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**RESEARCH ARTICLE** | *Control of Movement*

# Eye movements do not play an important role in the adaptation of hand tracking to a visuomotor rotation

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**Gouirand N, Mathew J, Brenner E, Danion FR.** Eye movements do not play an important role in the adaptation of hand tracking to a visuomotor rotation. *J Neurophysiol* 121: 1967–1976, 2019. First published April 3, 2019; doi:10.1152/jn.00814.2018.—Adapting hand movements to changes in our body or the environment is essential for skilled motor behavior. Although eye movements are known to assist hand movement control, how eye movements might contribute to the adaptation of hand movements remains largely unexplored. To determine to what extent eye movements contribute to visuomotor adaptation of hand tracking, participants were asked to track a visual target that followed an unpredictable trajectory with a cursor using a joystick. During blocks of trials, participants were either allowed to look wherever they liked or required to fixate a cross at the center of the screen. Eye movements were tracked to ensure gaze fixation as well as to examine free gaze behavior. The cursor initially responded normally to the joystick, but after several trials, the direction in which it responded was rotated by 90°. Although fixating the eyes had a detrimental influence on hand tracking performance, participants exhibited a rather similar time course of adaptation to rotated visual feedback in the gaze-fixed and gaze-free conditions. More importantly, there was extensive transfer of adaptation between the gaze-fixed and gaze-free conditions. We conclude that although eye movements are relevant for the online control of hand tracking, they do not play an important role in the visuomotor adaptation of such tracking. These results suggest that participants do not adapt by changing the mapping between eye and hand movements, but rather by changing the mapping between hand movements and the cursor's motion independently of eye movements.

**NEW & NOTEWORTHY** Eye movements assist hand movements in everyday activities, but their contribution to visuomotor adaptation remains largely unknown. We compared adaptation of hand tracking under free gaze and fixed gaze. Although our results confirm that following the target with the eyes increases the accuracy of hand movements, they unexpectedly demonstrate that gaze fixation does not hinder adaptation. These results suggest that eye movements have distinct contributions for online control and visuomotor adaptation of hand movements.

eye fixation; eye-hand coordination; gaze behavior; humans; sensorimotor adaptation

## INTRODUCTION

Because we are sometimes confronted with changes in our body, such as muscle fatigue, or with changes in the environment, such as those that occur when looking through a diving mask, we need to be able to adjust our motor commands to maintain accurate hand movements. Sensorimotor adaptation is the process that leads to the reduction in systematic errors induced by such altered conditions, thereby restoring the former level of performance (Krakauer 2009). The case of adaptation to a visuomotor rotation, a situation in which the visual feedback of hand movements is rotated, has been thoroughly studied over the last decades (Cunningham 1989; Krakauer 2009; Ogawa and Imamizu 2013; Prablanc et al. 1975; Scheidt and Ghez 2007). Although this field of research has produced substantial knowledge about the generalization of adaptation and consolidation of motor memory (Canaveral et al. 2017; Huang et al. 2011; Orban de Xivry and Lefèvre 2015), little is known about the possible contribution of eye movements to visuomotor adaptation despite the intricate relationship that is believed to exist between eye and hand movements (Crawford et al. 2004; Miall et al. 2001; Neggers and Bekkering 2000; Prablanc et al. 1979). The goal of the current study is to explore this issue.

Visuomotor adaptation has been studied with two types of motor tasks, namely, reaching tasks and tracking tasks. Although much is known about gaze behavior during visuomotor adaptation of hand reaching movements (de Brouwer et al. 2018; Rand and Rentsch 2015, 2016; Rentsch and Rand 2014), gaze behavior during the adaptation of hand tracking movements has been studied much less extensively. For reaching movements, it has been proposed that eye movements reflect the explicit component of visuomotor adaptation (de Brouwer et al. 2018; Rand and Rentsch 2015). Specifically, Rand and Rentsch (2015) showed that constraining gaze affected the explicit component of adaptation (aiming) but not the implicit component. Although these studies speak for a contribution of extraretinal signals (efference copy or ocular proprioception) to visuomotor adaptation for discrete movements with no feedback about the transformation until the end of the movement, whether this also extends to continuous manual tracking is not clear. Adaptation to visuomotor rotation has been described for tracking tasks (Ogawa and Imamizu 2013; Prablanc et al. 1975; Tong and Flanagan 2003), but no study has yet examined gaze behavior and its contribution to such adaptation. To date, we

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are only aware of a study that investigated the impact of gaze behavior in the context of a visual (left-right) inversion (Grigorova and Bock 2006), which might even rely on different neural mechanisms than adaptation to a visuomotor rotation (Telgen et al. 2014). In the study of Grigorova and Bock (2006), participants were either instructed to look at the target, look at the cursor, or fixate straight ahead, or received no instructions regarding eye movements. Surprisingly, fixating straight ahead did not impair the dynamics of adaptation to the inversion, questioning whether extraretinal signals play a role in visuomotor adaptation. In the current study we proposed to reinvestigate this issue in the context of a visuomotor rotation, avoiding some of the limitations of that earlier study and exploring some new issues.

Regarding limitations, in contrast to Grigorova and Bock (2006), who recorded eye movements by means of electrooculography, we used an eye tracking system that allows us to perform a more detailed analysis of the eye movements. In particular, we wanted to be sure that participants produce adequate gaze fixation. Moreover, we examined tracking of a target moving in two dimensions, making our visuomotor rotation presumably more challenging than a visual inversion along the horizontal axis. We reasoned that if task difficulty is not a key factor for the contribution of eye movements to visuomotor adaptation, the finding of Grigorova and Bock (2006) that gaze did not matter should also hold in this situation. One new issue that we wanted to examine, assuming that adaptation to a visuomotor rotation is possible with gaze fixed, is whether adaptation occurred in the same manner with gaze fixed as when the eyes were free to move. To address this issue, we examined whether adapting with gaze fixed would transfer to a context in which fixation was no longer a requirement, and vice versa.

During regular hand tracking, gaze is typically concerned with monitoring the target (Danion and Flanagan 2018). We reasoned that adaptation of hand tracking could be performed in two different ways. Because eye movements guide future or ongoing hand movement (Crawford et al. 2004; Gielen et al. 2009), a first possibility is that participants update the mapping between eye and hand movements. Not only does this predict that participants will keep their eyes on the target whenever they can, but adaptation is expected to be impaired in the absence of eye movements. Alternatively, participants might directly update the relationship between hand motor commands and cursor motion, independently of eye movements. If eye movements are not an integral part of visuomotor adaptation, adaptation should generalize across eyes fixed and eyes free conditions.

