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

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Abstract

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 participants' 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 to that in the opposite direction, as evidenced by decreased pursuit latency, increased lead of the eye to target in positions, 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.

New & Noteworthy

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

We constantly coordinate our eye 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; Scarchilli and Vercher 1999; Ross and Santos, 2014), decreased number of saccades (Mather and Lackner 1980; Steinbach and Held 1968; Steinbach 1969), 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 applying transcranial magnetic stimulation (TMS) 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, Hauschild, Wilke and Andersen (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 hand movement system and 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 showed that neural signals in the lateral intraparietal area (LIP) in the motor planning stage predicted eye movements made in coordination with 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 on-going motor execution also plays a role in coupling the 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 aim, 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 to the same direction, ensuring complete predictability of the target motion in either case. In the incongruent blocks low-level signals anchored to the finger motor commands would however be incompatible with the oculomotor task. Our results show improved tracking performance in the congruent blocks compared to incongruent blocks, suggesting that directly mapped low-level motor commands plays a role in the oculomotor anticipation of finger movements.


Method

Participants

Twelve observers (7 females, average age = 26.6, from 20 to 36) 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 approved by the local ethics committee.

Procedure

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 following 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 direction, and to move 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 deg, on either side). There were no further constraints on the amplitude or speed of their movement. Meanwhile, their gaze should keep following the tracking target, which could move either congruently with the finger, or incongruently across different blocks. 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, participants were explained the mapping of this block and were encouraged to try out before the block starts. The sequences of 4 blocks (left/right hand moving direction, congruent/incongruent gaze-hand mapping) were 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 re-calibrated 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 deg in a viewing distance of 30 cm. The Zebris marker was chosen as the pursuit target mostly for convenience. On one side 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. On the other side, its shape resembles the commonly used bull's eye fixation targets. A belt inside the device transmits 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 to the observer.

[-------------insert Fig 1 here-------------]

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, Isny im Allgäu, Germany). The Zebris marker was attached to the experimental device and served as pursuit target. Eye movements from the right eye were recorded at 1000 Hz using an Eyelink 1000 table-mounted eye tracker (SR Research, Missisauga, ON, Canada). We had to place the eye tracker behind the experimental device, as participants need to interact with the device. Positioning the eye tracker above the gaze, however, produced relatively noisy data. A chin rest was used to limit the 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 Zebris system as well as a potentiometer with a rotating sensor (Vishay Spectrol 534, Vishay Intertechnology, Inc., PA, USA). 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 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 manually checked the eye position and finger position traces for all trials. Trials with artifacts, e.g. participants' failure to make the correct movement or eye tracker data loss, were rejected (6.6%). We did no 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-passed 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 0 velocity was defined as the movement onset. Individual trials were visually inspected. When the estimated onset clearly missed the initial build-up stage of the velocity trace (e.g., it was located at the fixation stage or during on-going movement), we manually restricted the time window to a range near the velocity build-up stage and repeated the above procedure to detect the movement onset (we did this in 3.0% of trials for the finger onset detection; 28.7% for the eye onset detection). Results did not change whether these trials were included or not.

Saccades were detected using the Eyelink default algorithm, which uses a velocity threshold of 30 °/s and an acceleration threshold of 8000 °/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 1985; used in, e.g., Mergenthaler and Engbert, 2010), with a bootstrap sample size of 5000. Two tailed one sample t-test and paired-samples t-test were used in all analyses. In the result, we reported inter-individual standard deviation (SD) values together with the mean.
**Results**

On average, the finger movement length before turning back was 14.6 deg (7.7 cm, from 9.1 to 21.6 deg across participants, SD = 4.0 deg). The time of the turning point was 737 ms on average, which varied between 296 and 1844 ms across different trials and different participants. The average speed on the forward leg of the movement was 22.1 deg/s (between 14.1 and 36.8 deg/s across participants, SD = 8.6 deg/s). In Fig 2, we plotted 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 their 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 < .001) in congruent pursuit and 0.75 (SD = 0.15, from 0.55 to 0.96, all P < .001) in incongruent pursuit. Across participants, finger onset time highly correlated with eye onset time, both in the congruent condition (r = 0.94, P < .001, Fig 3A) as well as in the incongruent condition (r = 0.97, P < .001, Fig 3B). Moreover, the variability of finger onset time correlated with the variability of eye onset time in the congruent condition (r = 0.79, P = .002) and the incongruent condition (r = 0.91, P < .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 < .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
high correlated in both the congruent condition \(r = 0.94, P < .001\) and the
incongruent condition \(r = 0.76, P = .004\). 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) by 2 (finger vs. eye) ANOVAs over onset time revealed a significantly
earlier eye onset \((mean \pm SD, 341.7 \pm 71.7 \text{ ms})\) than finger onset \((360.9 \pm 69.3 \text{ ms}), F(1, 11) = 10.1, P = .009,\) and a significant interaction, \(F(1, 11) = 15.0, P = .003.\) The
main effect of congruency was not significant, \(F(1, 11) = 3.6, P = .085.\) Subsequently,
we first separately analyzed the congruent and incongruent condition. In congruent
condition, the eye onset \((315.3 \pm 68.6 \text{ ms})\) was significantly earlier than the finger
onset \((347.7 \pm 67.6 \text{ ms}), t(11) = -4.7, p = .001.\) In incongruent condition, the eye onset
\((368.0 \pm 93.9 \text{ ms})\) and finger onset \((374.1 \pm 96.3 \text{ ms})\) did not differ, \(t(11) = -0.9, p\)
\(= .40.\) We then separately looked at the two modalities. The finger onset did not differ
between congruent \((347.7 \pm 67.6 \text{ ms})\) and incongruent condition \((374.1 \pm 96.3 \text{ ms})\),
\(t(11) = -1.38, P = .19;\) while the eye onset was earlier in congruent \((315.3 \pm 68.6 \text{ ms})\)
than incongruent condition \((368.0 \pm 93.9 \text{ ms}), t(11) = -2.3, P = .043.\)

