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Role of motor execution in the ocular tracking of self-generated movements

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Chen J, Valsecchi M, Gegenfurtner KR. Role of motor execution in the ocular tracking of self-generated movements. *J Neurophysiol* 116: 2586–2593, 2016. First published September 14, 2016; doi:10.1152/jn.00574.2016.—When human observers track the movements of their own hand with their gaze, the eyes can start moving before the finger (i.e., anticipatory smooth pursuit). The signals driving anticipation could come from motor commands during finger motor execution or from motor intention and decision processes associated with self-initiated movements. For the present study, we built a mechanical device that could move a visual target either in the same direction as the participant's hand or in the opposite direction. Gaze pursuit of the target showed stronger anticipation if it moved in the same direction as the hand compared with the opposite direction, as evidenced by decreased pursuit latency, increased positional lead of the eye relative to target, increased pursuit gain, decreased saccade rate, and decreased delay at the movement reversal. Some degree of anticipation occurred for incongruent pursuit, indicating that there is a role for higher-level movement prediction in pursuit anticipation. The fact that anticipation was larger when target and finger moved in the same direction provides evidence for a direct coupling between finger and eye motor commands.

anticipatory smooth pursuit; ocular tracking of self-motion; congruency effect; eye-hand coordination

NEW & NOTEWORTHY

Humans constantly coordinate eye and hand movements. Here we asked observers to track their own finger movements and found that, for every parameter we measured, the tracking performance was better when the eye and hand were moving in a congruent direction. As we made sure that top-down predictability was identical, our results showed that directly mapped motor commands play a role in eye-hand coordination.

WE CONSTANTLY COORDINATE our eyes and hands when we interact with the world. One example of such coordination is when our gaze follows our moving hand. Studies have shown that the ocular tracking of self-generated movements is better than the tracking of external movements. The benefits include reduced pursuit latency (Gauthier and Hofferer 1976; Ross and Santos 2014; Scarchilli and Vercher 1999), decreased number of saccades (Mather and Lackner 1980; Steinbach 1969; Steinbach and Held 1968), and reduced delays at reversals (Mather and Lackner 1980; Steinbach 1969; Vercher et al. 1995). Two models have been proposed to explain these effects: the common controller model (Bock 1987) and the mutual coordination model (Lazzari et al. 1997; Scarchilli and Vercher 1999). The common controller model suggests that a common control signal is fed to both the pursuit system and the hand motor system for coordinated movements, without a direct link between two systems. Direct evidence for the common controller model comes from the observation that executing smooth pursuit eye movements modulates the excitability of the hand motor cortex, as evidenced by motor evoked potentials measured after application of transcranial magnetic stimulation to the primary motor cortex (Hiraoka et al. 2014; Maioli et al. 2007). The mutual coordination model does not include a common control stage and instead assumes that the two systems exchange information constantly and directly. For example, Scarchilli and Vercher (1999) showed that the somatomotor and oculomotor systems independently adapt to predictable mechanical perturbations applied to the hand, yielding optimal coordination. Hwang et al. (2014) investigated the role of the parietal reach region, an area responsible for hand reach movement in eye-hand coordination. They found that inactivation of the parietal reach region impairs coordination, revealing a direct interaction between the hand movement system and the eye movement system. These results thus support the mutual coordination model.

The two models are of course not mutually exclusive, since a common control signal for eye and hand movements could be fine-tuned by additional coordination signals. It is plausible that a common control signal resulting from motor decisions in the motor planning stage is followed by interactive coordination signals from the efference copy of the motor command in the motor execution stage. A preliminary report (Kowler et al. 2015) suggested a dominant role of the decision signals for eye-hand coordination by showing that pursuit could still be initiated with near-zero latency even when the efference copy signal was disrupted by mirroring the direction of the eye and the direction of the hand. Indeed, a recent primate study (Dean et al. 2012) showed that neural signals in the lateral intraparietal area (LIP) in the motor planning stage predicted eye movements made in coordination with the hand but not eye movements executed alone. These studies implied a crucial role of decision signals from hand motor preparation in the control of eye movement. It is unknown, however, whether coordination signals from ongoing motor execution also play a role in coupling eye and hand movement.

In the present study we aimed to separate the contribution of low-level signals coming from motor execution from the contribution of high-level decision-based signals. To this end, we built a mechanical device that could move a visual target either in the same direction as the participants' hand or in the opposite direction. In each block of trials, the finger and eye movement directions were either congruent or incongruent, and observers repeatedly moved their finger in the same direction, ensuring complete predictability of the target motion in either case. In the incongruent blocks low-level signals an-

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chored to the finger motor commands would, however, be incompatible with the oculomotor task. Our results show improved tracking performance in the congruent blocks compared with incongruent blocks, suggesting that directly mapped low-level motor commands play a role in the oculomotor anticipation of finger movements.

METHODS

Participants. Twelve observers (7 women, 5 men; average age = 26.6 yr, from 20 to 36 yr) participated in the experiment. They had normal or corrected-to-normal vision and were all right-handed. They signed written informed consent forms in agreement with the Declaration of Helsinki and in accordance with protocols reviewed and approved by the local ethics committee.