## METHODS

### *Participants*

Thirty-three healthy right-handed volunteers were recruited (18 women; 25 ± 4 yr of age; from here on this notation will be used to indicate mean ± SD). Handedness of participants was verified using the Oldfield Handedness Inventory (Oldfield 1971) and revealed a mean group laterality index of 91 ± 10. All participants gave written consent before participation. The experimental paradigm (2016-02-03-007) was approved by the local ethics committee of Aix Marseille University and complied with the Declaration of Helsinki.

### *Data Acquisition*

Figure 1*A* shows the experimental setup. Participants were seated comfortably in a dark room facing a screen (BENQ; 1,920 × 1,080 pixels, 27-in., 144 Hz) positioned in the frontal plane 57 cm from the participants' eyes. Note that 1° of visual angle is approximately equivalent to a distance of 1 cm on the screen at an eye-to-screen distance of 57 cm. 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. To block vision of their hands, a mask was positioned under the participants' chin. Participants were required to hold a joystick (Series 812; Megatron, Allinges, France; with ±25° of inclination along *x-y* axes) with their right hand positioned horizontally on a table in front of them, in line with their central sagittal plane. Both right and left forearms were resting on the table. The output of the joystick was fed into a data acquisition system (Keithley ADwin Real Time; Tektronixs) and was sampled at 1,000 Hz. Movements of the right eye were recorded using an infrared video-based eye tracker (desktop EyeLink 1000 system; SR Research). Horizontal and vertical positions of the right eye were recorded at a sampling rate of 1,000 Hz. The output from the eye tracker was calibrated before every block of trials by recording the raw eye positions as participants fixated a grid composed of nine known locations. The mean values during 1,000-ms fixation intervals at each location were then used off-line for converting raw eye tracker values to horizontal and vertical eye positions in degrees of visual angle.

### *Experimental Design*

Throughout the experiment, participants had to perform a tracking task (Fig. 1*B*) that consisted of moving the joystick with the right hand so as to keep the cursor (red disk, 0.5 cm in diameter) as close as possible to a moving target (blue disk, 0.5 cm in diameter). This task allowed us to probe the ability to master hand movement along a desired trajectory (Ogawa and Imamizu 2013; Tong and Flanagan 2003). The motion of the target resulted from a combination of sinusoids: two along the frontal axis (one fundamental and a second or third harmonic) and two on the sagittal axis (same procedure). The following equations determined the target's motion:

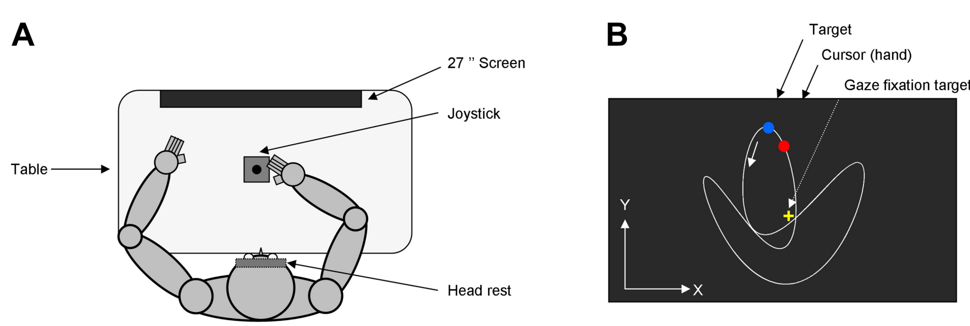


Fig. 1. Apparatus. *A*: top view of a participant sitting in the experimental setup. *B*: schematic view of the screen (see METHODS for further information).

Table 1. *Target trajectory parameters*

| Trajectory | $A_{1x}$, cm | $A_{2x}$, cm | $h_x$ | $\varphi_x$, ° | $A_{1y}$, cm | $A_{2y}$, cm | $h_y$ | $\varphi_y$, ° |
|---|---|---|---|---|---|---|---|---|
| *1* | 5 | 5 | 2 | 45 | 5 | 5 | 3 | −135 |
| *2* | 4 | 5 | 2 | −60 | 3 | 5 | 3 | −135 |
| *3* | 4 | 5.1 | 3 | −60 | 4 | 5.2 | 2 | −135 |
| *4* | 5 | 5 | 3 | 90 | 3.4 | 5 | 2 | 45 |
| *5* | 5.1 | 5.2 | 2 | −90 | 4 | 5 | 3 | 22.5 |

$$x_t = A_{1x}\cos\omega t + A_{2x}\cos(h_x\omega t - \varphi_x) \quad (1)$$

$$y_t = A_{1y}\sin\omega t + A_{2y}\sin(h_y\omega t - \varphi_y) \quad (2)$$

This technique was used to generate pseudorandom two-dimensional patterns while preserving smooth changes in velocity and direction (Danion and Flanagan 2018; Mrotek and Soechting 2007; Soechting et al. 2010). A total of five different patterns with a mean tangential velocity of 16°/s were used throughout the experiment (see Table 1 and Fig. 2). Mean target eccentricity was 6.0 ± 2.7 cm, with values ranging from 0.4 up to 11.8 cm. The time necessary to complete a full revolution was 5 s. Given that all trials had a duration of 10 s, each movement pattern was repeated twice during each trial, and they all had similar path length (160 cm). The order of patterns was randomized across trials while making sure that each experimental condition contained a similar number of each pattern.

Gaze behavior and the mapping between hand motion and cursor motion depended on the experimental conditions. Regarding gaze behavior, participants could either be asked to keep their gaze on a yellow fixation cross positioned at the center of the screen (gaze-fixed condition; see Fig. 1*B*) or did not receive any explicit instructions regarding eye movements (gaze-free condition) so that they were free to look at the target, the cursor, or both (Danion and Flanagan 2018). In the latter case, the fixation target was removed from the screen.

Regarding the hand-cursor mapping, we employed either a regular or rotated mapping. For both mappings, the gain of the joystick was such that a 25° change in the inclination of the joystick resulted in a change on the screen of 15 cm. This gain prevented the cursor from moving outside the screen. For the regular (or nonrotated) mapping, the relation between the joystick orientation and its visual consequences on the screen was intuitive: if the joystick was inclined to the left, the cursor on the screen also moved to the left. Under the rotated mapping, the relation between the joystick orientation and the position of the cursor was altered by a 90° anticlockwise visuomotor rotation (Ogawa and Imamizu 2013). As a result, if the participant moved the joystick forward, the cursor moved leftward on the screen.

