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Eye tracking a self-moved target with complex hand-target dynamics

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Landelle C, Montagnini A, Madelain L, Danion F. Eye tracking a self-moved target with complex hand-target dynamics. *J Neurophysiol* 116: 1859–1870, 2016. First published July 27, 2016; doi:10.1152/jn.00007.2016.—Previous work has shown that the ability to track with the eye a moving target is substantially improved when the target is self-moved by the subject's hand compared with when being externally moved. Here, we explored a situation in which the mapping between hand movement and target motion was perturbed by simulating an elastic relationship between the hand and target. Our objective was to determine whether the predictive mechanisms driving eye-hand coordination could be updated to accommodate this complex hand-target dynamics. To fully appreciate the behavioral effects of this perturbation, we compared eye tracking performance when self-moving a target with a rigid mapping (simple) and a spring mapping as well as when the subject tracked target trajectories that he/she had previously generated when using the rigid or spring mapping. Concerning the rigid mapping, our results confirmed that smooth pursuit was more accurate when the target was self-moved than externally moved. In contrast, with the spring mapping, eye tracking had initially similar low spatial accuracy (though shorter temporal lag) in the self versus externally moved conditions. However, within ~5 min of practice, smooth pursuit improved in the self-moved spring condition, up to a level similar to the self-moved rigid condition. Subsequently, when the mapping unexpectedly switched from spring to rigid, the eye initially followed the expected target trajectory and not the real one, thereby suggesting that subjects used an internal representation of the new hand-target dynamics. Overall, these results emphasize the stunning adaptability of smooth pursuit when self-maneuvering objects with complex dynamics.

smooth pursuit; saccade; prediction; object manipulation; eye-hand coordination; internal model

NEW & NOTEWORTHY

The ability to anticipate visual consequences resulting from our actions is fundamental. Human subjects have an excellent performance when visually tracking a self-moved target compared with an externally driven one. Here, we challenge this ability by imposing a nonlinear (elastic) mapping between hand and target. We show that, despite initial impairment, accurate eye tracking is restored within few minutes of practice, thereby emphasizing the stunning adaptability of smooth pursuit when manipulating objects with complex dynamics.

BECAUSE THE ABILITY to track with the eye a moving target is functionally important, eye tracking has often been studied (for recent reviews, see Barnes 2008; Spering and Montagnini 2011). Importantly, it has been observed that smooth pursuit is substantially improved when the target is moved by the subject's hand compared with when it is moved by an external agent: in the case of a self-moved target, eye tracking is characterized by a higher gain in smooth pursuit (Gauthier et al. 1988; Mather and Lackner 1975; Vercher et al. 1995), fewer saccades (Angel and Garland 1972; Mather and Lackner 1975; Steinbach 1969; Steinbach and Held 1968), and a shorter temporal lag between target and eye position (Domann et al. 1989; Gauthier and Hofferer 1976; Steinbach and Held 1968; Vercher et al. 1996). To account for these observations, it has been proposed that the oculomotor system has access to an estimate of the current hand position using predictive mechanisms (i.e., a forward model) combining sensory feedback and arm efferent copy in conjunction with acquired knowledge of the hand-target dynamics (Ariff et al. 2002; Scarchilli et al. 1999). In other words, it is hypothesized that eye tracking benefits from the ability to both predict future states of the limb (Ariff et al. 2002) and learn the mapping between hand movements and their visual consequences (Sailer et al. 2005). The goal of the present study was to investigate changes in eye tracking when human subjects have to cope with complex hand-target dynamics.

Previous studies have investigated eye-hand coordination when imposing a temporal delay (Angel and Garland 1972; Vercher and Gauthier 1992; Vercher et al. 1996), a visual inversion (Steinbach 1969; Vercher et al. 1995, 1996), or even a change in arm dynamics using a brake that delayed the initiation of arm movement (Scarchilli et al. 1999; Scarchilli and Vercher 1999). Initial eye tracking performance was systematically perturbed by these procedures. However, when subjects were repeatedly exposed to these constant perturbations, results showed that smooth pursuit adapted across successive trials (Scarchilli and Vercher 1999; Vercher et al. 1995), suggesting that the mapping between hand action and their visual consequences could be updated. Here, we investigated how the oculomanual coordination system might cope with a situation in which the hand-target dynamics mimicked the visual behavior of a mass-spring system. Specifically, when the hand was moving, we made the target behaving like a mass attached to the hand by means of a spring; however, haptic feedback was not provided. Our motivation was to construct a more challenging task than with an inversion or a temporal delay because of the nonlinearities inherent to the mass-spring dynamics but also presumably more challenging than the initial braking of the hand used by Scarchilli and collaborators (1999) in the sense that our visual perturbation persists throughout the ongoing movement. This interest in mass-spring dynamics was also encouraged by many studies showing that learning to move skillfully a nonrigid object can be a slow and difficult process (Dingwell et al. 2002; Venkadesan et al.

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2007; Winges et al. 2009). In some cases, it has been proposed that learning to control a nonrigid object is associated with the formation (or update) of some internal models that provide a mapping between hand movements and object motions (Danion et al. 2012; Dingwell et al. 2002, 2004; Nagengast et al. 2009).

The goal of the present study was to explore how the eye tracking system copes with, and possibly learns, a complex mapping between hand actions and their visual consequences. To this end, we designed a task in which subjects were asked to generate random oscillatory movements while tracking with their eyes the resulting target movement under the spring mapping. To provide some baseline measurements, eye tracking performance under this new mapping was compared with eye tracking performance under a simple (i.e., rigid) mapping in which the hand and target movements matched perfectly. To assess the effects of agency, we also included two conditions in which subjects tracked externally moved targets whose trajectories had been previously generated when self-moving the target under the rigid or spring mapping. Each subject performed a block of twenty 16-s trials in each of these four conditions to monitor possible improvements in performance. We reasoned that if some predictive mechanisms linking hand movement to visual target motion can be updated, despite low initial performance, eye tracking performance when the target is externally moved may be restored toward a level similar to self-moving the target under the rigid mapping. To further probe the update of predictive mechanisms underlying eye-hand coordination, we had the target transiently disappeared (blanks) and also catch trials in which the hand-target dynamics were unexpectedly switched (from spring to rigid or vice versa). We reasoned that if the predictive mechanisms can be updated to accommodate the spring mapping *1*) the ability to compensate for transient target disappearances should improve with experience and *2*) during catch trials smooth pursuit should initially follow the expected trajectory and rather than the real one. Finally, particular attention was devoted to determine whether the eventual update of predictive mechanisms underlying smooth pursuit benefited also to the control of saccades.

METHODS

Participants. Twelve self-proclaimed right-handed participants (5 men and 7 women) participated in this study (age: 22.0 ± 2.7 yr). None of the subjects had neurological or visual disorders. They were naïve as to the experimental conditions and hypotheses and had no previous experience of ocular motor testing. All participants gave informed written consent before the study. Participants received 10€ for their participation. The Aix-Marseille University local ethics committee approved the experimental paradigm (no. 2014-12-3-04), which complied with the Declaration of Helsinki.

Apparatus. The experimental setup is shown in Fig. 1. Subjects were comfortably seated in a dark room facing a screen positioned on the frontal plane 57 cm away from the subject's eye. To minimize measurement errors, subjects' head movements were restrained by a chin rest and a padded forehead rest so that the eyes in primary position were directed toward the center of the screen. A mask was positioned under the participants' chin to block vision of their hands. In some of the experimental conditions (see "Self" below), participants were required to insert their right index finger into a ring attached to two linear potentiometers (SX50, Draw Wire Waycon) positioned so that the ring could only slide horizontally in the frontal plane. The ring was positioned approximately midway between the eye and the screen. Shoulder and elbow joints were key contributors in sliding the ring. Hand movements were recorded at a sampling rate of 1,000 Hz with a resolution of 0.1 mm.