Procedures. The experiment took place in a lit room. Participants used their right index finger to control the device. Participants initiated a trial by pressing the space bar on the keyboard with their left hand. To correct gaze drift due to, e.g., minor eye movements, we measured the gaze positions for 400 ms after the bar pressing and subtracted the fixation error. After a 100-ms delay, an audio cue indicated the start of the trial. Participants then started to move their right finger to either the left or the right and back to center. The direction of motion was constant in a given block of trials and alternated between blocks. Participants were instructed to make a smooth movement; in particular, they were asked to turn smoothly without stopping the movement at the turning point. They were told not to move too far, so as not to reach the limit of the range enabled by the device (17 cm, i.e., 32.5°, on either side). There were no further constraints on the amplitude or speed of their movement. Meanwhile, their gaze had to keep following the tracking target, which could move either congruently with the finger or incongruently in different blocks of trials. Within a certain block, however, both the hand direction and gaze direction remained constant; participants thus were fully aware of the mapping between the tracking target and the hand. Before each block, the mapping of this block was explained to participants and they were encouraged to try it out before the block started. The sequence of the four blocks (left/right hand moving direction, congruent/incongruent gaze-hand mapping) was counterbalanced across participants. Participants underwent 320 trials in total (80 in each condition), except for *participant 1*, who completed 480 trials (120 in each condition). Participants took a short break and recalibrated the eye tracker every 40 trials.

Experimental device. We built a device that was controlled by the participants' finger (Fig. 1). When participants moved the finger horizontally, a marker for the Zebris motion tracker system (Zebris Medical, Isny im Allgäu, Germany) on top of the device moved either in the same direction as the finger or in the opposite direction. The marker served as the pursuit target, which was white in color and had a radius of 0.9° in a viewing distance of 30 cm. The Zebris marker was chosen as the pursuit target mostly for convenience: It would have been difficult to occlude it from the viewer's vantage point while leaving it in the field of view of the Zebris sensor. Also, its shape resembles the commonly used bull's eye fixation targets. A belt inside the device transmitted the finger position to the target. An electric magnet under the control of our experiment program engaged the target on different sides of the belt, so that it moved either in the same direction as the finger or in the opposite direction. This ensured that the mechanical resistance of the device was equated in both configurations. Only the tracking target was visible to participants. All mobile parts of the device and the hand were occluded from the observer.

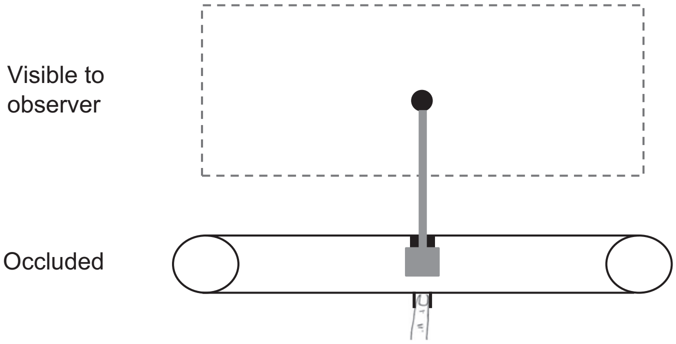

Fig. 1. Diagram of the device used in the experiment. The example setting shows the incongruent condition, where the tracking target is attached to the back side of the belt. As a result, the target always moves in the opposite direction when the finger moves. Note that the device and the hand were occluded, and only the tracking target was visible to the observer.

Target movement and eye movement recordings and analyses. Movements of the pursuit target, which was directly connected to the finger, were tracked at 100 Hz with a Zebris motion capture system (Zebris Medical). The Zebris marker was attached to the experimental device and served as pursuit target. Eye movements from the right eye were recorded at 1,000 Hz with an EyeLink 1000 table-mounted eye tracker (SR Research, Mississauga, ON, Canada). We had to place the eye tracker behind the experimental device because participants needed to interact with the device. Positioning the eye tracker above the gaze, however, produced relatively noisy data. A chin rest was used to limit head movements. The distance from the eye to the pursuit target was 30 cm.

External motion tracking systems inevitably add some delay between the real movement and the digital recording of the measurement. We estimated the delay of the Zebris system by simultaneously recording the same movement with the Zebris system as well as a potentiometer with a rotating sensor (Vishay Spectrol 534, Vishay Intertechnology). We then used the movement onset detection method (Schütz et al. 2007) described below to get the movement onset from both the distance data of the Zebris system as well as the voltage data of the potentiometer. With 100 measures, we estimated the delay as 9.0 ms (SD = 6.5 ms).

We visually checked the eye position and finger position traces for all trials. Trials with artifacts, e.g., participant failure to make the correct movement or eye tracker data loss, were rejected (6.6%). We did not discard trials where saccades occurred during fixation, as we expected eye movements to be executed anticipatorily. We used the regression-based method described in Schütz et al. (2007) to compute the finger and eye movement onset in individual trials. Position signals were low-pass filtered below 30 Hz. Velocity signals, which were calculated by differentiating the position data, were low-pass filtered below 20 Hz. We fitted regression lines with 80-ms length to the velocity trace and discarded regression lines with $R^2 < 0.7$ or with a slope below 10°/s^2 or above 200°/s^2. We then selected the regression line with the highest R^2 value. The time corresponding to zero velocity was defined as the movement onset. Individual trials were visually inspected. When the estimated onset clearly missed the initial buildup stage of the velocity trace (e.g., it was located at the fixation stage or during ongoing movement), we manually restricted the time window to a range near the velocity buildup stage and repeated the above procedure to detect the movement onset (we did this in 3.0% of trials for the finger onset detection and 28.7% for the eye onset detection). Results did not change whether these trials were included or not.