As summarized in Fig. 3, participants were split into three groups (*group 1*: $n = 11$, mean age = 24 ± 2 yr, 6 women; *group 2*: $n = 11$, mean age = 26 ± 5 yr, 5 women; *group 3*: $n = 11$, mean age = 24 ± 4 yr, 7 women). The first 22 participants that we recruited were assigned randomly to either *group 1* or *group 3*. Eleven additional participants were recruited later and assigned to *group 2*. To assess baseline performance and group homogeneity, all groups first performed a block of 10 trials with free gaze using the nonrotated cursor. Subsequently, *group 1* and *group 2* then performed 80 trials with the rotated mapping. *Group 1* first performed a block of 40 trials with gaze fixed and then a block of 40 trials with gaze free. *Group 2* first performed a block of 40 trials with gaze free and then 40 trials with gaze fixed. After this, without changing the gaze context, the rotated mapping was removed for a single trial to assess the magnitude of the aftereffect in each group. *Group 3* went through the same conditions as *group 1* except that there was no rotation during the first block of 40 trials, in which gaze was fixed. The first two groups allow us to assess how eye movements contribute to the learning and transfer of control of the cursor with the rotated mapping. The third group allows us to determine whether any difference in performance between the second block of trials of *group 1* and the first block of trials of *group 2*, both of which involved the rotated cursor mapping with gaze free, could be due to participants having practiced the tracking task with restrained gaze rather than to having practiced tracking with the rotated mapping. Overall, each participant completed a total of 91 trials. Before the experiment, each participant performed two or three practice trials to become familiarized with the setup and the tracking task.

The experiment was designed to address three main objectives. First, we wanted to compare whether *group 1* and *group 2* participants would adapt similarly to a visuomotor rotation with gaze fixed and gaze free, respectively. This will extend earlier findings to a more complex situation under controlled fixation. Second, we wanted to assess how *group 1* and *group 2* participants' performance would change when starting the second block of 40 trials under a different gaze context: to what extent does the adaptation suffer when gaze changes? This will reveal whether the adaptation to visuomotor rotation is linked to the eye movements. Third, we examined natural gaze behavior during adaptation to a visuomotor rotation. Do participants always track the target if they are allowed to? Do the participants of *group 1* try to keep fixating, despite the absence of a fixation point, in order not to lose their adaptation?

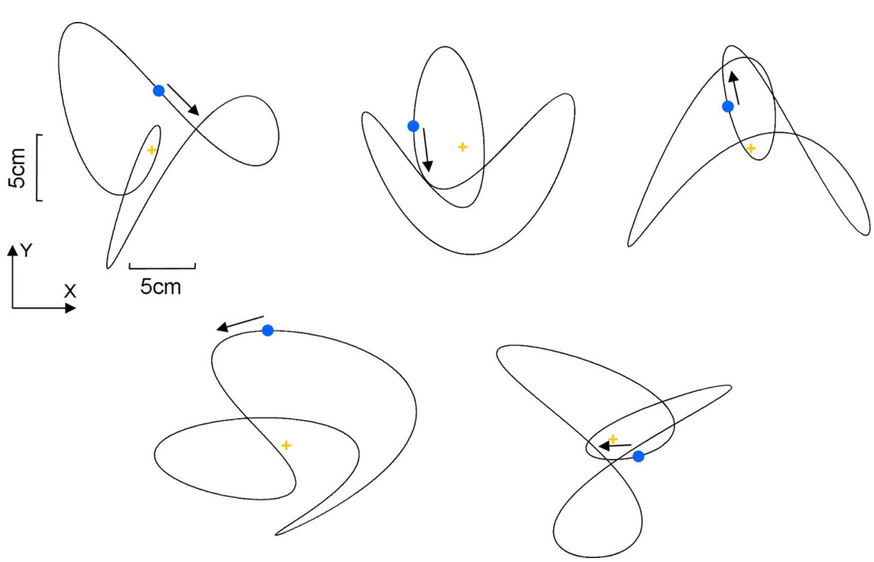


Fig. 2. Target trajectories used across all the experimental conditions. The blue dot shows the initial position of the target, and the arrow shows its initial motion direction. The yellow cross indicates the position of the fixation target when gaze was constrained.

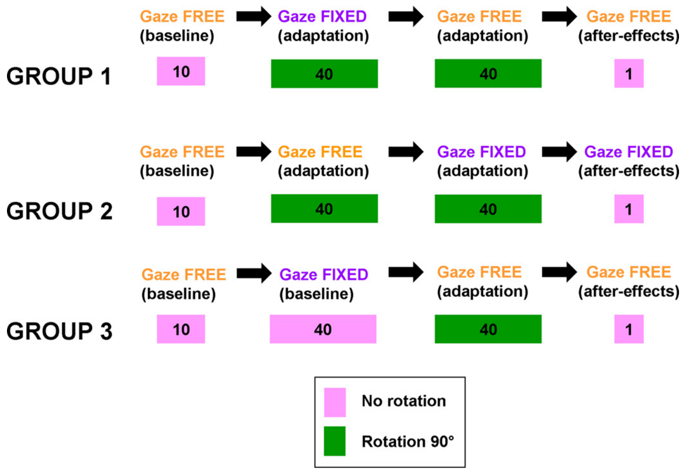


Fig. 3. Experimental design. The pink and green boxes represent blocks of trials, with the number of trials in each block indicated.

### Data Analysis

To quantify hand tracking error ($E$), we measured the distance in centimeters (in 2 dimensions, $x$ and $y$) between the cursor ($C$; moved by the hand) and the target ($T$) at each instant ($t$) using the following equation:

$$E_t = \sqrt{(C_{xt} - T_{xt})^2 + (C_{yt} - T_{yt})^2} \tag{3}$$

We averaged this error across time for each trial. To quantify the time course of adaptation, we fit an exponential function with three parameters to the change in error across trials for each participant:

$$E_{trial} = ae^{b \times trial} + c, \tag{4}$$

with $a$ accounting for the magnitude of the change, $b$ for the learning rate, and $c$ for the asymptotic performance ("trial" is the trial number).