The target was a red disk laser beam (0.5° in diameter) projected on the screen. The laser was moved by an optical scanner (GSI M2 series) servo-controlled by a PC. The delay in the servo-command was <2 ms. The optical scanner motion was restricted to one dimension so that the target moved only along the horizontal axis. Eye movements were recorded using an infrared video-based eye tracker (Eyelink Desktop-mounted system, SR Research). Horizontal and vertical positions of the right eye were recorded at a sampling rate of 1,000 Hz. Before each block of trials, we calibrated the output from the eye tracker by recording the raw eye positions as subjects fixated a grid composed of nine known locations. The mean values during 1,000-ms fixation intervals at each location were then used for converting offline raw eye tracker values to horizontal and vertical eye position in degrees of visual angles.

When subjects had to self-move the rigid target (Self-Rigid), its motion was a direct replicate of the actual hand trajectory (i.e., with a 2-ms delay): if the hand moved by 1 cm to the left, the target also moved by 1° (1 cm) to the left on the screen. When subjects had to self-move the nonrigid target (Self-Spring), the target was simulated as a mass-spring object with the following properties: mass = 3 kg,

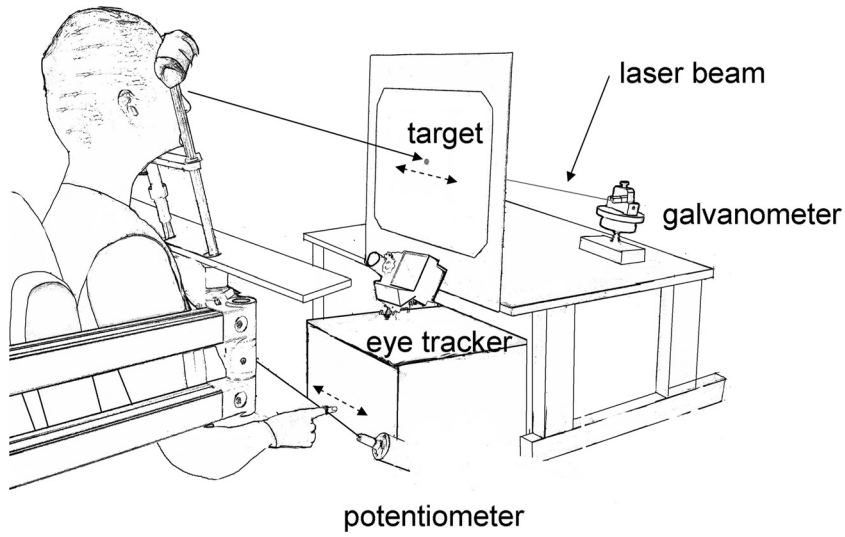


Fig. 1. Schematic drawing of the experimental setup. See text for more details. All parts of this figure were drawn by C. Landelle and F. Danion.

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stiffness = 120 N/m, damping = 5 N/m/s, and resting length = 0 m. These values are close to the values used in previous studies that investigated the manipulation of nonrigid objects (Danion et al. 2012; Dingwell et al. 2002, 2004; Nagengast et al. 2009). It is worth noting that the laws of physics impose that a mass-spring system acts as filter and carries a resonance frequency (F) that depends on its mass (m) and its stiffness (k) as exposed in the following equation:

$$F = (1/2\pi)\sqrt{(k/m)}$$

In our case, the current parameter setting imposes a resonance frequency of 1 Hz. Importantly, this means that even if subjects performed random hand motion over a large set of frequencies, this hand motion will result in a target motion that will be centered around 1 Hz. This is exactly what we observed. Figure 2 shows a comparison of the mean group power spectrum of hand and target motion under the Spring and Rigid mapping. As can be seen, despite the fact that the power spectra of hand motion had similar structure (Fig. 2*A*), this was not the case for the power spectra of target motion (Fig. 2*B*). Indeed, under the Spring mapping only, one can clearly notice the presence of a peak at 1 Hz, namely, at the resonance frequency of the mass-spring system. As will be discussed later, this overrepresentation of target motion at 1 Hz will be responsible for key differences in eye tracking performance under the Spring and Rigid mapping.

Procedures. In all trials, subjects were instructed to track as accurately as possible the target moving on the screen. Depending on the experimental condition, the target motion was either driven by the subject's moving finger (Self) or externally (External). In the Self conditions, the mapping between hand movement and target motion could either be rigid (Self-Rigid) or elastic (Self-Spring). In both cases, subjects were asked to perform random oscillatory movements to move the target (for similar procedures, see Angel and Garland 1972; Steinbach and Held 1968). The underlying motivation was to make target motion as unpredictable as possible when subsequently played back in the External conditions (see below). Subjects were encouraged to use the whole extent of the screen (±15°) while making sure that the target did not fall outside the screen boundaries. To facilitate the production of random movements, a template was given before each of the two Self blocks. During demonstration trials, subjects did not move their hand and simply had to observe the replay of a trial performed by one of the experimenters under the same mapping condition. During the experimental trials, we ensured that hand movement had a mean absolute target velocity close to 30°/s: mean target velocity was computed online, and the experimenters provided some verbal feedback to the subject, such as "please move faster" or "please slow down" when necessary. This procedure ensured minimal changes in mean target velocity across subjects (SD: 1.1°/s), experimental conditions (SD: 0.3°/s), and trials (SD: 0.9°/s). Each subject completed 1 block of 20 trials in the Self-Rigid and Self-Spring condition (preceded by a demonstration trial). Each trial was 16 s long (for a similar duration, see Steinbach 1969). Subjects were not explicitly informed about the nature of the mapping between their hand movement and the target motion before completing these experimental conditions.

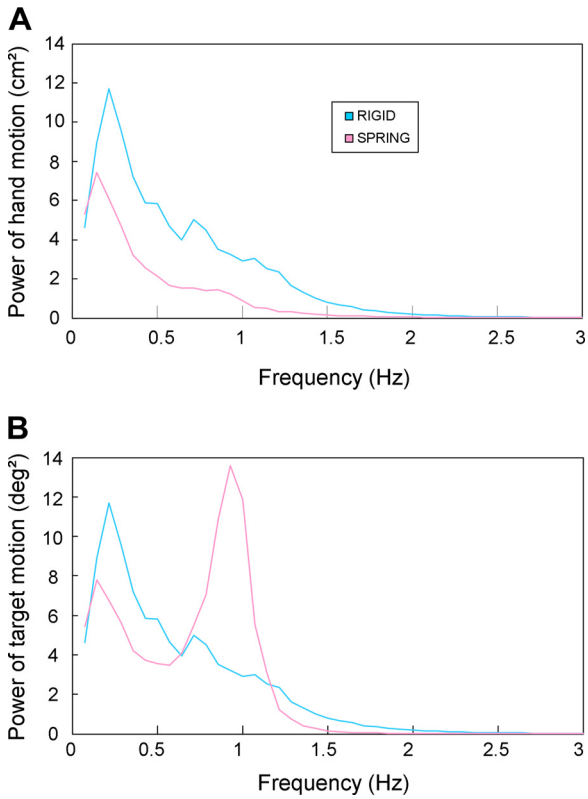


Fig. 2. Mean power spectrum of hand (*A*) and target motion (*B*) as a function of hand-target mapping. Individual power spectra were averaged across trials and subjects. Note the presence of a peak around 1 Hz in the target motion spectrum under the SPRING mapping.

When target motion was externally driven (External-Rigid or External-Spring), subjects were presented the target trajectories they previously generated in the corresponding Self conditions (for similar procedures, see Angel and Garland 1972), allowing within-subject comparisons and minimizing possible effects due to changes in target kinematics with respect to hand-target mapping. The order of trial presentation was identical within each block. This procedure imposed some constraints regarding the randomization of the four experimental conditions: subjects could only perform an External block after performing the associated Self block. Thus, participants always started the experiment by a Self condition. Each of the six possible conditions sequences was tested for two subjects.

