/s\(^2\); \( F_{(12,108)} = 5.0; P < 0.01 \)] as well as mean hand velocity [from 0.17 to 0.16 m/s; \( F_{(12,108)} = 3.6; P < 0.05 \)]. Peak hand acceleration also decreased across trials [from 1.78 to 1.58 m/s\(^2\); \( F_{(5,45)} = 7.5; P < 0.001 \)]. There was no significant interaction. There was no significant main or interaction effect on peak hand velocity (mean = 0.29 m/s; all values of \( P > 0.05 \)).

Figure 6 shows that in the last POST2 trial, the cursor preceded the target. An ANOVA with Trial (PRE, POST2) and Time bin (26 levels) as within-subject factors confirmed the significance of this anticipatory behavior by showing a main effect of Trial on the cursor–target lag [\( F_{(3,27)} = 32.7; P < 0.001 \)].
DELAYED VISUAL FEEDBACK AFFECTS GRIP FORCE CONTROL IN A NONTRACKING TASK. The main finding presented in Fig. 6A is that, within DELAY-noT trials, delayed visual feedback affected the grip–load lag. As the visual delay increased, GF preceded more LF. Then, as the visual delay decreased, the lag returned to original values. The two-way ANOVA with Delay (13 levels) and Trial (3 levels) as within-subject factors confirmed the effect of Delay on the grip–load lag \( F(12,108) = 8.5; \ P = 0.001 \). The trend analysis revealed a significant linear trend \( (P < 0.001) \): Fig. 7B shows the strong correlation between the visual delay and the grip–load lag. Concerning the coefficient of cross-correlation between GF and LF, \( R \) values were high in all DELAY-noT trials \( (mean = 0.93) \) and a Delay \( \times \) Trial ANOVA (on \( z \) scores) showed no significant effect \( (all values of \( P > 0.05 \)).

To assess whether tracking a target influences the effect of delayed visual feedback on the timing of grip force, we compared the effect of visual delay on the grip–load lag in DELAY and DELAY-noT trials \( (experiments 1 \ and \ 2, \ respectively) \). A \( t \)-test for independent samples did not reveal any significant difference \( (t = 1.1; \ P > 0.05) \) between the changes in grip–load lag induced by delayed visual feedback in DELAY and DELAY-noT trials \( (NORMAL \ trials \ serving \ as \ baseline) \). We also performed individual linear regressions between visual delay and grip–load lag and found no significant difference between the slopes in DELAY and DELAY-noT trials \( (t = 0.47; \ P > 0.05) \).

**DISCUSSION**

In the absence of visual delay, a tight coupling between grip force and load force was observed, as reflected by high coefficients of correlation \( (R > 0.9) \) and small temporal lags between the two signals \( (approximately \ -30 \ ms) \). Such small, possibly negative, lags are consistent with previous research \( (Danion \ and \ Sarlegna \ 2007; \ Davare \ et \ al. \ 2007; \ Flanagan \ and \ Wing \ 1997; \ Nowak \ 2004) \) and indicate that grip force was adjusted in anticipation, rather than in response, of the sensory consequences of load force \( (Kawato \ 1999; \ Wolpert \ and \ Flanagan \ 2001) \). In our experiment, participants received visual feedback of the object load force on a computer monitor \( (Dingwell \ et \ al. \ 2002; \ Flanagan \ et \ al. \ 2003) \). They also had tactile feedback of the object load force at the object–finger interface as well as proprioceptive feedback from muscular and joint receptors. The integration of these spatially segregated signals did not seem to substantially affect object manipulation during our simple, unidimensional movements, since the grip–load force coupling was similar to that in our previous experiments \( (Danion \ and \ Sarlegna \ 2007; \ Danion \ et \ al. \ 2009) \).

When we introduced a visual delay, we found that delayed visual feedback affects manual tracking performance, an observation consistent with previous research \( (Foulkes \ and \ Miall \ 2000; \ Langenberg \ et \ al. \ 1998; \ Smith \ 1972) \). The novel finding of the present study is that delayed visual feedback affects grip force control when participants move a handheld object. More specifically, the temporal synchrony between grip force and load force decreases as a function of the visual delay. Although previous studies investigated the effect of vision by comparing vision versus no-vision conditions and reported no significant differences in grip force control \( (Johansson \ and \ Westling \ 1988b; \ Nowak \ 2004) \), the present study shows for the first time \( (to \ our \ knowledge) \) that visual feedback of object motion influences grip force control. In the following discussion, we will consider possible mechanisms accounting for our findings.