We also investigated the influence of target position on hand tracking, because an obvious consequence of not following the target with one's eyes, in addition to extraretinal signals not providing useful information about the target's motion, is that the target's position has to be judged using information from a higher retinal eccentricity. For each trial in the gaze-fixed blocks, data points were split into two sets: those in which the target was near the fixation point, and therefore also near the origin of the rotation (<6 cm), and those in which it was far from the fixation point, and therefore at a larger retinal eccentricity (>6 cm). The rotation obviously alters the position of the cursor more strongly when it is farther from the origin, but it alters the relationship between the direction in which the cursor moves and the orientation of the joystick to the same extent everywhere.

Gaze behavior during sessions with gaze free was assessed by comparing the mean distances between where on the screen participants were looking with respect to the target, and where they were looking with respect to the cursor (each determined using a method similar to that used to determine the distance between cursor and target). During sessions with gaze fixation, the quality of eye fixation was evaluated by measuring the spread (standard deviation) of gaze along the horizontal and vertical axis within each trial.

### Statistics

ANOVAs with group as a factor and sometimes with individual participants' values on different trials as a repeated measure were the main tool for statistical analyses. The threshold of significance was always set at 0.05. We tested whether fixating influenced performance when there was no rotation, whether fixating influenced the rate of adaptation when the rotation was introduced, and whether performance changed when fixation was imposed or no longer required after participants had adapted to the rotation. We also tested whether participants' gaze was closer to the cursor or to the target when they were free to move their eyes.

## RESULTS

### Representative Trials

Figure 4 plots representative trials collected from one participant from each group in various experimental conditions and at various stages of exposure. As can be seen in Fig. 4*C*, hand tracking with no rotation was poorer with fixed gaze. Tracking was even poorer when the rotation was introduced, under both gaze-free and gaze-fixed conditions (see Fig. 4, *A* and *B*). In both cases, hand tracking performance improved across trials as suggested by the comparison between early and late trials. It also can be noted that whenever eyes were free to move, gaze focused more on the target than on the cursor (gaze curves closer to the target curves than to the cursor curves during free gaze in Fig. 4). These observations are analyzed in more detail below.

### Evaluating Hand Tracking

*Baseline hand tracking.* During the first block, all participants performed the tracking task with their gaze free and no visuomotor rotation. We found no systematic difference in hand tracking performance between the groups before we introduced any gaze constraints or visuomotor rotation. Averaged across groups, mean cursor-target distance during baseline trials was 1.65 cm.

*Impact of gaze fixation without rotation.* We first consider the case of *group 3* in which hand tracking under gaze-fixed and gaze-free conditions could be compared in the absence of visuomotor rotation. When participants switched from the gaze-free to the gaze-fixed condition (*trial 11*; Fig. 5), the cursor-target distance increased by ~1 cm [from 1.64 to 2.77 cm; $F(1,10) = 121.5$; $P < 0.001$]. Improvements in hand tracking were observed between the 1st and 40th trials [from 2.77 to 2.22 cm; $F(1,39) = 3.54$; $P < 0.001$], but the value quickly reached a plateau. It never returned to baseline performance. This shows that under normal hand-cursor mapping, eye movements help to keep the cursor close to the target.

*Adaptation under gaze-free and gaze-fixed conditions.* When participants were first exposed to the visuomotor rotation, their hand tracking performance deteriorated markedly. Compared with baseline performance, the cursor-target distance initially increased by a factor of 6 (*group 1* from 1.54 to 9.05 cm; *group 2* from 1.45 to 9.21 cm; *group 3* from 1.64 to 9.53 cm). Participants' tracking performance improved substantially over the 40 trials of exposure, with tracking error decreasing by ~60–70% (reaching 3.29 cm for *group 1*, 2.63 cm for *group 2*, and 3.05 cm for *group 3*). Tracking performance never returned to the baseline performance (or even to what was observed under fixation with no rotation).

To examine whether adaptation of hand tracking has a similar time course under gaze-free and gaze-fixed conditions, we compared the time course of hand tracking errors for *group 1* under fixed gaze (*block 2*) and for *group 2* under free gaze (*block 2*). An ANOVA comparing the parameters of the exponential fits of the learning curves (*Eq. 2*) showed no significant difference across groups for the amplitude of the change