To further investigate the nature of the predictive mechanisms involved in smooth pursuit, we used transient target disappearances (Becker and Fuchs 1985; Gauthier and Hofferer 1976; Orban de Xivry et al. 2008, 2009). The duration of occlusion (400 ms) was chosen to be in the range of values used by others (Bennett and Barnes 2003; Madelain and Krauzlis 2003; Mehta and Schaal 2002; Orban de Xivry et al. 2008, 2009). Within each block, the last 15 trials (i.e., *trials 6–20*) had four occlusions each. We did not use occlusions in the first five trials to limit the difficulty of the task and to familiarize the subjects with the task. The following constraints were applied to trigger target occlusions: *1*) occlusions were never initiated during the first 5 s of the trial, *2*) consecutive target occlusions were separated by at least 1.5 s, and *3*) occlusions were contingent on current target velocity and acceleration. We explored two types of occlusion. In the first type, occlusions were set around movement reversals, that is, when target velocity was close to zero (<0.1°/s) and target acceleration was high (>50°/s^2). In the second type, occlusions were triggered around the center of oscillation, that is, when target velocity was high (>20°/s) and target acceleration was low (<1°/s^2). Each trial had a total of four target occlusions, with two of each type. The order of occlusion types was randomized across trials. Before the beginning of the sixth trial, subjects were instructed that the target would occasionally disappear for short periods of time in the remaining trials of the block. Subjects were encouraged to keep tracking the target as if it was still present on the screen. The typical instruction was: "Follow the target the best you can and try to carry on when the target is masked." Because of our External procedure, the periods of target occlusion were identical in the Self (Self-Rigid or Self-Spring) and External (External-Rigid and External-Spring) trials for each subject. Overall, a total of 60 target occlusions (4 × 15 trials) were used for each subject in each of the experimental conditions.

The procedure for catch trials (Scarchilli et al. 1999; Vercher et al. 1996;) consisted in unexpectedly changing the object/target dynamics (Dingwell et al. 2002) from Rigid to Spring or from Spring to Rigid. For the External blocks, the trajectory of the catch trial was taken from the 20th trial performed in the complementary Self block. This means

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that the catch trial inserted at the end of the External-Spring block consisted in playing back the target trajectory produced by the subject at the end of the Self-Rigid block (conversely, the catch trial at the end of the External-Rigid block used the target trajectory produced at the end of the Self-Spring block).[1] To preserve the novelty of these changes in dynamics, catch trials had a shorter duration (4 s) than regular trials.

Overall, each participant performed a total of 84 trials (4 × 21) in a single session averaging 60 min. Participants could request additional breaks at any time, but most of them only took the break offered between blocks.

Data analysis. Because the stimuli were moving exclusively along the horizontal meridian, we focused our analyses on the horizontal component of eye movements. The beginning of a trial was based on the initiation of target motion, namely, when the absolute target velocity first exceeded 2°/s. We then performed a sequence of analysis to separate periods of smooth pursuit, saccades, and blinks form the raw eye position signals. The identification of the blinks was performed by visual inspection. This procedure led to the removal of ~1% of eye recordings. Eye position time series were then low-pass filtered with a Butterworth (fourth order) using a cutoff frequency of 25 Hz. The resultant eye position signals were differentiated to obtain the velocity traces. The eye velocity signals were low-pass filtered with a cutoff frequency of 25 Hz to remove the noise from the numerical differentiation. The resultant eye velocity signals were then differentiated to provide the accelerations traces that we also low-pass filtered at 25 Hz to remove the noise. A dedicated Matlab script was run to identify the beginning and end of each saccade. This identification was based on the acceleration and deceleration peaks of the eye (>1,500°/^{2}). Further visual inspection allowed to identify smaller saccades (<1°) that could not be identified automatically by our program. Based on these computations, epochs of pursuit and of saccades were extracted. We distinguished regular pursuit from the periods of target occlusion (from the 6th trial to the 20th trial): the 400-ms segments of occlusions as well as the subsequent 600 ms were therefore marked so as to allow sufficient time to restore regular eye tracking; a total of 4 s of signal were marked in the last 15 trials of each block. These segments of eye and target motion were analyzed separately.

To assess the participants' ability to predict the dynamics of the target or hand-target during visually guided tracking, we computed several dependent variables. First, we computed the mean absolute position error (PE) by averaging the absolute difference in position between the target and the eye. Second, we computed the mean absolute velocity error (VE), i.e., the average absolute difference between the eye and target velocity. Note that although PE was evaluated over the whole trial (i.e., including both periods of saccades and smooth pursuit[2]), VE was computed only during smooth pursuit periods. Third, to evaluate the temporal relationship between the eye and target movements, we computed the lag between eye and target velocity signals using a cross-correlation (a positive lag corresponding to the eye lagging behind the target). This lag computation was based on the eye signal excluding saccades.

To better characterize saccades and smooth pursuit, the following dependent variables were computed. First, we computed for each trial the average saccade rate, that is, the average number of saccades initiated per second (Angel and Garland 1972; Steinbach 1969). Second, we computed the smooth pursuit gain by averaging the ratio between instantaneous eye and target velocities during phases of smooth pursuit (to avoid numerical instabilities, only situations where absolute target velocity was >10°/s were considered). Third, to evaluate the accuracy of saccade, PE was computed at the end of each saccade. Finally, to assess the relative contribution of saccades and smooth pursuit, we computed for each trial the total distance travelled by the eye with saccades (Orban de Xivry et al. 2006) and then expressed this as a percentage of the total distance travelled by the eye using both saccades and smooth pursuit.

To compare the complexity of target motion under the Rigid and Spring mapping, approximate entropy (ApEn) was used as an index that characterizes the unpredictability of a signal (Pincus 1991); the larger the ApEn, the more unpredictable the signal is. To compute ApEn, we used the following Matlab function: https://fr.mathworks.com/matlabcentral/fileexchange/32427-fast-approximate-entropy [with the following settings: embedded dimension = 2, tolerance = 0.2 × STD(target trajectory)].

We investigated the trajectory of the eye at the initiation of the catch trial, i.e., trials in which the target dynamics unexpectedly changed after a 20-trial block. Particular attention was devoted on catch trials that followed the Self-Spring block so as to determine whether the eye followed the real target (i.e., using the rigid mapping) or the expected one (i.e., using the spring mapping). To address this issue, we compared PE during the first 200 ms with respect to the real and expected target. Following the same logic, we also compared the accuracy of saccades with respect to the real and expected target.

Transient target blankings during more standard ocular tracking tasks are known to induce a reduction of velocity gain in eye motion (Becker and Fuchs 1985). To investigate whether a similar effect was found in our task, we computed the absolute smooth pursuit velocity signal during each of the 400-ms blanking periods as well as during equivalent periods (i.e., periods during which the criteria to trigger the target disappearance were fulfilled but the target remained visible). To assess whether prior experience could help limiting the negative impact of target blanking, mean absolute smooth pursuit velocities over the last 200 ms of the blanks were compared between early and late trials (i.e., *trials 6–8* vs. *trials 18–20*). This procedure was performed separately for the accelerating and decelerating blanks. In addition, we compared tracking performance during blanks across agency conditions to test whether the negative impact of blanks is reduced in the more predictive situation of self-driven motion. Because the accuracy of saccades initiated during blanks is also informative about the knowledge acquired by the subjects about target trajectory (Bennett and Barnes 2003; Orban de Xivry et al. 2006), rather similar analyses were conducted on PE at the end of saccades during blanking periods.

Statistical analysis. Repeated-measures three-way ANOVA was used to assess the effects of Agency (Self vs. External), target Mapping (Rigid vs. Spring), and Trial. The Trial factor compared the mean performance over the first three trials with the mean performance over the last three trials to assess changes over time in eye movement performance. Data normality was probed with Shapiro tests. Tukey corrections were used for post hoc *t*-tests to correct for multiple comparisons. A conventional 0.05 significance threshold was used for all analyses.

RESULTS

Typical trials. Figure 3 shows four typical trials performed by the same subject illustrating several key differences across experimental conditions. Importantly, one should notice the quite complex relationship between the hand (in green) and the target (in red) in the Self-Spring trial. First, hand movement and target motion were loosely correlated ($R = 0.72$, mean group: 0.67 ± 0.12, hereafter SD is across subjects) compared with the Self-Rigid trial ($R = 1$). Second, the mean (absolute) distance between hand and target position was 5.2° (mean group: 4.9 ± 0.4°). Third, cross-correlation analyses revealed that, on average, target motion lagged behind hand movement by ~154 ms (mean group: 160 ± 41 ms). Fourth, we observed

[1] In 4 of 24 cases, the order of the blocks did not allow us to follow this procedure. In these few cases, we used the 20th trial performed by the preceding subject.

[2] Excluding saccades from PE evaluation did not change our findings.