Saccades were detected with the EyeLink default algorithm, which uses a velocity threshold of 30°/s and an acceleration threshold of 8,000°/s^2. The eye movement latency was defined as the eye movement onset time relative to the finger movement onset time (i.e., the visual target's movement onset time). Negative latencies thus indicate anticipatory eye movements. Bimodality was statistically tested with Hartigan's dip test (Hartigan and Hartigan 1985; used in, e.g., Mergenthaler and Engbert 2010), with a bootstrap sample size of 5,000. Two-tailed one-sample *t*-test and paired-samples *t*-test were used in all analyses. In RESULTS, we report interindividual standard deviation (SD) values together with means.

RESULTS

On average, the finger movement length before turning back was 14.6° (7.7 cm, from 9.1° to 21.6° across participants, SD = 4.0°). The time of the turning point was 737 ms on average, which varied between 296 and 1,844 ms across different trials and different participants. The average speed on the forward leg of the movement was 22.1°/s (between 14.1 and 36.8°/s across participants, SD = 8.6°/s). In Fig. 2, we plot the average position and average velocity profile for one example observer. We did not observe any significant difference between hand movements to the left and to the right; thus we grouped them together in all analyses.

We first explored how well participants coordinated their finger and eye movements. For each participant, we correlated the finger onset time (relative to the audio cue) and the eye onset time in both the congruent condition and the incongruent condition. The correlation coefficient was on average 0.69 (SD = 0.17, from 0.36 to 0.91 across participants, all $P < 0.001$) in congruent pursuit and 0.75 (SD = 0.15, from 0.55 to 0.96, all $P < 0.001$) in incongruent pursuit. Across participants, finger onset time highly correlated with eye onset time, both in the congruent condition ($r = 0.94$, $P < 0.001$; Fig. 3*A*) and in the incongruent condition ($r = 0.97$, $P < 0.001$; Fig. 3*B*). Moreover, the variability of finger onset time correlated with the variability of eye onset time in the congruent condition ($r = 0.79$, $P = 0.002$) and the incongruent condition ($r = 0.91$, $P < 0.001$). Furthermore, we computed the peak velocities of finger movement and eye movement in the outgoing leg of the movement in individual trials. Within each participant, the peak velocity correlation between finger and eye was on average 0.42 (SD = 0.19) in congruent pursuit and 0.25 (SD = 0.14) in incongruent pursuit. The correlations were significant ($P < 0.05$) except in the case of one participant in the congruent condition and except for two participants in the incongruent condition. Across participants, the peak velocities of eye and finger were highly correlated in both the congruent condition ($r = 0.94$, $P < 0.001$) and the incongruent condition ($r = 0.76$, $P = 0.004$). These results demonstrated that participants coordinated the finger and eye movements in both the congruent and incongruent conditions.

Eye latency was reduced in congruent pursuit. We compared the onset times relative to the audio cue across conditions. Repeated-measures 2 (congruent vs. incongruent) × 2 (finger vs. eye) ANOVAs over onset time revealed a significantly earlier eye onset (mean ± SD, 341.7 ± 71.7 ms) than finger onset (360.9 ± 69.3 ms) [$F(1,11) = 10.1$, $P = 0.009$] and a significant interaction [$F(1,11) = 15.0$, $P = 0.003$]. The main effect of congruency was not significant [$F(1,11) = 3.6$, $P = 0.085$]. Subsequently, we first analyzed the congruent and incongruent conditions separately. In the congruent condition, the eye onset (315.3 ± 68.6 ms) was significantly earlier than the finger onset (347.7 ± 67.6 ms) [$t(11) = -4.7$, $P = 0.001$]. In the incongruent condition, the eye onset (368.0 ± 93.9 ms) and finger onset (374.1 ± 96.3 ms) did not differ [$t(11) = -0.9$, $P = 0.40$]. We then looked at the two modalities separately. The finger onset did not differ between congruent (347.7 ± 67.6 ms) and incongruent (374.1 ± 96.3 ms) conditions [$t(11) = -1.38$, $P = 0.19$], while the eye onset was earlier in the congruent (315.3 ± 68.6 ms) than the incongruent (368.0 ± 93.9 ms) condition [$t(11) = -2.3$, $P = 0.043$].

We calculated eye latencies as defined by eye onset time relative to finger onset time (Fig. 3, *C* and *D*). Eye latencies