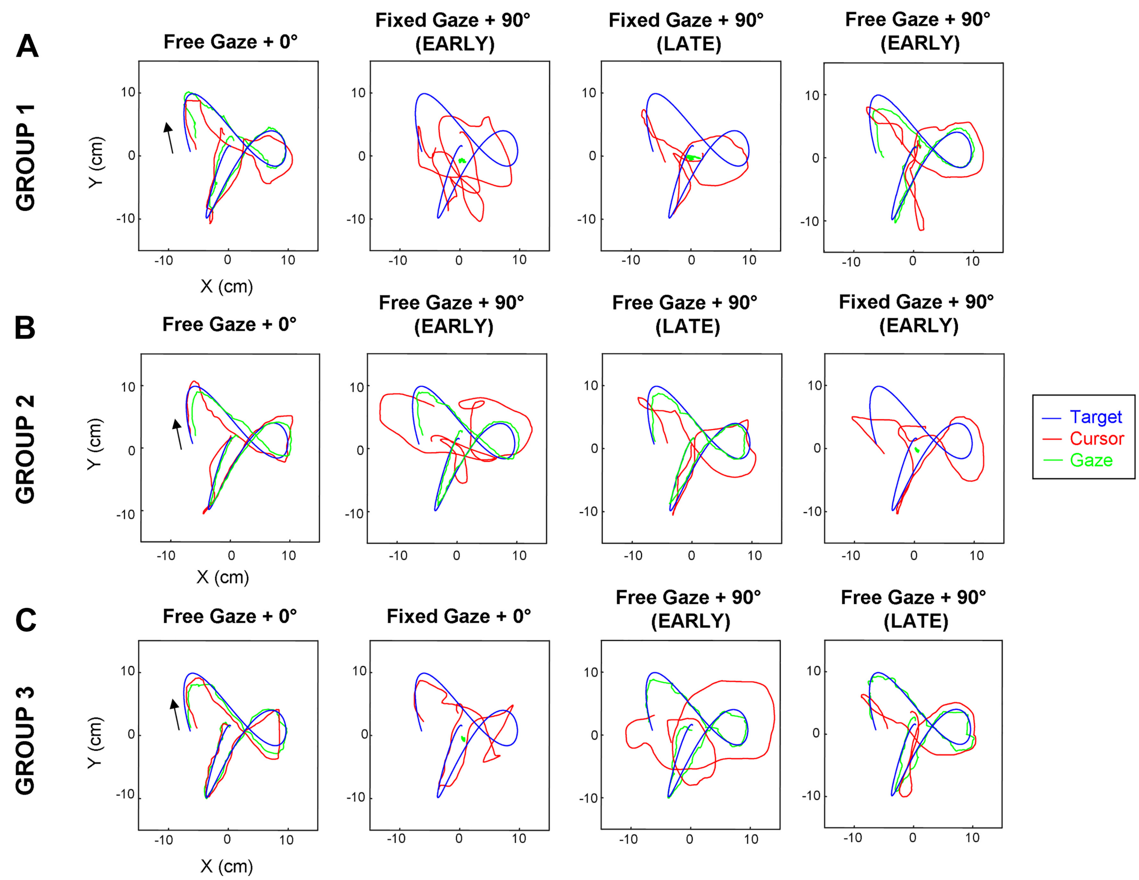


Fig. 4. Typical trials by 3 participants at various stages of the experiment. Target, cursor, and eye position signals are shown. *A*: data for a participant of *group 1* during free gaze with no rotation, as well as during exposure to the rotation under fixed gaze and then free gaze. *B*: data for a participant of *group 2* during free gaze under no rotation, as well as during early and late exposure to the rotation with free gaze and then fixed gaze. *C*: data for a participant of *group 3* during free gaze, during fixed gaze under no rotation, and then during free gaze under rotation. Although each trial was 10 s long, only 4 s of signals are displayed for clarity. To make the comparison easier, we display trials with the same target trajectory. The arrow shows the initial target motion direction. The small gaps in some eye movement traces are due to blinks.

[parameter *a*; $F(1,20) = 0.07$; $P = 0.79$] or the learning rate [parameter *b*; $F(1,20) = 1.89$; $P = 0.18$]. The only difference was that the asymptote was higher under gaze-fixed conditions [parameter *c*; $F(1,20) = 4.24$; $P = 0.05$]. This can be observed in *trials 40–50* of Fig. 5 where tracking error was smaller under gaze-free (*group 2*) than gaze-fixed (*group 1*) conditions.

Overall, *group 1*, whose participants adapted while fixating, did not stand out as being particularly different from *group 2*,

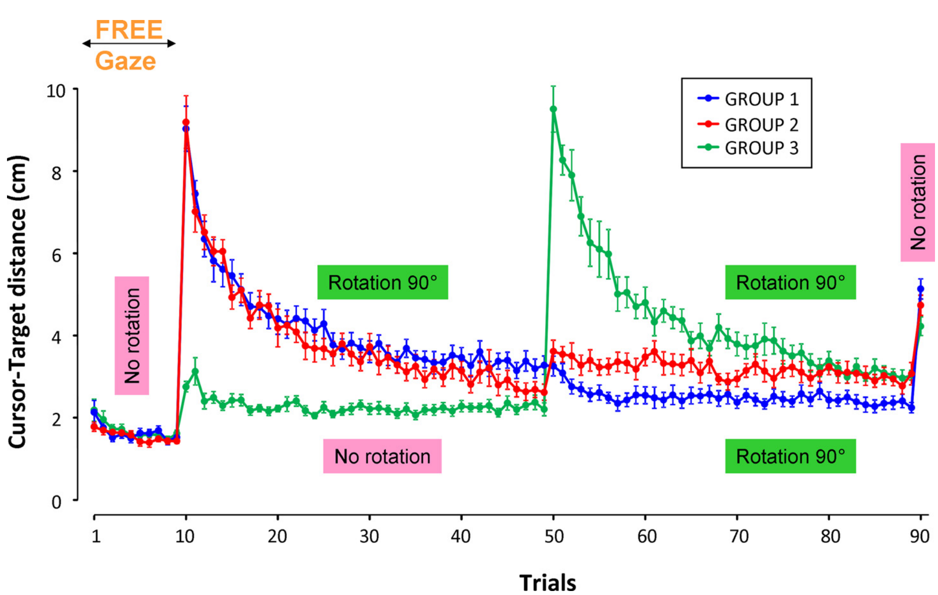


Fig. 5. Mean cursor-target distance as a function of trial number and experimental *group 2*. Error bars represent SE of the mean across participants.

whose participants adapted while pursuing the target. The only difference is the extent of final adaptation, with *group 2* reaching better tracking performance at the end of the second block. Those differences are consistent with our earlier observation (based on *group 3*) that when there is no rotation, hand tracking is better under gaze-free than under gaze-fixed conditions. This difference can easily be explained by the quality of the feedback, which differs due to the retinal resolution and extraretinal information not being the same when participants are fixating as when they are pursuing the target. Thus we do not consider it to indicate that the adaptation mechanisms themselves are different. We can conclude from these comparisons that eye movements have minimal impact on the time course of the initial adaptation of hand tracking to a visuomotor rotation.

*Transfer of adaptation between fixed gaze and free gaze.* To determine whether adaptation under fixed gaze transfers to free gaze, and vice versa, we first examined the hand tracking performance of *group 1* when participants switched from fixed gaze to free gaze (see Fig. 5). We found no significant difference in cursor-target distance between the last trial performed under fixed gaze (*trial 50*) and the first trial performed under free gaze [*trial 51*; 3.29 vs. 3.27 cm; $F(1,10) = 0.01$; $P > 0.91$], providing support for a full transfer of adaptation. Subsequent improvements were observed after gaze was no longer fixed, with cursor-target distance decreasing from 3.27 to 2.37 cm within eight trials. No further improvement was seen during the remaining 32 trials. Thus adaptation with fixed gaze transfers well to gaze-free conditions. Finally, performance with free gaze (*trials 51–90*) was clearly better for *group 1* than for *group 3*, showing that the improvement was really due to transfer of the adaptation rather than simply to increased experience with the task.

To determine whether adaptation also transfers from free gaze to fixed gaze, we examined the hand tracking performance of *group 2* (see Fig. 5). We found an increase in cursor-target distance between the last trial performed under free gaze and the first trial performed under fixed gaze [2.63 vs. 3.63 cm; $F(1,10) = 20.81$; $P = 0.001$]. Although tracking performance did become worse when fixation was imposed, performance was still much better than the initial performance when participants were exposed to the rotation (distance of ~9 cm). The sudden increase in error (by ~1 cm) is consistent with the sudden increase that was observed when participants switched from free to fixed gaze under no rotation (*group 3*). During the subsequent trials, hand tracking accuracy improved, with cursor-target distance decreasing from 3.63 to 3.09 cm between the first and last trial with fixed gaze, an effect that was also observed for *group 3* (before the rotation was imposed).