We calculated eye latencies as defined by eye onset time relative to finger onset
time (Fig 3C and 3D). Eye latencies were smaller in congruent condition \((mean \pm SD,
-32.4 \pm 23.9 \text{ ms})\) than that in incongruent condition \((-6.1 \pm 24.2 \text{ ms}), t(11) = -3.87, P\)
\(= .003.\) Note that absolute latency should be treated with caution, as we may
underestimate it due to the delay in Zebris motion tracker system \(9.0 \text{ ms based on our\)
estimate, see Method section). To quantify the variability of eye latencies, we
computed the standard deviations in each condition and for each participant, and
found no significant difference between the congruent condition \((75.4 \pm 24.6 \text{ ms})\) and
the incongruent condition \((78.7 \pm 35.0 \text{ ms}), t(11) = -0.39, P = .70.\) We tested the
bimodality of eye latency distributions (Fig 3D 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 both the congruent condition (all P > .52) and the incongruent condition (all P > .50).

Congruency effect does not quickly disappear with adaptation. A previous study suggest that the incongruency cost may be limited to the first few trials (Vercher, Quaccia and Gauthier, 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 condition (Fig 4). A 2 (congruent vs. incongruent) by 4 (trial order) ANOVA revealed a main effect of congruency, F(1,11) = 17.2, P = .002. The main effect of trial order was approaching significance, F(3, 33) = 2.26, P = .099, while the interaction was not significant, F(3, 33) = 1.12, P = .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) than incongruent pursuit (mean = -18.8 ms, SD = 18.7 ms), t(11) = -2.69, P = .021.

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 on-going pursuit. We measured how much the eye led the finger in both congruent pursuit and incongruent pursuit (Fig 5A). In the [0 400] ms window, the lead was on average 0.29 deg in congruent pursuit (SD = 0.41 deg; larger than 0, t(11) = 2.49, P = .03) and 0.03 deg in incongruent pursuit (SD = 0.55 deg; not different from 0, t(11) = 0.21, P = .84). The lead was significantly larger in congruent pursuit than that in incongruent pursuit, t(11) = 2.96, P = .013. We measured the temporal lead by calculating the asynchrony
between the time the eye and the finger reached a given position (from 0.5 to 5 deg, in 0.02 deg bins, Fig 5B). In the [0.5 2] deg 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 < .001) and 8.7 ms in incongruent pursuit (SD = 17.5 ms; not different from 0, t(11) = 1.73, P = .11). The lead was larger in congruent pursuit than that in incongruent pursuit, t(11) = 2.53, P = .028.

The increased position lead in congruent pursuit may be merely consequences 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, the position lead difference was correlated with pursuit latency difference, r = 0.71 P = .0099. For [100 200] ms window, r = 0.68, P = .015. However, 200 ms after finger onset (about 200-240 ms after pursuit onset), the correlation disappeared. In the [200 300] ms window, they were not correlated, r = -0.017, P = .96; in [300 400] ms window, r = 0.011, P = .97. These results suggest that the position lead in congruent versus incongruent pursuit was not merely a by-product of decreased pursuit latency, especially after the open-loop phase of pursuit.

Pursuit gain 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). Due to 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 congruent condition (mean = 0.92, SD = 0.11) than that in the incongruent condition (mean = 0.83, SD = 0.19), t(11) = 2.90, P = .014.
The increased gain in congruent condition versus incongruent condition was due to a higher eye velocity (congruent vs. incongruent: 27.1 ± 10.2 vs. 21.9 ± 9.6 deg/s; t(11) = 3.64, P = .004), rather than a lower finger movement velocity (congruent vs. incongruent: 30.4 ± 14.1 vs. 28.2 ± 15.1 deg/s; t(11) = 1.09, P = .40). Further, we correlated the difference in gain and the difference in pursuit latency between congruent and incongruent condition (Fig 6B), and observed a significant correlation, r = -0.60, P = .040 (r = -0.28, P = .41 if the data point in the bottom right corner is not considered). This suggests that same factors may lead to anticipatory pursuit initiation and to the improvement in on-going pursuit control in the congruent condition.