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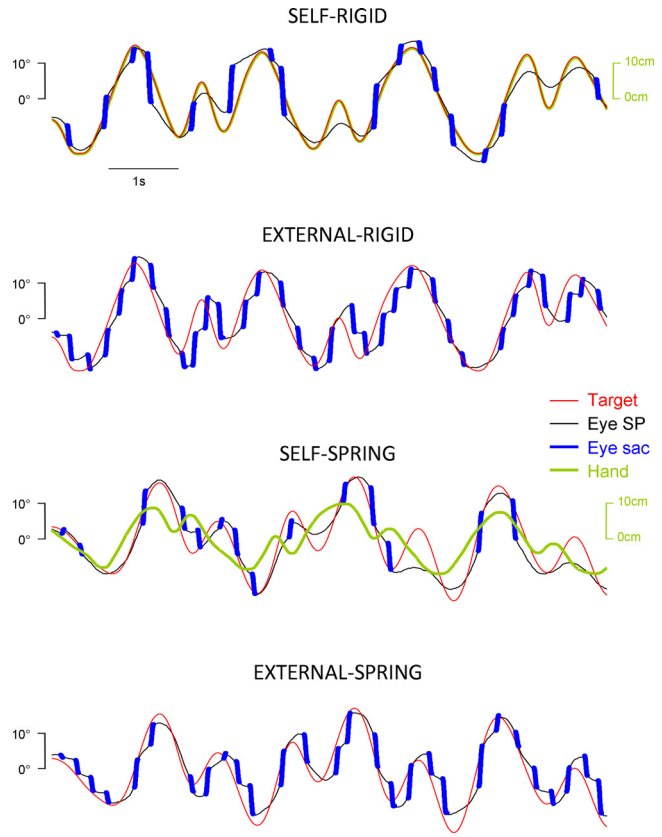


Fig. 3. Typical early trials in each experimental condition. All trials were performed by the same subject and had the same rank within each experimental block (fifth trial). Only the first 8 s of each trial are shown. Saccadic (sac) eye movements are depicted in blue. Note the larger number of saccades during External conditions. SP, smooth pursuit.

that the elastic mapping somehow amplified the visual consequences of hand movement in the sense that subjects were able to achieve the intended mean absolute target velocity while using a mean absolute hand velocity ~50% smaller compared with Self-Rigid (15.4 ± 2.3 vs. 30.4 ± 1.0 cm/s); this observation is consistent with the power spectral analysis of hand motion shown in Fig. 2*A*. However, these strong differences in hand-target movement coordination did not induce any obvious differences in the eye movements themselves. Indeed, the most striking effects seem to be due to the control of the target displacement (or Agency): when the target is moved by the subject (Self conditions), the saccades rates appear much lower than when the target is externally moved (External conditions). Importantly, the results shown in Fig. 3 clearly indicate that our subjects were able to track the target with a combination of saccades and smooth pursuit. In the subsequent sections, we will describe in more detail eye tracking performance in each experimental condition and its evolution across trials.

Eye tracking performance and eye movements. Figure 4 shows the main eye movements' variables across conditions as a function of trials. To assess the significance of the effects, we performed for each variable three-way ANOVA with the factors of Agency, Mapping, and Trial. Taking the control of the target allowed the participants to decrease PE [$F(1,11) = 97.34$, $P < 0.001$; see Fig. 4*A*]. However, this decrease in PE was more pronounced under the Rigid mapping than the Spring mapping [Agency × Mapping interaction, $F(1,11) = 184.29$, $P < 0.001$]. We also found a decrease in PE across successive trials [$F(1,11) = 14.63$, $P < 0.01$], but this effect was larger when the subject controlled the target than when it was externally moved [Trial × Agency interaction, $F(1,11) = 34.71$, $P < 0.001$] and also when the mapping was spring-like rather than when it was rigid [Trial × Mapping interaction, $F(1,11) = 10.06$, $P < 0.01$]. Post hoc analyses indicated that Self-Spring was the only condition in which a significant decrease in PE was observed across trials ($P < 0.001$): on average, PE decreased by ~30% between early and late trials (2.79 ± 0.68° vs. 1.94 ± 0.43°). Post hoc comparisons across conditions showed that initial PE in Self-Spring was similar to External-Spring (2.79 ± 0.43° vs. 2.58 ± 0.26°, $P > 0.05$) and greater than in Self-Rigid (2.05 ± 0.29°, $P < 0.001$). In contrast, in late trials, PE became similar in Self-Spring and Self-Rigid (1.94 ± 0.43° vs. 1.81 ± 0.26°, $P > 0.05$) and smaller than in External-Spring (2.54 ± 0.35°, $P < 0.01$). Computing PE after realigning eye and target signals (i.e., by subtracting the temporal lag between the two) allowed us to reduce PE but did not change the ranking of the conditions.

We also found that taking control of the target allowed the participants to decrease VE [$F(1,11) = 113.60$, $P < 0.001$; Fig. 4*B*] and that this benefit was more pronounced under the Rigid mapping than the Spring mapping [Agency × Mapping interaction, $F(1,11) = 44.99$, $P < 0.001$]. VE was stable across trials [$F(1,11) = 2.98$, $P > 0.05$] except in the Self-Spring condition [Trial × Agency × Mapping interaction, $F(1,11) = 7.88$, $P < 0.05$], in which VE decreased by ~30% (early = 19.1 ± 4.4°/s vs. late = 13.7 ± 2.6°/s, $P < 0.001$). Although VE was similar between Self-Spring, Self-Rigid, and External-Spring in early trials ($P > 0.05$), VE in Self-Spring was significantly smaller than in Self-Rigid (18.5 ± 2.4°/s) and External-Spring (18.9 ± 2.2°/s) in late trials ($P < 0.001$).

Concerning the temporal relationship between eye and target, the eye was always lagging behind the target, albeit with different delays depending on the experimental conditions (Fig. 4*C*). As expected, the eye-target lag was substantially smaller for the Self conditions compared with the External conditions [24.9 ± 8.5 vs. 60.0 ± 9.6 ms, $F(1,11) = 110.29$, $P < 0.001$]. However, as for PE and VE, the benefit associated with self-moving the target was greater under the Rigid mapping than the Spring mapping [Agency × Mapping interaction, $F(1,11) = 72.04$, $P < 0.001$]. Indeed, although the lag decreased by ~50 ms when switching from External-Rigid to Self-Rigid (79.5 ± 13 vs. 28.7 ± 10.1 ms), it decreased by only 20 ms when switching from External-Spring to Self-Spring (vs. 40.5 ± 8.0 ms and vs. 21.2 ± 10.5 ms). We also found a main effect of Trial consistent with a reduction of eye-target lag across trials [$F(1,11) = 27.41$, $P < 0.001$]. However, further analyses showed that this decrease in lag was significant only for the Self conditions [Agency × Trial interaction, $F(1,11) = 14.51$, $P < 0.01$], resulting in almost synchronous eye and target motions by the end of the blocks (lag: 20.0 ± 7.9 ms).

The smooth pursuit gain (Fig. 4*D*) was also affected by the control over the target movement. ANOVA revealed main effects of Agency [$F(1,11) = 67.39$, $P < 0.001$] and Mapping [$F(1,11) = 38.85$, $P < 0.001$] accounting, respectively, for greater gains in Self conditions and with the Spring mapping. We found no main effect of Trial; however, double and triple interactions with this factor were all significant [$F(1,11) >$