Thus visuomotor adaptation transfers almost completely between gaze-fixed and gaze-free conditions. Such transfer implies that the same mechanisms are involved in visuomotor adaptation under gaze-fixed and gaze-free conditions.

*Aftereffects.* At the end of the third block, when the rotation was unexpectedly removed, all groups exhibited clear impairments in hand tracking, as one would expect (see the points on the extreme *right* in Fig. 5). Aftereffects of adaptation were greater for *groups 1* and *2* than for *group 3*, presumably because *group 3* participants had only been exposed to the rotation for 40 trials, whereas the others had been exposed to the rotation for 80 trials.

*Impact of target eccentricity.* As already mentioned, we found poorer performance when gaze was fixed, irrespective of the rotation. To what extent is the poorer performance in the gaze-fixed condition a result of the larger retinal eccentricities that arise from not following the target with one's eyes? Considering that target eccentricity changes substantially within each trial in the gaze-fixed condition, we compared hand tracking performance for intervals with high (>6 cm) and low (<6 cm) target eccentricity (Fig. 6). In the absence of visuomotor rotation (*group 3* in Fig. 6), a modest detrimental effect of target eccentricity was found, with cursor-target distance being 16% greater for the higher target eccentricities (2.46 vs. 2.11 cm). In the presence of visuomotor rotation (*group 1* in Fig. 6), hand tracking was consistently less accurate for the higher target eccentricities (4.67 vs. 3.74 cm). The rotation obviously influences eccentric positions far more than positions in the vicinity of gaze fixation, so these differences are not surprising. The fact that hand tracking precision is

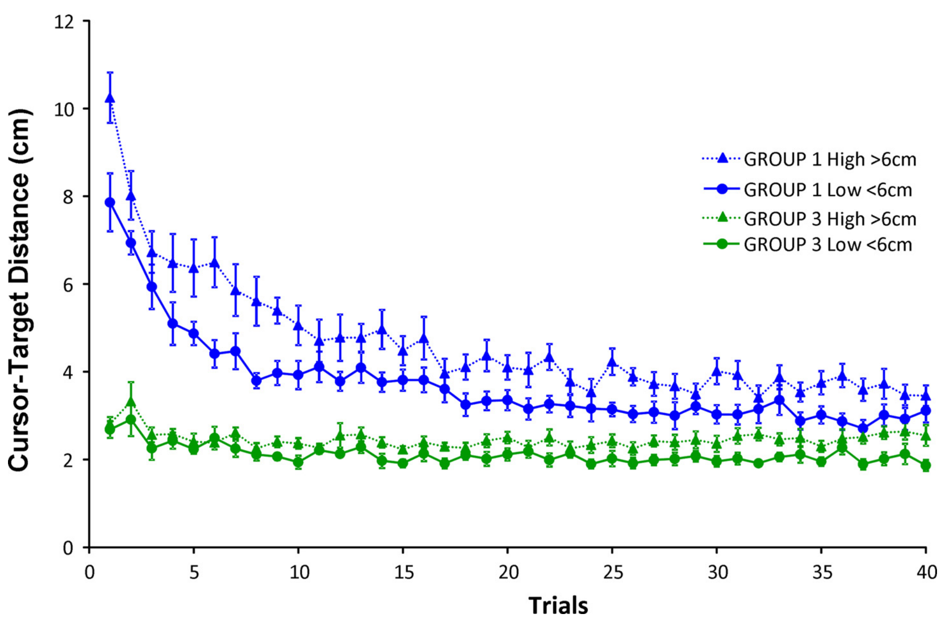


Fig. 6. Changes in the mean cursor-target distance when the target was near (low eccentricity) or far (high eccentricity) from fixation for *group 1* and *group 3* participants when subjected to the first block of trials in which gaze was fixed. Solid lines and circles indicate hand tracking under low target eccentricity. Dashed lines and triangles indicate hand tracking under high target eccentricity. Error bars represent SE of the mean across participants.

poorer when gaze is fixating than when gaze is free, irrespective of any rotation, can therefore at least partially be attributed to the larger target eccentricities of the target and cursor (assuming that gaze follows the target, as we will show next).

### *Evaluating Gaze*

*Accuracy of gaze fixation.* We first investigated how well participants coped with the instruction to keep gaze straight ahead. Each group completed one block of 40 trials under gaze-fixed conditions. Averaged across trials, the resulting standard deviation of gaze position was 0.29, 0.26, and 0.26 cm, respectively, for *group 1*, *group 2*, and *group 3* (1 cm corresponds with ~1° at the viewing distance that we used; we report gaze in cm on the screen to make it easier to compare values related to gaze with the tracking values). For comparison, standard deviations under free gaze were much larger, reaching 4.46, 4.23, and 4.63 cm, respectively, for *group 1*, *group 2*, and *group 3*. Because asking participants to fixate reduced gaze excursion to ~6% of the value when not instructed to fixate, and this value includes measurement noise, we conclude that participants coped rather well with our instruction to keep their eyes fixed. Moreover, those values indicate that when switching from the gaze-fixed block to the gaze-free block, *group 1* participants did not try to keep fixating to maintain the adaptation (to the rotation) that they had achieved while fixating. Similarly, when switching from the gaze-free block to the gaze-fixed block, *group 2* participants were able to maintain the adaptation while coping rather well with the requirement to fixate gaze. These observations confirm that transfer of adaptation truly occurred across gaze conditions.

*Free gaze behavior during adaptation of hand tracking.* As suggested by the typical trials displayed in Fig. 4, when participants could freely move their eyes, their gaze seemed more concerned with the target than with the cursor. This view is confirmed by an analysis of the eye-cursor and eye-target distances when *group 2* participants first encountered the rotated mapping with gaze free (Fig. 7). Throughout the block, the eye-cursor distance was consistently and substantially larger than the eye-target distance. Averaged across trials, the eye-target and eye-cursor distances were respectively 1.57 and 3.52 cm [$F(1,10) = 67.99$; $P < 0.001$]. A similar difference was found for performance in this condition after participants had learned the rotation with eyes fixed [*group 1*; 1.49 and 2.42 cm; $F(1,10) = 53.51$; $P < 0.001$].