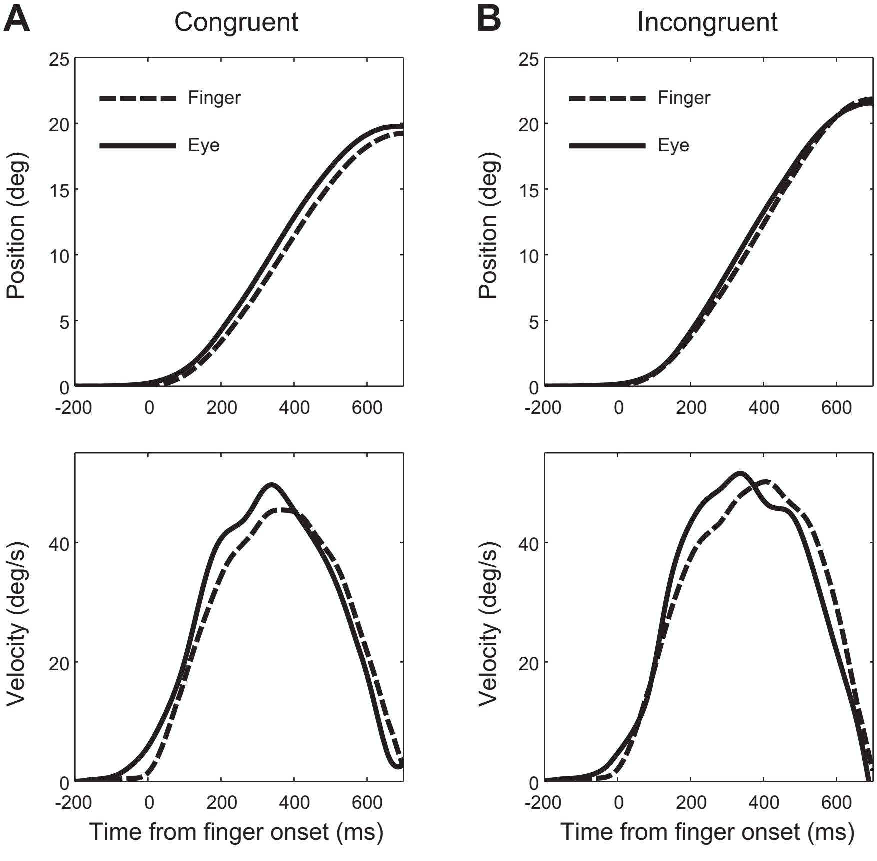

Fig. 2. Average position (*top*) and average velocity (*bottom*) for the eye and finger for 1 example observer in the congruent (*A*) and incongruent (*B*) conditions.

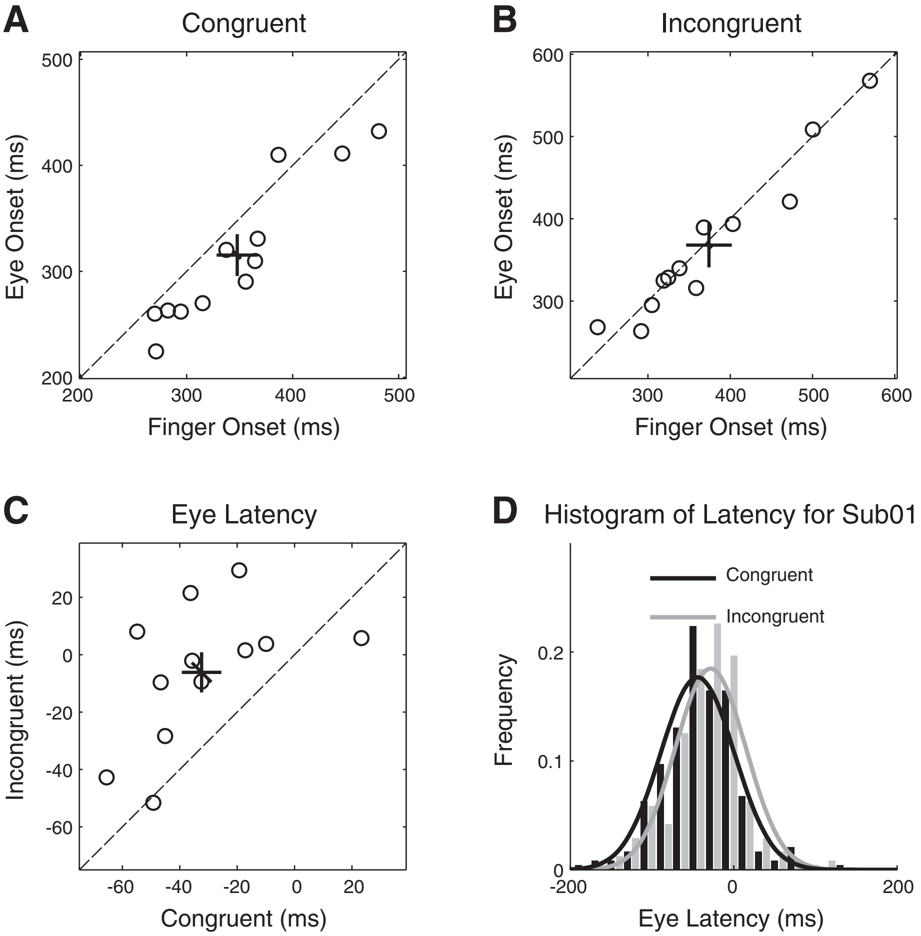

Fig. 3. *A* and *B*: eye onset time plotted against finger onset time for individual participants in the congruent (*A*) and incongruent (*B*) conditions. Eye onset was earlier than finger onset in *A* but not in *B*. *C*: eye latency in incongruent pursuit plotted against eye latency in congruent pursuit for individual participants. Eye latency was smaller in congruent pursuit. *D*: frequency plot of eye latencies in all trials of 1 example participant. Eye latency was reduced overall in the congruent condition. The cross in *A*–*C* shows the average value ± SE.

were smaller in the congruent condition (mean ± SD, −32.4 ± 23.9 ms) than in the incongruent condition (−6.1 ± 24.2 ms) [$t(11) = -3.87$, $P = 0.003$]. It should be noted that absolute latency should be treated with caution, as we may underestimate it because of the delay in the Zebris motion tracker system (9.0 ms based on our estimate; see METHODS). To quantify the variability of eye latencies, we computed the SDs in each condition and for each participant and found no significant difference between the congruent condition (75.4 ± 24.6 ms) and the incongruent condition (78.7 ± 35.0 ms) [$t(11) = -0.39$, $P = 0.70$]. We tested the bimodality of eye latency distributions (see Fig. 3*D* for one example participant's latency distributions). To avoid artifacts from averaging across participants, we ran the analysis for each condition of individual participants. We did not find any significant deviation from unimodality for any observer in either the congruent condition (all $P > 0.52$) or the incongruent condition (all $P > 0.50$).