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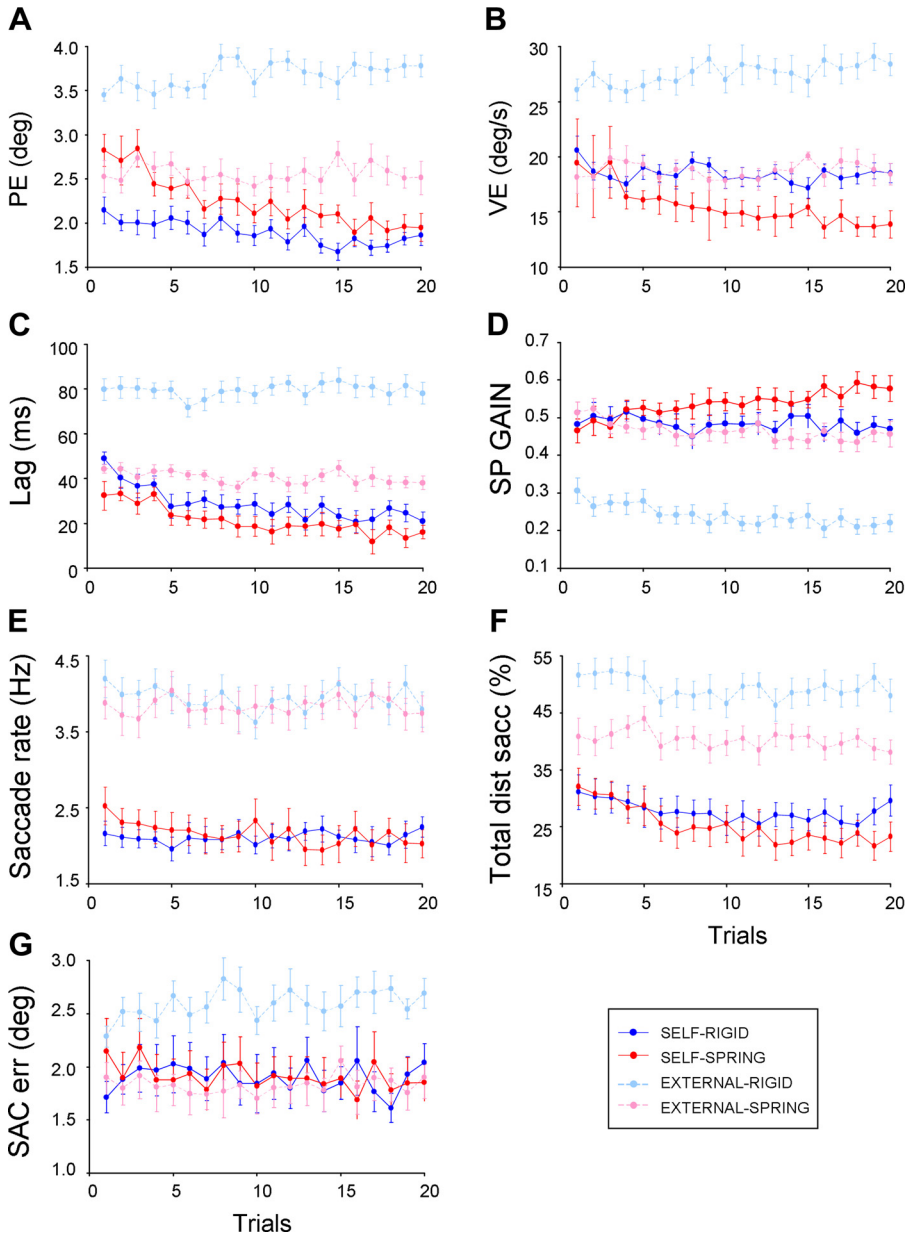


Fig. 4. Average eye tracking performance as a function of experimental condition and trial number. *A*: position error (PE). *B*: velocity error (VE). *C*: temporal lag between eye and target (a positive lag indicates that the eye is lagging behind the target). *D*: SP gain. *E*: number of saccades per second. *F*: percentage of total distance covered by saccades. *G*: terminal position error of saccades. Error bars represent SEs. For most indexes, note the improvements across trials in Self-Spring.

5.53, $P < 0.05$]. Post hoc analyses of the triple interaction indicated that although smooth pursuit gain increased significantly between early and late trials for the Self-Spring condition (0.48 ± 0.11 vs 0.58 ± 0.10, $P < 0.001$) but remained stable (or eventually decreased) in the other conditions. Finally, although in early trials the smooth pursuit gain in Self-Spring was similar to both Self-Rigid and External-Spring ($P > 0.05$), in late trials the smooth pursuit gain was significantly greater in Self-Spring (0.58 ± 0.10) than in Self-Rigid (0.47 ± 0.08, $P < 0.001$) and External-Spring (0.45 ± 0.08, $P < 0.001$).

We also found that, on average, subjects initiated almost twice more saccades in External conditions compared with Self conditions [Agency, $F(1,11) = 243.8$, $P < 0.001$, 3.88 ± 0.69 vs. 2.13 ± 0.50; Fig. 4*E*]. However, in contrast to previous dependent variables, the saccadic rate did not depend on the target mapping [Mapping: $F(1,11) = 0.51$, $P > 0.05$]. Finally, the saccadic rate remained quite stable across trials [Trial: $F(1,11) = 1.04$, $P > 0.05$], but there was a tendency for a drop in Self-Spring (−12%) that was not observed in the other conditions [Trial × Mapping × Agency, $F(1,11) = 4.74$, $P = 0.052$].

The relative contribution of saccade and smooth pursuit to eye tracking (Fig. 4*F*) depended largely on the way the target was controlled [Agency: $F(1,11) = 164.51$, $P < 0.001$]. Consistent with what we observed for the saccadic rate, the percentage of total distance covered by saccades was nearly divided by 2 when the target was self-moved compared with when being externally moved (26.4 ± 7.8 vs 44.8 ± 6.9%). In addition, we also found that the saccadic contribution was greater for the Rigid mapping than the Spring mapping [Mapping: $F(1,11) = 37.06$, $P < 0.01$, 38.4 ± 6.9 vs. 32.7 ± 7.3%]. We also found evidence for a reduction of this index across trials [Trial: $F(1,11) = 30.50$, $P < 0.001$], but this reduction depended on both the target mapping and the mode of target control [Trial × Mapping × Agency: $F(1,11) = 5.47$, $P <$

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0.05]. Post hoc analyses of the triple interaction showed that Self-Spring was the only condition in which the saccadic contribution decreased significantly across trials ($P < 0.001$). In this condition, the saccadic contribution dropped from 31 ± 9% to 23 ± 8% between early and late trials.

Finally, the analysis of saccade accuracy (Fig. 4*G*) revealed that postsaccadic PE was similar in Self-Spring, Self-Rigid, and External-Spring (PE: 1.9 ± 0.1°). However, saccade accuracy was lower in External-Rigid (PE: 2.6 ± 0.1°) compared with the other conditions [Mapping × Agency: $F(1,11) = 35.72$, $P < 0.001$]. In contrast to possible improvements in smooth pursuit, the accuracy of saccades did not change over successive trials.

Catch trials. The analyses of catch trials after External blocks revealed no obvious carryover effects on eye tracking. This view was supported by the fact that eye tracking performance (in terms of PE) was similar during both regular (expected) and unexpected (catch) External-Rigid trials [$F(1,11) = 2.38$, $P > 0.05$] as well as during regular and unexpected External-Spring trials [$F(1,11) = 2.59$, $P > 0.05$]. In contrast, when hand-target mapping was unexpectedly changed after a Self block, we found strong carryover effects at trial initiation, thereby suggesting that subjects relied more on priors when the target was self-moved than when it was moved externally. In these trials, subjects tended to track the anticipated target trajectory, i.e., the one that would correspond to their actual hand movements if the mapping had remained unchanged rather than the actual target trajectory. For instance, when switching from Self-Rigid to Self-Spring conditions, PE was 20% smaller when computed with respect to the expected (rigid) trajectory than with the actual (spring) one [$F(1,11) = 4.95$, $P < 0.05$]. Similarly, a bias in eye motion was observed when switching from Self-Spring to Self-Rigid. This is apparent in Fig. 5*A*, in which we plotted eye and target positions during a typical catch trial, superimposed with the target position that would have been observed if the Spring mapping had been unchanged (i.e., the expected target trajectory): initially, the eye position closely followed the expected (Spring) target trajectory before getting closer to the actual target trajectory.