## DISCUSSION

Our main objective was to investigate the contribution of eye movements to visuomotor adaptation of hand tracking. Our results can be summarized with the following key findings. First, we observed that normal hand tracking was more accurate when participants' eyes were free to move than when they had to fixate. Second, not only is it possible to adapt one's hand movements to a rotation without making eye movements, but the time course of this adaptation (and resulting aftereffects) is similar to that when gaze is free. Third, when participants adapt to the rotation under gaze-fixed conditions, most if not all of the adaptation is transferred to gaze-free conditions, despite the freedom being used to pursue the target with their gaze. Similarly, when participants adapt to the rotation under gaze-free conditions, most if not all of the adaptation is transferred to gaze-fixed conditions. Fourth, there is a detrimental effect of target eccentricity on hand tracking, but seeing the target at large eccentricity part of the time does not seem to affect the time course of visuomotor adaptation. Fifth, when gaze is free, it follows the target rather than the cursor, even during initial exposure to the rotation when the cursor is not moving as the participant would anticipate. We will discuss the implications of these findings in more detail below.

### *Contribution of Eye Movements to Normal Hand Tracking*

In the absence of visuomotor rotation, we observed that participants tracked the target more accurately with their hand when their eyes were free to move than when the eyes had to stay immobile. This observation extends earlier observations made in the context of hand reaching movements (Abrams et al. 1990; Neggers and Bekkering 1999; Prablanc et al. 1979; Vercher et al. 1994). Our results are also consistent with those of Grigorova and Bock (2006), who showed that hand tracking error was nearly doubled when participants had to keep their eyes fixed. They are consistent with the latency of hand tracking increasing under eyes-fixed conditions (Engel and Soechting 2003; Miall and Reckess 2002). Overall, the results

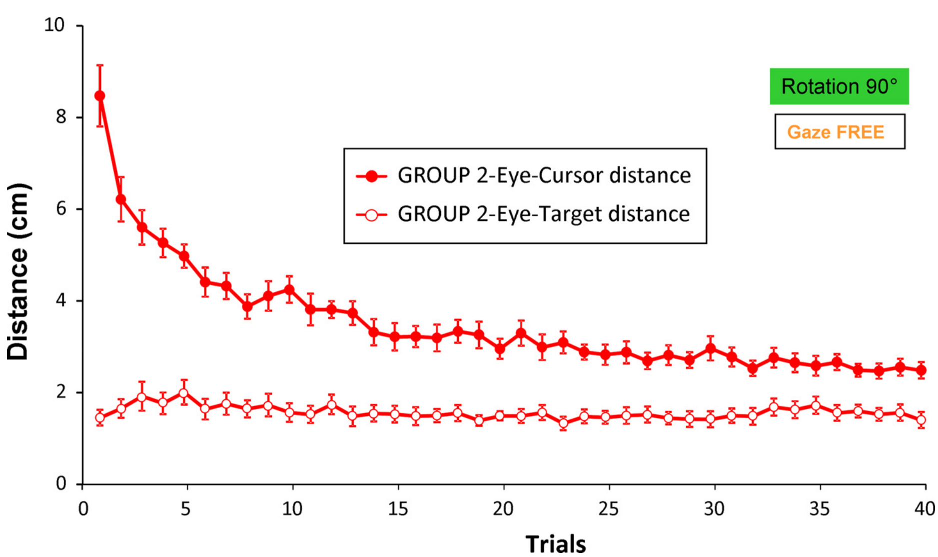


Fig. 7. Mean eye-cursor and eye-target distance as a function of trial number during adaptation to the visuomotor rotation with gaze free (*group 2*). Error bars represent SE of the mean across participants. Note how gaze is consistently closer to the target than to the cursor.

confirm that eye movements are critical for the online control of spatially accurate hand movements. We show that at least part of the reason why eye movements are critical is that they reduce the retinal eccentricity of the target and cursor.

### *Limited Contribution of Eye Movements to Visuomotor Adaptation*

In the INTRODUCTION, we contrasted two possible ways of adapting hand tracking to a rotation: either by updating the mapping between eye and hand movements or by updating the mapping between hand and cursor motion. Although, as predicted by the first scheme, participants kept their gaze on the target when the rotation was introduced, the fact that participants adapted in a rather similar way under gaze-free and gaze-fixed conditions suggests that eye movements do not play an important role in this form of visuomotor adaptation. This supports the second scheme in which participants update the relation between their hand motor commands and the anticipated cursor motion. The strongest support for the second scheme is the observation that adaptation transfers well across gaze conditions. Indeed, not only does adaptation with the eyes fixed transfer to performance with the eyes free, but a rather similar transfer exists when participants adapt with the eyes free and then switch to an eyes-fixed condition. All these observations suggest that visuomotor adaptation of hand tracking is not linked to eye movements per se. This conclusion fits well with the seminal study of Grigorova and Bock (2006) in which gaze fixation did not prevent participants from adapting to a left-right inversion of hand visual feedback. Our results extend their findings to a two-dimensional task (rather than a one-dimensional one) and to a more complex hand-cursor mapping (90° rotation rather than left-right inversion) that might rely on different adaptive mechanisms (Telgen et al. 2014).

Our results seem to be at odds with recent studies that investigated free gaze behavior when people adapted to a visuomotor rotation when making hand reaching movements (de Brouwer et al. 2018; Rand and Rentsch 2015, 2016; Rentsch and Rand 2014). In that case, it was proposed that eye movements might reflect the explicit component of visuomotor adaptation (de Brouwer et al. 2018; Rand and Rentsch 2015). In the current study, in which participants had to perform a continuous hand movement (tracking task), we show that the rate of adaptation is virtually unaffected by eye movements. However, because reaching and tracking rely on different gaze behaviors (i.e., different contribution of saccades, fixation, and smooth pursuit), it is possible that limiting eye movements interferes differently with the adaptation of these two types of hand movements. In tracking tasks, both the eyes and the hand are constantly guided by the anticipation of how the target will move. In aiming tasks, the target position is usually evident, and gaze is directed accordingly well before the hand reaches its goal.

Finally, although perturbing hand visual feedback by means of cursor rotation is a common technique to investigate visuomotor adaptation, other techniques are available, for instance, biasing hand-cursor gain (Pine et al. 1996), hand-cursor temporal relationship (Foulkes and Miall 2000; de la Malla et al. 2014), or even wearing prism glasses (Redding et al. 2005). Considering that some features of adaptation seem restricted to one form of adaptation (Petitet et al. 2018; Pine et al. 1996), future studies are necessary to assess whether the current results extend to other forms of visuomotor adaptation.