Congruency effect does not quickly disappear with adaptation. A previous study suggested that the incongruency cost may be limited to the first few trials (Vercher et al. 1995). We thus examined the eye latencies in the first 10 trials (*1–10*), the following 70 trials (*11–80*), the following 40 trials (*81–120*), and the last 40 trials (*121–160*), separately in congruent and incongruent conditions (Fig. 4). A 2 (congruent vs. incongruent) × 4 (trial order) ANOVA revealed a main effect of congruency [$F(1,11) = 17.2$, $P = 0.002$]. The main effect of trial order was approaching significance [$F(3,33) = 2.26$, $P = 0.099$], while the interaction was not significant [$F(3,33) = 1.12$, $P = 0.35$]. Although some degree of adaptation might take place, participants were not able to fully adapt to the incongruent condition, as evidenced by the fact that in the last 40 trials we still observed a reduced eye latency in congruent pursuit (mean = −35.2 ms, SD = 30.3 ms) compared with incongruent pursuit (mean = −18.8 ms, SD = 18.7 ms) [$t(11) = -2.69$, $P = 0.021$].

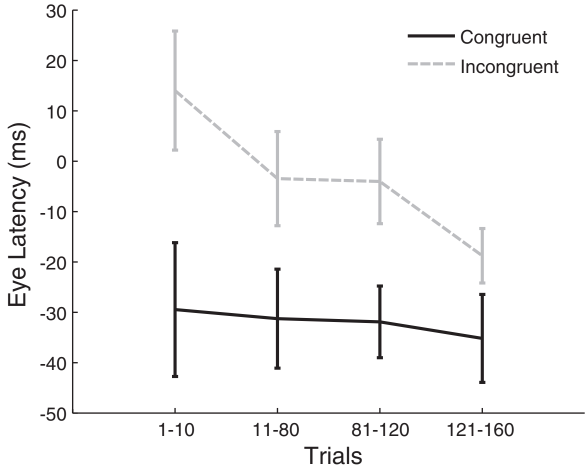

Fig. 4. Eye latency in congruent and incongruent conditions with increasing number of trials. Some adaptation may take place in the incongruent condition. The congruency effect, however, still held even in the last 40 trials. Error bars indicate ±SE.

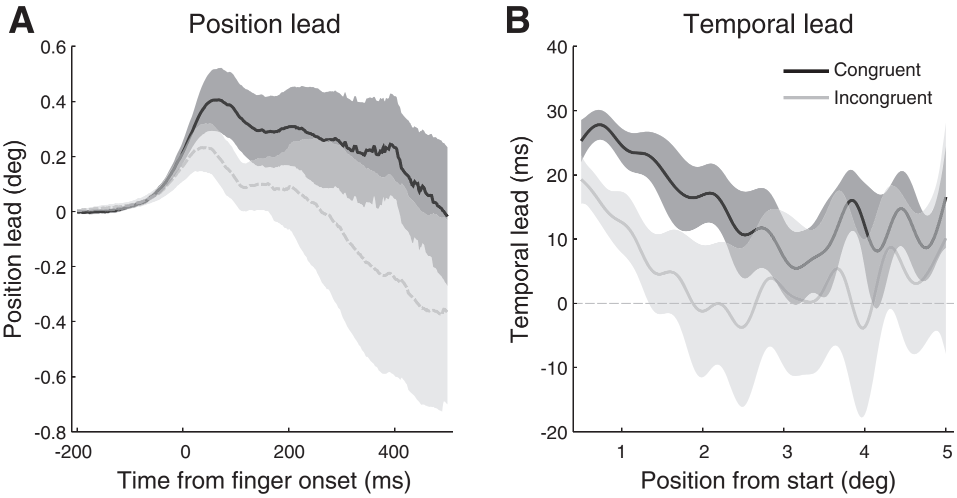

Fig. 5. *A*: position lead of the eye relative to the finger in congruent pursuit and incongruent pursuit. *B*: temporal lead of the eye relative to the finger (asynchrony between eye and finger reaching a given position). Shaded areas indicate ±SE.

Position lead was larger in congruent pursuit. Not only did the eye start to move before the finger, the eye also led the finger in position during ongoing pursuit. We measured how much the eye led the finger in both congruent pursuit and incongruent pursuit (Fig. 5*A*). In the [0 400] ms window, the lead was on average 0.29° in congruent pursuit [SD = 0.41°; larger than 0, $t(11) = 2.49$, $P = 0.03$] and 0.03° in incongruent pursuit [SD = 0.55°; not different from 0, $t(11) = 0.21$, $P = 0.84$]. The lead was significantly larger in congruent pursuit than in incongruent pursuit [$t(11) = 2.96$, $P = 0.013$]. We measured the temporal lead by calculating the asynchrony between the times the eye and the finger reached a given position (from 0.5° to 5°, in 0.02° bins; Fig. 5*B*). In the [0.5 2]° window, the temporal lead was 22.5 ms on average in congruent pursuit [SD = 12.1 ms; larger than 0, $t(11) = 6.44$, $P < 0.001$] and 8.7 ms in incongruent pursuit [SD = 17.5 ms; not different from 0, $t(11) = 1.73$, $P = 0.11$]. The lead was larger in congruent pursuit than in incongruent pursuit [$t(11) = 2.53$, $P = 0.028$].