To better characterize this effect, we first investigated the time course of the pursuit bias induced by the catch trials. We computed PE associated with the real trajectory and the predicted one. Figure 5*B* shows the group-average temporal profiles of PE from movement initiation: during the first 200 ms, PE computed with respect to the predicted target trajectory was indeed smaller than when taking in account the actual target trajectory, as one would expect if the eye initially tracked the predicted trajectory. However, after ~200 ms, the two curves intersect, and the real PE becomes smaller than the predicted PE, suggesting that after this delay the eye is tracking the real trajectory. This strongly suggests that the bias in eye trajectory we observed during the catch trial lasts ~200 ms. Second, to investigate whether saccades were also biased during these catch trials, we investigated the characteristics of the first saccade with respect to both the real and predicted targets. Importantly, the mean latency of these saccades was 208 ± 11 ms, a value that closely matches the timing of the change in pursuit. Presaccadic PE was substantially larger when computed with respect to the real target than when using the predicted target (real PE: 2.3 ± 0.3° vs. predicted PE: 0.6 ± 0.2°), whereas the opposite was observed for the postsaccadic error (real PE: 1.1 ± 0.2° vs. predicted PE: 3.7 ± 0.4°). Analysis of the subsequent saccade further confirmed the view that saccades were initiated to reduce PE relative to the real target position and not the predicted target position. Altogether, this strongly suggests that for the first 200 ms, eye movements were driven by the predicted target trajectory resulting from hand motion. However, rapidly after, both the pursuit and saccadic systems switched modes to track the actual target trajectory.

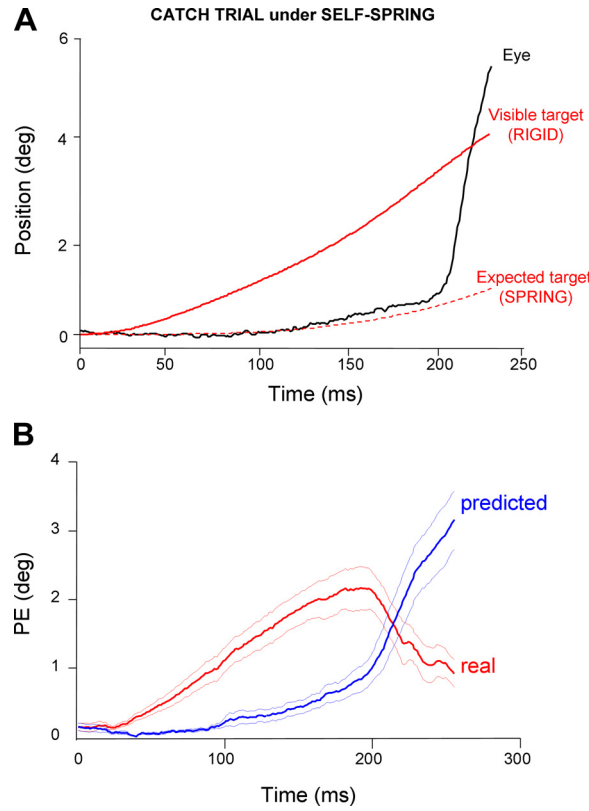


Fig. 5. Effect of catch trials on eye tracking performance at the end of the Self-Spring block. *A*: catch trial from a representative subject. During the first 200 ms, the eye follows the expected (Spring) target trajectory not the real (Rigid) target trajectory. *B*: group-average PE computed with respect to real and predicted target trajectory. The thin lines indicate SEs. Note how during the first 200 ms predicted PE was smaller than real PE.

Transient target disappearance. Masking the target impaired the tracking behavior, leading to a reduction of absolute eye velocity. Figure 6 shows the absolute smooth pursuit velocity for both the blanking epochs and corresponding control epochs in our four experimental conditions either in the decelerating mask condition (*A*) or in the accelerating mask conditions (*B*).

Compared with control epochs, it is apparent that eye velocity started to decrease ~150–200 ms after target masking and that this decrease continued for the remaining of the masked period. When computing the mean absolute velocity during the last 200 ms of these masking and control epochs, we found that this reduction in eye velocity was similar in decelerating and accelerating masking conditions (−56% and −59%, respectively), but it was smaller in Self compared with External [−52% vs. −62%, $F(1,11) = 37.50$, $P < 0.001$]. Subsequent analyses of the masking epochs showed no im-

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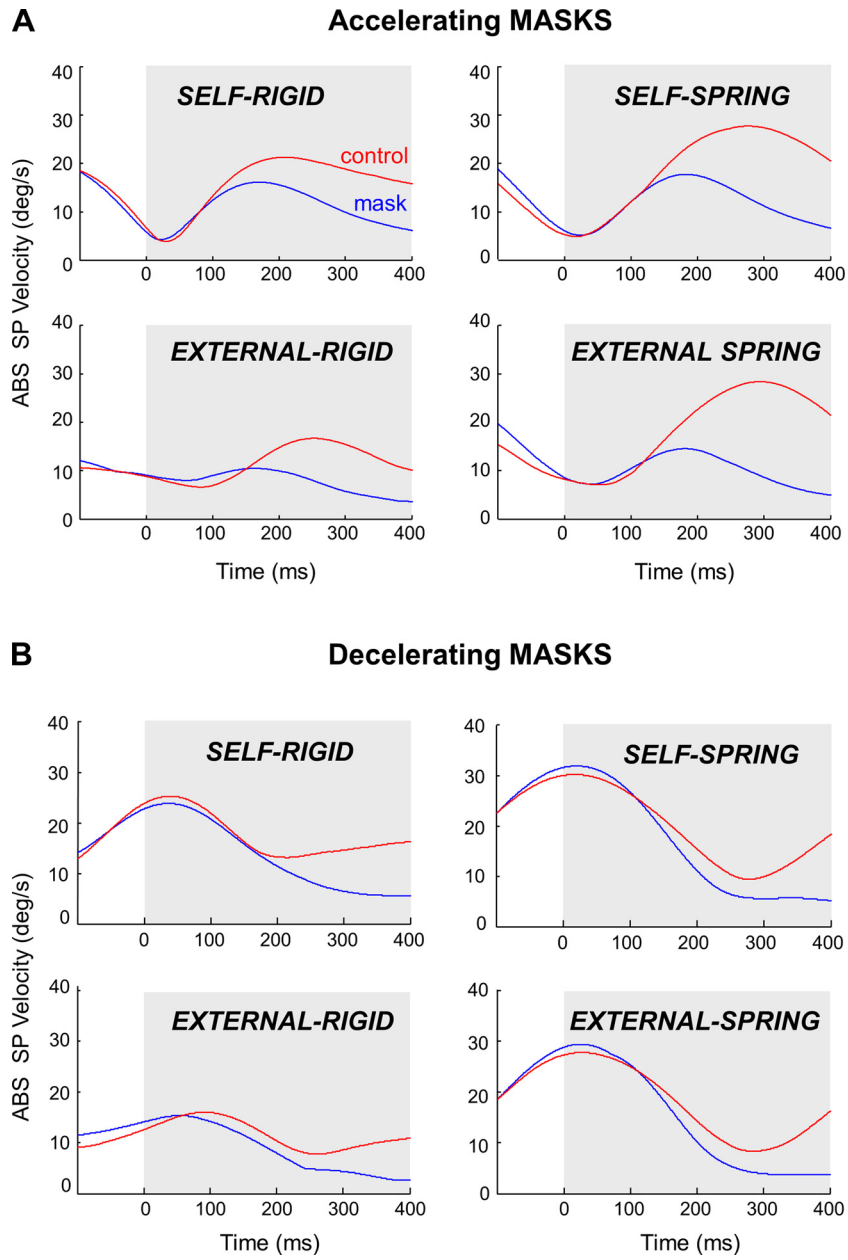


Fig. 6. Effect of target masking on SP velocity. *A*: mean absolute SP velocity as a function of experimental condition during accelerating masks and similar control epochs. The gray shading indicates the blanking period. *B*: same as in *A* but for decelerating masks. Note how in both cases masking the target progressively altered SP velocity.

provement in eye velocity across trials except in the Self-Spring condition, in which eye velocity increased substantially between early and late trials (see Fig. 7), by 43% and 51% in decelerating and accelerating epochs, respectively ($P < 0.01$). Similar analyses during control epochs showed no improvement in eye velocity across trials. Finally, the accuracy of saccades occurring after the first 200 ms of the target blankings was also investigated by comparing postsaccadic PE during masked and control epochs. The accuracy of saccades dropped substantially in all conditions under blanking periods, with PE increasing from 2.0 ± 0.3° to 3.3 ± 0.6° ($P < 0.001$), but we found no evidence that PE decreased across trials. Again, this analysis suggests that the saccadic system did not benefit much from experience.