**Does task complexity influence the predictive control of grip force?**

The present study revealed a strong correlation between the visual feedback delay and the grip–load lag. Surprisingly, grip force was more ahead of the load force when the visual delay increased. Indeed, the grip–load lag shifted from approximately \(-30 \ to \ -80 \ ms\) when the visual delay shifted from \(0 \) to \(300 \ ms\). Such an effect was surprising since, to our knowledge, only virtual lesions of cortical motor areas \( (by \ transcranial \ magnetic \ stimulation; \ Davare \ et \ al. \ 2006, \ 2007) \) and corticospinal lesions \( (Duque \ et \ al. \ 2003) \) have been shown to result in earlier grip force modulations relative to load force. However,
increasing the visual delay also increased the complexity of the manual tracking task, as reflected by tracking errors. To assess the influence of task complexity on grip force control, we investigated two other experimental conditions in experiment 2. In the first condition, task complexity was manipulated through target motion. Despite the fact that task complexity was matched with experiment 1 (in terms of tracking error and cursor–target lag), we did not find any significant changes in the temporal relationship between grip force and load force; such a result obtained with continuous and unpredictable target displacement extends our previous finding obtained with discrete and unpredictable target displacement (Danion and Sarlegna 2007). In the second condition, task complexity was decreased by removing the visual target, so that participants only had to oscillate the handheld object with delayed visual feedback. Despite the absence of explicit tracking and visual error signals, we observed that the visual delay affected the temporal lag between grip force and load force, to the same extent as that in experiment 1. Altogether, both experiments indicate that the visual delay, not task complexity or manual tracking, influences the temporal coupling between grip force and load force.

How independent is grip force control from the adaptation of hand movements?

In agreement with previous findings, we observed that hand movement control adapted to the delayed visual feedback. First, we observed a general reduction in tracking errors across trials (Foulkes and Miall 2000; Miall and Jackson 2006). Second, we observed significant aftereffects in manual tracking (Cunningham et al. 2001; Miall and Jackson 2006; Smith and Bowen 1980) despite the fact that those could have been washed off due to our experimental design (i.e., the visual delay being reset to 0 at the end of each trial). These findings are consistent with the idea that introducing a visual delay leads to an adaptive modification of the visuomotor transformations (Miall and Jackson 2006). On the other hand, our protocol never changed the relationship between arm motor commands and the resulting load force (and thus somatosensory consequences). Therefore there was a priori no need to modify the predictive control of grip force. Still, changes in the relation between grip force and load force were observed and these were always observed concurrently with adaptation in manual tracking. This raises a question: Could adaptation of hand movement to delayed visual feedback have caused changes in the control of grip force?

We believe this is unlikely for the following reasons. First, changes in manual tracking performance and grip force control exhibited different patterns. Indeed, in the main experiment, the effect of delayed visual feedback on the grip–load lag did not significantly change throughout the trials, whereas the effect on cursor–target lag did change. Second, although we found differences in hand movement control between PRE and POST trials, no such significant differences were found in grip force control (although a possible washout due to our procedure cannot be discarded). Third, we did not find a significant correlation between subjects’ ability to compensate for the visual delay (as reflected by the cursor–target lag) and grip–load force synchrony. In other words, the subjects who compensated the most efficiently for the visual delay were not necessarily those who exhibited the largest changes in grip force control.

Altogether, these findings suggest that the adaptation of hand movements did not critically influence grip force control, which may have theoretical implications. Indeed, it has been suggested that both grip force control and arm movement control rely on forward models predicting action consequences (Desmurget and Grafton 2000; Flanagan et al. 2003; Kawato 1999; Miall and Jackson 2006). Here, since adaptation was observed only for the manual tracking movements, one can hypothesize that distinct forward models underlie the control of grip force and visually guided arm movements. This idea of multiple predictors is reminiscent of a previous proposal by Miall et al. (1993) who suggested that the brain predicts separately the visual and somatosensory consequences of actions. Neurophysiological support for this hypothesis was later provided by Liu et al. (2003) who showed that in the cerebellum, distinct neurons code for the visual and somatosensory consequences of limb motion.

How does visual feedback affect the predictive control of grip force?