The increased position lead in congruent pursuit may be merely a consequence of decreased pursuit latency, as earlier pursuit initiation definitely leads to larger position lead. We calculated the correlation across observers between the increased position lead (congruent vs. incongruent) and the decreased pursuit latency (congruent vs. incongruent). They were significantly correlated, but only for the first 200 ms of pursuit. For example, in the [0 100] ms window, position lead difference was correlated with pursuit latency difference ($r = 0.71$, $P = 0.0099$). For the [100 200] ms window, $r = 0.68$ and $P = 0.015$. However, 200 ms after finger onset (~200–240 ms after pursuit onset), the correlation disappeared. In the [200 300] ms window, they were not correlated ($r = -0.017$, $P = 0.96$); in the [300 400] ms window, $r = 0.011$ and $P = 0.97$. These results suggest that the position lead in congruent vs. incongruent pursuit was not merely a by-product of decreased pursuit latency, especially after the open-loop phase of pursuit.

Pursuit gains were larger in congruent pursuit. The position measurement is not optimal for pursuit quality, as saccades also contribute to position data. Here we computed finger/eye velocities and pursuit gain (eye velocity/finger velocity) after excluding saccades in velocity traces (Fig. 6). Because of anticipatory eye movement, the gain was extremely high in the beginning (<50 ms after finger onset). In the [100 300] ms window, the gain was larger in the congruent condition (mean = 0.92, SD = 0.11) than in the incongruent condition (mean = 0.83, SD = 0.19) [$t(11) = 2.90$, $P = 0.014$]. The increased gain in congruent condition vs. incongruent condition was due to a higher eye velocity [congruent vs. incongruent: 27.1 ± 10.2 vs. 21.9 ± 9.6°/s; $t(11) = 3.64$, $P = 0.004$] rather than a lower finger movement velocity

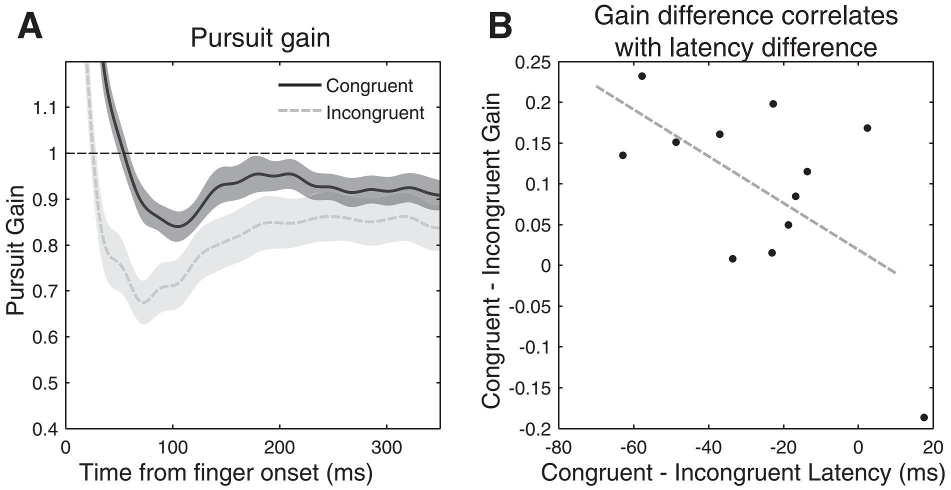

Fig. 6. *A*: pursuit gain for congruent and incongruent conditions. The gain was larger in the congruent condition. Shaded areas indicate ±SE. *B*: the increased gain in congruent vs. incongruent conditions was correlated with the decreased pursuit latency, suggesting similar underlying factors for anticipatory pursuit initiation and improvement in ongoing pursuit control.

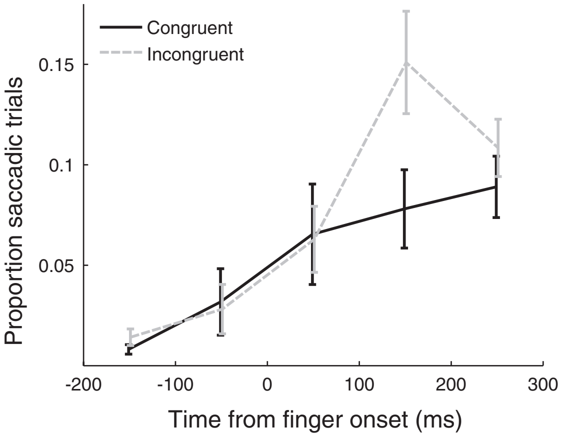

Fig. 7. Proportion of trials that have saccades for every 100-ms time window separately for the congruent and incongruent conditions. Error bars indicate ±SE.

[congruent vs. incongruent: 30.4 ± 14.1 vs. 28.2 ± 15.1°/s; $t(11) = 1.09$, $P = 0.40$]. Furthermore, we correlated the difference in gain and the difference in pursuit latency between congruent and incongruent conditions (Fig. 6*B*) and observed a significant correlation ($r = -0.60$, $P = 0.040$; $r = -0.28$, $P = 0.41$ if the data point in the bottom right corner of Fig. 6*B* is not considered). This suggests that the same factors may lead to anticipatory pursuit initiation and to the improvement in ongoing pursuit control in the congruent condition.