Complexity of target motion and eye tracking performance. The finding that many aspects of the tracking performance was better for the External-Spring condition than for the External-Rigid condition (see Fig. 4, *A–D*) was somewhat unexpected. To better understand this, we performed two additional analyses. First, by computing ApEn, we sought to examine the unpredictability of target motion under the two mapping conditions. Two-way ANOVA with the factors of Mapping and Trial revealed that target motion was less complex under Spring than Rigid [ApEn: 0.56 ± 0.03 vs. 0.70 ± 0.07; Mapping: $F(1,11) = 68.35$, $P < 0.001$]. However, we found no main effect of Trial [$F(1,11) = 0.916$, $P > 0.05$] or significant interaction between Mapping and Trial [$F(1,11) = 0.827$, $P > 0.05$], suggesting that target trajectories did not become more predictable with experience.

Second, we performed a simulation-based analysis by implementing a simple well-established model of visually guided smooth pursuit (Goldreich et al. 1992), which operates as a delayed low-pass filter on target retinal velocities and accelerations and then combines these outputs with an oculomotor

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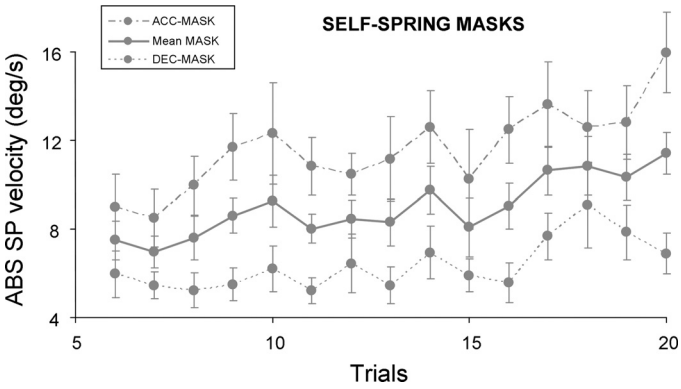


Fig. 7. Effect of target masking on mean absolute SP velocity in Self-Spring as a function of trial number and type of mask. The thick lines represent the average of the accelerating (dashed line) and decelerating (dotted line) masks. Error bars represent SEs. Note how in all cases SP velocity improved across trials.

positive feedback to accurately mimic smooth pursuit velocity properties. Importantly, this class of models generate a time series of simulated continuous smooth eye velocity but does not account for saccades. We then fed this model with all the target trajectories experienced by our participants under the External-Rigid and External-Spring conditions. We used parameters tuned to previously optimized fit of smooth pursuit of constant velocity targets (see Bogadhi et al. 2011). To avoid possible discontinuities in target velocity, we did not exclude blanking periods for these simulations. The results showed that the temporal lag between the simulated tracking velocity and target velocity was significantly larger for the External-Rigid condition than for the External-Spring condition (one-tailed paired *t*-test: $P < 0.05$ for all subjects, mean difference: 26.4 ± 4 ms), much as in our experimental findings. For both conditions, the estimated time lag was larger for the simulated data than for the experimental data, which may result from the general simplicity of the model and the lack of any predictive or learned guidance for the simulated eye movements. Our simulations also accounted for the larger VE in External-Rigid for all subjects (one-tailed paired *t*-test: $P < 0.05$, mean difference: 11.5 ± 4.5°/s). Finally, the model also predicted a lower smooth pursuit gain (i.e., the mean of the instantaneous simulated eye velocity by target velocity ratio, excluding all data points with absolute target velocity lower than 10°/s) in External-Rigid (one-tailed paired *t*-test: $P < 0.05$; mean difference: −0.33 ± 0.18). Overall, we conclude that the improved eye tracking performance under External-Spring may be attributed to key differences in the target's dynamics, even when possible effects of motion prediction or learning are not taken into account.

DISCUSSION

The goal of the present study was to determine whether human subjects could accommodate a complex mapping between hand movements and their visual consequences when the task requires to track with the eyes a self-moved target. To achieve this goal, we monitored changes in eye tracking performances when subjects moved a target with mass-spring-like dynamics. For comparison purposes, eye tracking was also monitored using a simple (rigid) hand-target dynamics as well as tracking target trajectories that subjects had previously generated when self-moving the target with the spring and rigid mapping. Overall, our key findings are as follows. First, in agreement with earlier studies, our results showed that, when using a rigid mapping, eye tracking was more accurate when the target was self-moved than when it was moved by an external agent. Second, for the spring mapping, the benefit of agency was not immediate (except for the time lag) and required some experience to build up. After 20 trials, all indexes revealed better performance in Self-Spring than in External-Spring, to the point that in many cases their values became similar, and sometimes better, compared with the values collected in Self-Rigid trials. Third, we observed that when, at the end of the Self-Spring block, the hand-target dynamics unexpectedly switched to rigid, initial smooth pursuit followed the expected target trajectory rather than the actual trajectory. Fourth, as transient target disappearances were repeated in Self-Spring trials, smooth pursuit velocity became less and less altered by the target occlusion. Fifth, in contrast to smooth pursuit, the accuracy of saccades during Self-Spring did not improve with experience. Finally, as an aside, we noticed that during the External conditions, eye tracking performance was consistently better when subjects followed target trajectories originating from the spring mapping than from the rigid mapping. In both cases, no improvement in eye tracking was seen across trials. We will now discuss in more details these findings and their implications.

Effect of agency under the rigid mapping. For all our performance indexes, we found that, when using the rigid mapping, eye tracking performance was more accurate when tracking the self-moved target than the externally moved target. These observations fit well with previous studies showing that smooth pursuit gain, saccade rate, and eye target lag all benefit from self-moving the target (Angel and Garland 1972; Steinbach and Held 1968; Vercher et al. 1995). Note that even the nearly doubling in the saccade rate in External is consistent with the studies of Steinbach and Held (1968) (1.87 vs. 3.7 Hz) and Angel and Garland (1972) (2.17 vs. 3.58 Hz). However, our study provides two main novel contributions. First, we show that the greater performance in Self-Rigid compared with External-Rigid is hardly influenced by training. Second, we show that the advantages provided by self-moving the target extend to other performance variables such as PE and VE.

Tracking an externally moved target: why is there an effect of target dynamics? We consistently found that eye tracking performance was better in External-Spring than in External-Rigid, as demonstrated by a smaller eye target lag (40 vs. 80 ms), a lower PE (2.6 vs. 3.7°), and a lower VE (19 vs. 28°/s). What can be the reasons leading to more accurate eye tracking in External-Spring given that in both cases target motion was intended to be random and with similar 30°/s mean absolute speed? As previously discussed (Fig. 2), in contrast to the monotonically decreasing power spectrum observed when using the rigid mapping, the power spectrum obtained under the spring mapping exhibits a clear peak around 1 Hz, namely, the resonant frequency of the mass-spring system that we simulated. The fact that a significant fraction of the power is concentrated around the resonant frequency makes the target motion more predictable, in the sense that there are fewer possible trajectories for the upcoming movement with the spring mapping than with the rigid mapping. This view was supported when comparing the complexity (i.e., unpredictability) of Spring and Rigid trajectories by means of ApEn (Pincus

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1991). Indeed, we found that ApEn of target trajectories was, on average, 20% smaller under Spring than Rigid. As a result, the somewhat more regular motion of the target under External-Spring facilitates eye tracking. The fact that our simulations based on a simple model of visually guided smooth pursuit (Goldreich et al. 1992) accounted for many of the differences in eye tracking performance (lag, VE, and smooth pursuit gain) further support for this view. This scheme is also consistent with previous studies showing that eye tracking is more accurate for a sinusoidal signal than a random signal (Dallos and Jones 1963; Stark et al. 1962) or a signal with a decreasing bandwidth in temporal frequency (Michael and Jones 1966). Finally, it is worth pointing that the oculomotor system was very fast at picking up the greater regularity of the Spring trajectories since eye tracking performance was substantially better under External-Spring than External-Rigid from the very first trial (see Fig. 4).