### *Free Gaze Behavior During Visuomotor Adaptation*

When participants could freely move their eyes, we observed that gaze was consistently oriented toward the target, not the cursor, as was observed previously when participants used a straightforward hand-cursor mapping (Danion and Flanagan 2018) or even a delayed hand-cursor mapping (Cámara et al. 2018). This observation contrasts markedly with the changes in gaze behavior observed during the adaptation of hand reaching movements (Rentsch and Rand 2014). In the latter case, it has been reported that gaze was directed to the cursor during early practice but progressively shifted toward the target as experience built up (see also Sailer et al. 2005). On the basis of this observation, we considered that participants might be tempted to direct their gaze more equally between the cursor and the target during early exposure of hand tracking. However, the current study clearly showed that this was not the case (Fig. 7). We conclude that even during challenging conditions, fixating the moving target seems to be the adequate behavior for accurate hand tracking. One possible reason for favoring target fixation might be that relying on visual information is the only way to monitor target position, whereas participants can also rely on hand proprioception and efference copy to monitor cursor position.

### *Separate Contribution of Eye Movements to Hand Tracking and Its Adaptation*

Although following the target with one's eyes increases the precision of hand tracking, such increased precision does not speed up the adaptation of hand tracking to an imposed rotation. Apparently, tracking precision and visuomotor adaptation are rather independent. Ongoing hand movements may rely heavily on continuous control and benefit from both retinal and extraretinal information (such as eye efference copy) for a variety of reasons (de la Malla et al. 2017). In contrast, updating the mapping between movements of the hand and the cursor is probably guided by sensory prediction errors (Tseng et al. 2007): the mismatch between expected and observed visual consequences of hand motor commands, irrespective of any eye movements.

To what extent do gaze fixation and exposure to a visuomotor rotation induce independent detrimental effects on hand tracking? Assuming that the errors arising from imposing gaze fixation and from introducing a visuomotor rotation are independent, we expect to observe the quadratic mean of the two effects rather than their arithmetic mean (because they are not guaranteed to be in the same direction) so that if the error introduced by one of the two source is much larger than the other, we do not expect to see any influence of errors from the smaller source. This explains why we do not observe an upward shift of the learning curves under gaze-fixed conditions (compared with learning under gaze-free conditions), but only see an upward shift during late exposure, once adaptation to the visuomotor rotation has reduced the error introduced by the rotation to a level that no longer overshadows the effect of gaze fixation.

Considering imposing fixation and the visuomotor rotation to have independent detrimental effects on hand tracking can also explain some of the patterns of hand tracking behavior that we observed when switching between gaze-free and gaze-fixed conditions. If one has to learn to deal with both, we expect to see an asymmetry between introducing and removing both the fixation requirement and the rotation. This is indeed what we observed (Fig. 5). When fixation is introduced after adaptation, performance initially deteriorates somewhat, but improves again to some extent during subsequent trials. When fixation requirements are removed, performance does not deteriorate. Similarly, performance deteriorates much more markedly after the rotation is introduced than when it is removed (final trial). Thus the notions of independent effects of gaze fixation and of introducing a visuomotor rotation on hand tracking account for a substantial fraction of our observations, although we cannot exclude the possibility that additional effects or interactions are at play, especially considering that the neurophysiology allows for such interactions.

From a neurophysiological standpoint, the posterior parietal cortex (PPC) is often considered to be a key structure both for eye-hand coordination (Dean et al. 2012; Hwang et al. 2014; Van Donkelaar et al. 2000) and for adaptation to visuomotor rotation (Haar et al. 2015; Mutha et al. 2011; Savoie et al. 2018). Many neurons in PPC are influenced by both eye and hand actions (Carey 2000). Moreover, functional MRI activity in PPC correlates rather well with adaptation to a visuomotor rotation (Haar et al. 2015). Nevertheless, our results speak in favor of rather independent neural circuits for the online control and the adaptation of visually guided hand movements. Similar reasoning applies to the cerebellum, another structure that is often linked to both eye-hand coordination (Miall et al. 2001; Vercher and Gauthier 1988) and visuomotor adaptation (Rabe et al. 2009; Tseng et al. 2007).

### *Implicit vs. Explicit Adaptation*

Although adaptation was conceptualized in terms of a single (implicit) process that reflects the updating of an internal model, growing evidence suggests that (explicit) strategies can also play a role in sensorimotor learning (Huberdeau et al. 2015; Taylor and Ivry 2012). Our experiment was not designed to assess the separate contributions of explicit and implicit processes, but we would like to point out the following observations. First, aftereffects were observed in all our gaze conditions despite the fact that the final aftereffect trials were quite long (10 s), so there was ample time for any strategic effect to disappear. That the aftereffects were still present at the end of the final trials (not shown) suggests that the adaptation involved implicit mechanisms. Note that in a recent experiment performed by our group, aftereffects were still visible when a secondary catch trial was delivered (Mathew et al. 2018). Second, neural activity of the cerebellum and the sensorimotor cortex is consistent with the acquisition of an internal model when people are learning to use a rotated joystick to track a moving target (Imamizu et al. 2000; Ogawa and Imamizu 2013). Third, posttest interviews of the participants revealed that most of them were unable to explain verbally how the behavior of the cursor had been altered. Finally, although the subtle differences in the magnitude of aftereffects across groups can follow from different contributions of implicit and explicit processes, they can also stem from different amounts of practice, or from the gaze conditions. Overall, although we are not interested in claiming that there can be no strategic component to this task, such a component is probably minor or temporary. Still, future experiments investigating in detail the relative contribution of implicit and explicit processes will be helpful to validate this position.

### *Concluding Comments*

Although many studies have emphasized an intricate relationship between eye and hand movements (Carey 2000; Crawford et al. 2004; Johansson et al. 2001; Land and McLeod 2000; Li et al. 2018; Miall et al. 2001), the current study shows that eye movements are not mandatory for the adaptation of visually guided hand movements. Even though our results confirm that gaze contributes to the accuracy of hand tracking, gaze does not seem to play an important role in visuomotor adaptation because retinal signals alone (gaze-fixed condition) provide sufficient information to update the mapping between hand movements and their visual consequences. Moreover, adaptation under an eye-fixed condition transfers to an eye-free condition, and vice versa. Overall, for hand tracking movements, it would appear that signals about how the target is tracked with the eyes do not play an important role in visuomotor adaptation.

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## DISCLAIMERS

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## DISCLOSURES

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

## AUTHOR CONTRIBUTIONS

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

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