Saccades were fewer in congruent pursuit. The number of saccades is another measurement of pursuit performance. We plot in Fig. 7 the proportion of saccadic trials in each 100-ms window. In a given time window (e.g., [−200 −100] ms), we counted the number of trials that had at least one saccade within the time window and divided this by the total number of trials to calculate the proportion of saccadic trials. The proportions were generally low, around 7.8% (SD = 6.0%) in congruent pursuit and 10.7% (SD = 5.3%) in incongruent pursuit on average in the [0 300] ms window. The congruent condition had significantly fewer saccadic trials than the incongruent condition [$t(11) = -2.44$, $P = 0.033$].

Reversal delay was less in congruent pursuit. Finally, we computed the time point where the finger reversed direction (i.e., the peak in position trajectories) and compared it to the time point where the eye reversed direction in individual trials. Reversal delay was defined as the delay of eye reversal time relative to finger reversal time (Fig. 8). The delay was small, 1.9 ms on average in congruent pursuit [SD = 10.9 ms; not different from 0, $t(11) = 0.61$, $P = 0.56$] and 12.3 ms in incongruent pursuit [SD = 16.3 ms; larger than 0, $t(11) = 2.61$, $P = 0.024$]. The reversal delay was significantly smaller in congruent pursuit than in incongruent pursuit [$t(11) = -3.71$, $P = 0.004$]. The decreased reversal delay in congruent pursuit vs. incongruent pursuit may be a consequence of decreased pursuit latency. If so, we would expect a positive correlation between the congruency effect in reversal delay and that in pursuit latency. They were, however, not significantly correlated ($r = -0.47$, $P = 0.12$), and, if anything, the correlation is negative rather than positive as would have been expected. The decreased reversal delay was thus not driven by the decreased pursuit latency.

The difference in pursuit quality between congruent and incongruent trials could not be explained simply by a difference in finger motion speed. The average speed in the outgoing leg of the motion in congruent trials (mean = 22.5°/s, SD = 8.4°/s) did not differ from incongruent trials (mean = 21.7°/s, SD = 9.2°/s) [$t(11) = 0.79$, $P = 0.45$]. In the first 200 ms after finger onset, finger speed in congruent trials (mean = 16.2°/s, SD = 8.4°/s) also did not differ from incongruent trials (mean = 14.8°/s, SD = 9.0°/s) [$t(11) = 1.08$, $P = 0.20$].

DISCUSSION

Our main observation was an overall enhancement of smooth pursuit performance when the eye and the hand moved in a congruent direction compared with the case when finger and eyes moved in opposite directions. The enhancement of performance included reduced eye latency, increased lead of the eye in position, increased pursuit gain, fewer saccades, and reduced reversal latency. The effect could not be explained by the predictability of the pursuit target, as directions of both eye and finger motions were constant in each block of trials and thus completely predictable. The two conditions differed in the low-level, directional congruency of the two movements. Hand motor commands could be directly converted into eye motor commands in the congruent condition, whereas the mapping was reversed in the incongruent condition. This result suggests that the specific signal that leads to finger movement execution contributes to eye-hand coupling in finger tracking.

A few previous studies examined finger pursuit in incongruent conditions similar to ours. In their setups, the hand movements were monitored and were reproduced on a computer screen in near real time. Domann et al. (1989) reported that human participants as well as primates are capable of tracking a target that moves oppositely to the hand. They reported close to zero eye latencies in both congruent and incongruent conditions but did not explicitly compare them. They concluded that motor intention signals drive pursuit in finger tracking. Vercher et al. (1995) subsequently reported similar results in incongruent pursuit blocks. They also tested the condition in which the mapping of the target to the hand was randomized across trials. They found that in incongruent trials the eye

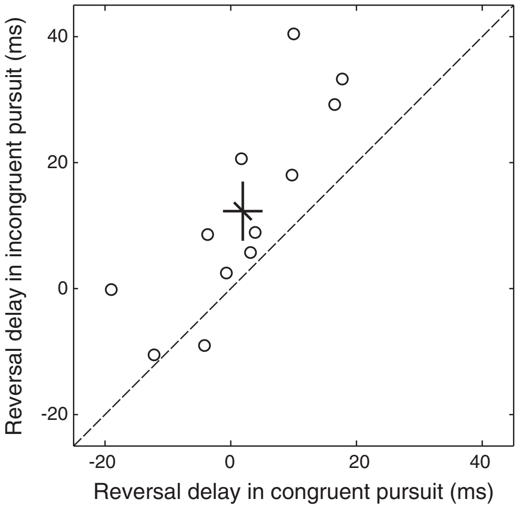

Fig. 8. Reversal delay in congruent and incongruent pursuit. Open circles indicate individual participants. The cross shows the average value ± SE.

started to move in the direction of the arm for the first ~140 ms. Afterwards, the eye reversed direction to catch up with the visual tracking target. In a preliminary report, Spitschan and Vishwanath (2011) varied hand-target gain and observed the best pursuit performance for the 1:1 direct mapping compared with the reverse 1:1 and other gain conditions. Independently of the target speed, they also reported better performance (in terms of pursuit gain and number of saccades) when the target was controlled by the finger movement compared with when the target motion was controlled externally. A recent preliminary report (Kowler et al. 2015) also found anticipatory pursuit eye movements in incongruent tracking.