The current study showed a continuous change in grip force control as visual feedback was progressively delayed. Having discarded an influence of task complexity and arm movement adaptation, we now consider the possible mechanisms by which delayed visual feedback could act on grip force control. A first possibility could be that delayed visual feedback influenced grip force control because, under challenging conditions, the visual position of the object started being used to infer the current tension of the elastic, i.e., the load force. Assuming that grip force became adjusted with this “visually perceived load” offers a rationale for the increased asynchrony between grip force and load force. However, this scheme predicts delayed grip force adjustments (relative to load force) when the visual delay increases. The fact that the opposite pattern was observed indicates that grip force was not timed to the visual feedback of object motion.

It is possible that the effect of delayed visual feedback on the grip–load lag could reflect a subject’s response to the uncertainty caused by the spatial and temporal mismatch between visual and real object motion (i.e., visuoproprioceptive mismatch; Langenberg et al. 1998). One could reason that earlier grip force adjustments represent a safety measure to ensure that the object does not slip. However, the load force was constantly oscillating (i.e., increasing and decreasing) in our task. Although earlier grip force adjustments could be viewed as a safety measure when the load force is about to increase, it should be pointed out that grasp stability is threatened when the grip force starts decreasing while the load force is still increasing.

Because delayed visual feedback influenced hand movement kinematics, one may question whether kinematic changes could be responsible for changes in grip–load force coupling. The fact that similar effects were observed on grip force control in both DELAY and DELAY-noT trials, despite opposite changes in kinematics, does not support this hypothesis. Furthermore, this scheme also has difficulties to account for the observation that movement speed and acceleration increased in DELAY and COMPLEX trials, whereas distinct effects were obtained on the grip–load lag. Altogether, it seems that movement kinematics did not critically influence the temporal coupling between grip force and load force. This conclusion fits rather well with previous studies showing that the grip–load lag is not significantly influenced by movement speed (Uygur et al.
Could delayed visual feedback modify the internal representation of object dynamics?

Earlier studies showed that visual feedback of object motion can alter object representation (Lecuyer et al. 2001), even with simplistic visual stimuli such as in the “rubber pencil illusion” (Pomerantz 1983). Here, we explored the possibility that the introduction of a delay between cursor and hand movement may have been perceived as the adjunction of a novel mass-spring system whose (virtual) load force was also taken into account to control grip force. Interestingly, one feature of a mass-spring system is that when being oscillated (at a constant frequency), the mass is lagging behind the imposed motion (by a constant delay). Moreover, recent studies showed that humans can extract relevant properties of mass-spring systems via visual information only (Israr et al. 2009; Norman et al. 2007). To assess whether the adjunction of a novel, virtual mass-spring system would have similar effects on the load force as a visual delay, we used a mechanical model (see the APPENDIX) in which a damped mass-spring system was attached to the hand (in addition to the real elastic). Our simulations (see also Fig. A2 in the APPENDIX) showed that if the virtual load force is alternating between positive and negative values (mean = 0) and 2 there is a phase lag between the virtual and the real, elastic load. Therefore contrary to intuition, the adjunction of a mass-spring system does not necessarily increase the combined (real + virtual) load force. However, one critical effect of summing the real elastic load force with the virtual load force is a forward shift of the combined load force with respect to the real load force. We reason that if grip force is modulated as a function of this combined load force, this should also result in a forward shift of grip force (i.e., earlier modulations). To obtain a 50 ms forward shift (as observed in experiments 1 and 2), the model provided a set of parameters for the mass-spring system that did not appear unrealistic (mass = 0.5 kg, stiffness = 3.1 N/m, damping = 1.5 N m s⁻¹).

Altogether, the model suggests that earlier grip force modulations could result from the visually induced illusion of a mass-spring system attached to the handheld object, thereby affecting the representation of the object dynamics. This scheme would be consistent with another study in which participants felt that “when the visual delay is of the order of 250 ms, one’s arm and hand movements take on a peculiar ‘rubbery’ quality” (Smith 1972; see also Vercher and Gauthier 1992). One may speculate that such visually induced illusion contributes to the detrimental effects of visual delays during teleoperation (e.g., Kim et al. 2005).