Tracking a self-moved target under complex hand-target dynamics. The key experimental condition in our study was the Self-Spring condition. Our main goal was to investigate changes in eye tracking performance when the mapping between hand movement and target motion is complex. A key variable, PE, indicated that initial tracking performance during Self-Spring was similar to External-Spring. In other words, during the initial exposure, apart from the eye target lag, it did not really matter whether the target was self-moved or externally moved. However, after successive trials, PE with Self-Spring decreased considerably and became similar to what was observed with Self-Rigid. In fact, all performance indexes that we explored improved under Self-Spring when we compared early and late trials (see Fig. 4). This observation strikingly contrasts with the rare and modest changes in performance observed in the other experimental conditions.

Importantly, as revealed by our ApEn measurements, the improvements observed in Self-Spring were not associated with a reduction in target motion complexity across trials. Overall, those results are consistent with the view that subjects have acquired some knowledge allowing them to better predict the future state of the target as a consequence of their hand movements. This accumulated knowledge accounts not only for improvements in eye tracking performance when the target is visible (see Fig. 4) or blanked (see Fig. 7) but also for carryover effects when the mapping was unexpectedly changed (see Fig. 5). Recent modeling studies have proposed that when the reliability of prediction is high, its weight for eye movement control becomes more important with respect to sensory cues (Bogadhi et al. 2013; Orban de Xivry et al. 2013). The following facts are consistent with this scheme. First, in contrast to the self-moved conditions, we found virtually no carryover effects after catch trials in externally moved conditions. Second, the reduction in smooth pursuit velocity induced by target blanks was smaller in self-moved conditions compared with externally moved conditions.

Results from previous studies have shown that subjects can accommodate changes in hand-target dynamics due to a visual delay (Vercher and Gauthier 1992; Vercher et al. 1996) or an inversion (Vercher et al. 1995, 1996), but, to our best knowledge, our study is the first in which such a nonlinear mapping was investigated. Although eye tracking initially benefited from the existence of a resonant frequency (see our earlier comments), it is noteworthy that the elastic mapping also introduced some important distortions between hand movement and target motion (see Fig. 3*C*). Still, despite those distortions, we found that within ~20 trials (~5 min) of tracking, subjects were able to capture these dynamics and performed at least as well as with the rigid mapping. Although this rather fast learning seems to conflict with previous observations focusing on manual dexterity with nonrigid objects (Dingwell et al. 2002; Venkadesan et al. 2007; Winges et al. 2009), there are also reports suggesting that predicting and controlling the movement of an object may be governed by distinct neural processes (Danion et al. 2013; Flanagan et al. 2003).

The update in eye-hand coordination seen in our study is reminiscent of two other studies in which subjects had to perform a visuomotor task that did not explicitly require some eye tracking (Rentsch and Rand 2014; Sailer et al. 2005). In the Sailer et al. (2005) study, subjects had to make pointing movements as quickly as possible to hit visual targets successively using a cursor that was moved by applying isometric forces and torques with the fingers, another type of challenging mapping. The results showed that as learning improved, saccades made to the target switched from a reactive to a more predictive mode. In the Rentsch and Rand (2014) study, a similar change in the control of saccadic eye movements was observed when subjects adapted to visuomotor rotations while making hand pointing movements toward visual targets. Our study further extends the range of adaptability of predictive mechanisms beyond saccade control to more general tracking abilities.

Finally, in some occasions, it is worth noting that, after prolonged experience, eye tracking performance under Self-Spring could actually exceed pursuit under Self-Rigid (see Fig. 4, *B* and *D*). This observation may seem counterintuitive given that the rigid mapping is presumably the most experienced in real life. We propose that eye tracking performance under Self-Spring benefited from the separate contributions of Mapping and Agency. The former contribution relates to the less complex target trajectories under Spring (i.e., as evidenced by lower ApEn), and it is not surprising that these low-level visual signal properties acted rapidly on pursuit (i.e., from the very first trial). The second contribution relates to the buildup of agency, an arguably slower process (i.e., requiring 20 trials in our experiment) allowing Self-Spring to progressively outperform External-Spring. In the specific cases of VE and smooth pursuit gain, the benefits of simpler trajectories were strong enough to equalize performance at the beginning of the External-Spring and Self-Rigid blocks. As the second mechanism (agency) started to build up, we found that eye tracking performance under Self-Spring could outperform performance under Self-Rigid.

Dissociation between the update of smooth pursuit and saccades. Except for a marginal decrease in saccade rate across trials, prolonged experience during Self-Spring did not benefit much to saccades, which is in apparent contrast with the numerous improvements found in smooth pursuit, as evidenced by changes in smooth pursuit gain, VE, and eye target lag. In particular, we found that PE at the end of saccades did not improve across trials, both during regular and blanked periods. In addition, we did not find evidence that saccades were biased in catchup trials. Note that the latter observation is consistent with the fact that adaptation of smooth pursuit to visual

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inversion did not seem to bias saccades (see Fig. 4*D* in Vercher et al. 1995). Overall, although our results on smooth pursuit show that subjects acquired some knowledge about the relation between their hand and the target's movement, this knowledge was apparently not accessible for the control of saccades. We propose that the update of the predictive neural mechanisms engaged in eye tracking of a self-moved target is dissociated for smooth pursuit and saccades. This conclusion may seem at odd with several evidences of a synergistic behavior between smooth pursuit and saccades (Orban de Xivry and Lefèvre 2007; Orban de Xivry et al. 2006), one possibility could be that the saccade-smooth pursuit synergy previously described when tracking an externally moved target does not extend to a self-moved target. The fact that catch trials specifically biased Self conditions but not External conditions strongly suggests that distinct predictive mechanisms are indeed engaged in both cases. Another possibility could be that the timeline of the experiment was too short to allow an update of the saccadic system. In this context, it is worth reporting that the update of saccades when learning a novel mapping between manual actions and their visual consequences (Sailer et al. 2005) was a rather slow process compared with the update of smooth pursuit seen in our study. Finally, this lack of transfer is reminiscent of one of our study in which subjects learned to manipulate an object with novel dynamics (Danion et al. 2013). Indeed, in that study, we showed that, despite well-established synergies between hand grip force and arm movement, the knowledge acquired by the gripping hand system was not accessible for updating arm movement control.

Perspectives

In our study, we simulated the visual behavior of a mass-spring system but did not provide haptic feedback that was consistent with a physical hand-target interaction. Although previous studies have shown that people can learn to control nonrigid objects both when appropriate haptic feedback is provided (Dingwell et al. 2002; Nagengast et al. 2009) and when it is not (Mah and Mussa-Ivaldi 2003; Mehta and Schaal 2002), we have previously observed that initial and late performance were better with haptic feedback (Danion et al. 2012), presumably because such feedback improves sensory estimates of the state of the object. At this stage, whether eye tracking performance under complex hand-target mapping could benefit or not from haptic feedback remains to be probed. Another important issue in motor control is to determine to what extent learning in one context can be generalized to other contexts (Shadmehr 2004). With respect to the present study, it would be particularly interesting to assess whether training under one particular spring dynamics can subsequently benefit to learning other spring dynamics as well as whether the knowledge acquired when moving the target with one hand is accessible for moving the target with the other hand. Another interesting development would be to experimentally probe the relative effects of informational transfer between the hand and eye versus target and eye on pursuit, by independently manipulating their signal-to-noise ratio. Answering these questions should provide critical information to assess the nature of the knowledge acquired by the subjects.

Final comments. In these experiments, we explored the ability to track a self-moved target under complex hand-target dynamics. We showed that, despite low initial eye tracking performance, subjects managed to improve their performance within a few minutes of practice. Results from the catch trials after practice suggest that subjects have acquired an internal forward model of the hand-target dynamics allowing more efficient smooth pursuit based on predicted visual consequences of hand actions. Altogether, this study extends the view that humans can build internal models of nonrigid objects not only for efficient manipulation (Danion et al. 2012; Dingwell et al. 2002, 2004; Mehta and Schaal 2002) but also to proficiently coordinate eye and hand movements.

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DISCLOSURES

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

AUTHOR CONTRIBUTIONS

C.L., A.M., L.M., and F.D. conception and design of research; C.L. and F.D. performed experiments; C.L., A.M., and F.D. analyzed data; C.L., A.M., L.M., and F.D. interpreted results of experiments; C.L. and F.D. prepared figures; C.L., A.M., L.M., and F.D. edited and revised manuscript; C.L., A.M., L.M., and F.D. approved final version of manuscript; F.D. drafted manuscript.

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