In general, previous studies have shown that the pursuit system can anticipate the future target movement even if the mapping is incongruent. This is consistent with our results, as we observed very low eye latency, few saccades, and a small reversal delay in the incongruent condition. High-level signals related to motor intention/decision are used for the eye to anticipate finger movements. However, our study further showed that the anticipation was enhanced even further if the target motion was congruent with the finger motion compared with incongruent mapping. This means that predictive signals tightly bound to motor execution also play a role in finger tracking. While this notion has been suggested before (e.g., Vercher et al. 1996), to our knowledge it has not been tested directly by dissociating motor execution from motor intention while maximizing target motion predictability.

Vercher et al. (1995) observed an adaptation effect after the mapping was reversed. In their study, in the first few trials the gaze was initiated in the direction of the hand rather than the visual target. In <10 trials, participants learned the reversed mapping and initiated pursuit with zero latency. The learning/adaptation effect was also observed in the study of Domann et al. (1989). They trained nonhuman primates to track hand movements with gaze in a reversed mapping condition and observed decreasing pursuit latencies with training. In addition, they observed a bimodal distribution in pursuit latency, one visual-driven component with 100- to 200-ms latency and one nonvisual driven component with 0-ms latency. The learning effect was associated with increased occurrence of a non-visual-driven component and decreased occurrence of a visual-driven component. In the present study, there might have been some adaptation effect in the incongruent condition. The adaptation, however, was not complete, and the congruency effect held throughout the experiment. Previous studies, in fact, were not designed to test the congruency effect and did not explicitly report the comparison. Our results complemented these studies by showing that the adaptation to incongruent mapping does not easily abolish the incongruency cost. Domann et al. (1989) in addition showed bimodal distribution in pursuit latency while training nonhuman primates to do the reversed-mapping tracking task. Neither our study nor that of Vercher et al. (1995) found bimodality. One possible explanation lies in the difference between human participants and nonhuman subjects. Humans may instantly learn the reversed mapping in few trials, while nonhuman primates require days of gradual training, which results in a coexistence of both components.

One alternative explanation for the decreased pursuit performance is that attention allocated to the pursuit system might be reduced in incongruent pursuit, as it is likely that the hand movement in the opposite direction would require a certain amount of attentional resources. The effect of dividing attention on smooth pursuit eye movements has been investigated in a few studies. Van Gelder et al. (1995) and Kathmann et al. (1999) added a secondary auditory task on top of the pursuit task. They did not find any dual-task interference; if anything, tracking error during pursuit decreased in the dual-task condition. Later, Hutton and Tegally (2005) showed that a more demanding secondary task, i.e., tapping a fixed number sequence with the finger, reduced pursuit gain and increased tracking error. Easy secondary tasks neither increased nor decreased pursuit performance. Recently, Seya and Mori (2015) used a manual reaction time task during smooth pursuit and set different deadlines (300, 400, or 500 ms) for the manual response. They found significantly increased tracking error with a 300 ms deadline but no difference between 400 ms and 500 ms deadlines. These results consistently suggest that smooth pursuit performance is largely unharmed until the secondary task becomes very demanding. The finger movements required from our observers were very repetitive and stereotyped, and the timing constraints were quite loose, meaning that the task was far from attentionally demanding. It should also be noted that we found an increase in eye latency, among other performance measures, in the incongruent pursuit. Souto and Kerzel (2008) found that divided attention particularly affected closed-loop pursuit, but it had little effect on smooth pursuit latency and early open-loop response. Overall, it seems rather unlikely that the comparatively worse pursuit performance in incongruent pursuit is due to divided attention.

Our findings have implications for the debate on models of eye-hand coordination in finger tracking. Two prominent proposals are the common controller model (Bock 1987) and the mutual coordination system (Lazzari et al. 1997). In our study, the motor execution signals, which directly originate from the hand motor system, were found to be able to influence the pursuit performance. This seems to support the mutual coordination system hypothesis, as the common controller model assumes no direct interactions between two systems (Scarchilli and Vercher 1999). Our results fit well with recent neurophysiology results showing mutual influences between the hand movement system and eye movement system under coordination. Yttri et al. (2013) recorded from LIP, a region associated with saccadic eye movements. They reported that whereas inactivation of LIP did not affect hand reach movements made in isolation, the inactivation did impair reach movements when made in coordination with saccades. This suggests that the saccade system does interact with the hand reach movement system during eye-hand coordination. Similarly, inactivation of the parietal reach region had an influence on coordinated saccades but not saccades executed in isolation (Hwang et al. 2014; but see Yttri et al. 2014). This study shows that the reach system interacts with the saccade system when they are coordinated. While these studies dealt with saccade/reach movements, we recently (Chen et al. 2016) showed that lateralized readiness potentials predict smooth pursuit latency in finger tracking. As lateralized readiness potentials are motor preparation signals originating mainly from the primary motor cortex (Coles 1989; de Jong et al. 1988), this finding suggests a direct interaction by linking motor commands responsible for finger movements with onset of the pursuit system. The present study is consistent with this finding and extends it by showing that even a simple change in the mapping between finger and pursuit target motion, such as mirroring, prevents the oculomotor system from fully exploiting the interactive signals attached to finger motor commands.

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DISCLOSURES

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

AUTHOR CONTRIBUTIONS

J.C., M.V., and K.R.G. conception and design of research; J.C. performed experiments; J.C. analyzed data; J.C., M.V., and K.R.G. interpreted results of experiments; J.C. prepared figures; J.C. and M.V. drafted manuscript; J.C., M.V., and K.R.G. edited and revised manuscript; J.C., M.V., and K.R.G. approved final version of manuscript.

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