Concluding remarks

The present study showed that the predictive control of grip force was influenced by delayed visual feedback. The fact that visual feedback is important for internal representations prior to picking up an object has been reported earlier (Cole 2008; Flanagan and Beltzner 2000; Gordon et al. 1991; Lukos et al. 2008). The novelty of the current study is to show that vision still contributes to grip force control after the object has been grasped (i.e., when somatosensory feedback is available). Although earlier studies showed that grip force adjustments are similar when eyes are closed or open (Johansson and Westling 1988b; Nowak 2004), the present study demonstrates that a subtle perturbation can still reveal the influence of visual feedback.

APPENDIX

In the DISCUSSION, we indicated that delaying the visual feedback may have modified the representation of object dynamics. In other words, participants may have perceived that they manipulated an object with time-varying physical properties and adjusted the grip force in consequence. Here, we show that it is possible to replace the visual delay by a damped mass-spring system and to predict a forward shift of the grip force.

The delayed visual feedback (cursor motion) corresponds to the motion of a damped mass-spring

In our model, we first assumed that the hand trajectory was sinusoidal. Formally, the hand trajectory \( y(t) \) is defined as

\[
y(t) = A_H \sin(\omega t)
\]

\[(A1)\]

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frequency of the target motion and 1.8 s). Note how

$\theta = 0.17 \pm 0.30$ s on May 28, 2017 http://jn.physiology.org/ Downloaded from

\[ F_{\text{ext}} = mx'' = k(y - x) + c(y' - \dot{x}) \]  

where $\theta$ is the negative time shift, or lag, that corresponds to the visual delay, which varied between 0 and 300 ms in this study ($0 < \theta > -0.3$ s). We now show that the mass of a virtual damped mass-spring system (Fig. A1) can move exactly like a delayed cursor.

The equation of motion of this system is

\[ m\ddot{x} + c\dot{x} + kx = k\sin(\omega t) + c\omega \cos(\omega t) = f(t) \]

with a sine/cosine forcing term $f(t)$. The steady-state solution of this equation has the same form as the cursor motion (Eq. A2)

\[ x = A_M \sin[\omega(t + \theta_M)] \]  

The lag $\theta_M$ and amplitude $A_M$ of the mass of this virtual damped mass-spring system are

\[ \omega_A \theta_M = \arctan\left(\frac{c\omega}{k}\right) - \arctan\left(\frac{c\omega}{k - m\omega^2}\right) \]  

\[ A_M = \frac{A_H \sqrt{k^2 + c^2\omega^2}}{\sqrt{(k - m\omega^2)^2 + c^2\omega^2}} \]  

Computation of the combined load force

The core idea of this model is that the grip force is not coupled with the real load force but is coupled with the combined load force $F_C$.
that results from adding the load force of the elastic (F_E) to the load force of the virtual mass-spring system (F_M). More specifically, the load force of the elastic (F_E) is
\[ F_E = -k_E y(t) - y_0 = -k_E A_H \sin(\omega t) + y_H - y_0 \] (A8)

F_E is proportional to the distance between the static position y(t) = A_H sin(\omega t) + y_H (with y_H = 0.15 m) and the rest point y_0 = 0 of the spring with a stiffness k_E = 33 N/m.

By definition, the load force of the virtual mass-spring system (F_M) is equal and opposite to the force applied to the mass (F_{ext})
\[ F_M = -F_{ext} = -m \ddot{x} = m \omega^2 A_M \sin[\alpha(t + \theta)] \] (A9)

where \( x(t) = A_M \sin[\alpha(t + \theta)] \) is the motion of the mass.

The combined load is thus a sine function
\[ F_E + F_M = -k_E A_H \sin(\omega t) + m \omega^2 A_M \sin[\alpha(t + \theta)] + k_E(y_0 - y_H) = A_M \sin(\omega t + \theta_0) + k_E(y_0 - y_H) \] (A10)

with amplitude
\[ A_L = \sqrt{k_E^2 A_H^2 + m^2 \omega^4 A_M^2 - 2k_E m \omega A_M A_H \cos(\omega \theta)} \] (A11)

and lag (relative to the real load force)
\[ \omega \theta_L = \arctan \left[ \frac{m \omega^2 A_M \sin(\omega \theta)}{m \omega^2 A_M \cos(\omega \theta) - k_E A_H} \right] \] (A12)

This equation shows that the lag \( \theta_L \) of the combined load depends directly on the mass \( m \) and indirectly on the stiffness and damping coefficient (through the amplitude of the mass motion \( A_M \); see Eq. A6). To model our results, the lag \( \theta_L \) of the combined load must be positive to lead the hand. Since the numerator is negative when the visual feedback is delayed (\( \theta < 0 \)), the denominator must also be negative, which is true as long as \( m \omega^2 A_M \cos(\omega \theta) < k_E A_H \).

Computation of the parameters of the damped mass-spring system

The parameters \( m, k, \) and \( c \) of the damped mass-spring system have to be selected so that the steady-state solution (Eq. A4) corresponds to the cursor motion (Eq. A2). In other words, the amplitude of the mass motion \( A_M \) (Eq. A5) must correspond to the amplitude of the cursor motion \( A_c \), and the lag of the mass \( \theta_m \) (Eq. A6) must correspond to the visual delay \( \theta \). In addition, the parameters of the damped mass-spring system must also be selected so that the phase shift \( \theta_0 \) of the combined load (Eq. A12) corresponds to the forward shift of the grip force. After these substitutions, Eqs. A5, A6, and A12 fully constrain the three parameters of the mass-spring system.

Assuming that the amplitude of the hand movement \( A_H \) is equal to that of the cursor motion \( A_c \) allows one to compute more easily the parameters of the mass-spring system.\(^2\) Substituting \( A_M \) with \( A_H \) in Eq. A6 yields the following formula for the stiffness
\[ k = \frac{1}{2} m \omega^2 \] (A13)

Similarly, substituting \( k \) in Eq. A13 and \( \theta_m \) in Eq. A5 yields a formula for the damping coefficient
\[ c = \frac{m \omega}{2 \tan(-\frac{1}{2} \omega \theta)} \] (A14)

Finally, assuming \( A_M = A_h \) in Eq. A12 yields a formula to compute the mass
\[ m = \frac{1}{\omega^2 \cos(\omega \theta)} \tan(\omega \theta_0) - \sin(\omega \theta) \] (A15)

that corresponds to a given grip-force lag \( \theta_0 \). Note that the mass is positive if and only if \( \theta_0 > \theta \), which is the case since \( \theta_0 \) is positive and \( \theta \) is negative. Altogether, Eqs. A13, A14, and A15 fully specify the parameters of the virtual mass-spring system when \( A_H = A_C \).

For example, for a visual delay of 300 ms (\( \theta = -0.3 \) s) and a 50 ms (\( \theta_0 = 0.05 \) s) forward shift of the grip force, these formulae yield a mass \( m = 0.5 \) kg, a stiffness \( k = 3.1 \) N/m, and damping \( c = 1.5 \) N-m^{-1}s^{-1}. The corresponding load forces are presented in Fig. A2, which also shows that the force \( F_M \) generated by this virtual system is quite limited (max \( F_M = 0.7 \) N) compared with the original load force (max \( F_E = 7 \) N). Note that because \( F_M \) is a force oscillating between positive and negative values (as opposed to \( F_E \)), it does not affect the mean combined load force and consequently should not affect the mean grip force. The adjunction of the small virtual load is sufficient to shift forward the combined load force and thus encourages earlier grip force modulations.

Figure A3A shows that the phase shift of the combined load is always positive even when the visuomotor gain (\( A_c/A_H \)) differs from one. Similarly, slight variations of movement amplitude (\( A_c \)) do not qualitatively change the results of this simulation. The other panels illustrate how the parameters of the mass-spring system must change to obtain a phase shift of the combined load that corresponds to the grip–load lag observed in this study (white line). These figures indicate that the direction of phase shift of the combined load does not critically depend on the parameter values of the virtual mass-spring system. In summary, the model shows that the perception of an additional mass-spring system (instead of a visual delay) could explain the forward shift of grip force in our study.

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Disclosure

No conflicts of interest, financial or otherwise, are declared by the author(s).

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\(^1\) We neglected the inertial load of the handheld object because its maximum value was very small: \( F_{\text{max}} = m a_{\text{max}} = 0.034 \) N, where \( m = 0.056 \) kg and \( a_{\text{max}} = \max(\ddot{x}^2 dy/dt) = A/2(2 \pi f_r)^2 = 0.102(2 \pi 0.556)^2 = 0.61 \) m/s\(^2\). \( F_E \) is thus considered as an elastic load force.

\(^2\) Using the actual visuomotor gain (\( A_c/A_H = 0.92 \); see METHODS) makes the resolution of Eqs. A5, A6, and A12 more difficult, but do not qualitatively change the results (see Fig. A3).