[S---insert Fig 6 here---]

Saccades were fewer in congruent pursuit. The number of saccades is another measurement of pursuit performance. We plotted 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 = .033.

[R---insert Fig 7 here---]

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, \( t(11) = 0.61, P = .56 \) and 12.3 ms in incongruent pursuit (SD = 16.3 ms; larger than 0, \( t(11) = 2.61, P = .024 \)). The reversal delay was significantly smaller in congruent pursuit than that in incongruent pursuit, \( t(11) = -3.71, P = .004 \). The decreased reversal delay in congruent pursuit versus incongruent pursuit may be consequences of decrease 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 (\( r = -0.47, P = .12 \), 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 deg/s, SD = 8.4 deg/s) did not differ from incongruent trials (mean = 21.7 deg/s, SD = 9.2 deg/s), \( t(11) = 0.79, P = .45 \). In the first 200 ms after finger onset, finger speed in congruent trials (mean = 16.2 deg/s, SD = 8.4 deg/s) also did not differ from incongruent trials (mean = 14.8 deg/s, SD = 9.0 deg/s), \( t(11) = 1.08, P = .20 \).
**Discussion**

Our main observation was an overall enhancement of smooth pursuit performance when the eye and the hand moved in a congruent direction, compared to 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, fewer saccades, and reduced reverse 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, Bock and Eckmiller (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, Quaccia and Gauthier (1995) subsequently reported similar results in incongruent pursuit blocks. They also tested the condition where the mapping of the target to the hand was randomized across trials. They found that in incongruent trials the eye 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 to 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 to 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 reverse 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 to 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, Quaccia and Gauthier (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 hand, rather than the visual target. In less than 10 trials, participants learned the reversed mapping and initiated pursuit with zero latency. The learning/adaptation effect was also observed in Domann, Bock and Eckmiller (1989)'s study. They trained non-human primates to track hand movements with gaze in 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 100-200 latency and one non-visual driven component with 0 latency. The learning effect was associated with increased occurrence of non-visual driven component and decreased occurrence of 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, Bock and Eckmiller (1989) in addition showed the
bimodal distribution in the pursuit latency while training non-human primates to do
the reversed-mapping tracking task. Neither our study nor Vercher, Quaccia and
Gauthier (1995) found bimodality. One possible explanation lies in the difference
between human participants and non-human subjects. Humans may instantly learn the
reversed mapping in few trials, while non-human primates have to take days of
gradual training, which resulted in a co-existence 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 resource. The effect of dividing attention on smooth pursuit eye
movements has been investigated in a few studies. Van Gelder et al (1995) and
Kathmann, Hochrein and Uwer (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 significant
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, stereotyped
and the timing constraints were quite loose, meaning that the task was far from
attentionally demanding. Also notice that we found a decrease in eye latency, among
other performance measures, in the incongruent pursuit. Souto and Kerzel (2008)
found that divided attention particularly affected close-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, was found 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, Liu and Snyder (2013) recorded from lateral intraparietal area (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. It suggests that saccade system does interact with hand reach movement system under 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 reach system interacts with saccade system when they are coordinated. While these studies dealt with saccade/reach movements, we recently showed that lateralized readiness potentials (LRPs) predict smooth pursuit latency in finger tracking. As LRPs are motor preparation signals originating mainly from the primary motor cortex (Coles 1989; de Jong et al. 1988), this finding suggest 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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References


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**Figure captions:**

Fig 1. The diagram of 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 moves always in the opposite direction when the finger moves. Note that the device and the hand were occluded, while only the tracking target was visible to the observer.

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

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 one example participant. Eye latency was overall reduced in the congruent condition. The cross in (A-C) shows the average value ± SEM.

Fig 4. Eye latency in congruent and incongruent condition 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 ± SEM.

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 ± SEM.

Fig 6. (A) The pursuit gain for congruent and incongruent condition. The gain was larger in the congruent condition. Shaded areas indicate ± SEM. (B) The increased gain in congruent versus incongruent condition was correlated with the decreased pursuit latency, suggesting similar underlying factors for anticipatory pursuit initiation and improvement in on-going 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 ± SEM.

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

Occluded
(A) Congruent

- Position (deg)
- Velocity (deg/s)

Time from finger onset (ms)

(B) Incongruent

- Position (deg)
- Velocity (deg/s)

Time from finger onset (ms)
(A) Congruent

(B) Incongruent

(C) Eye Latency

(D) Histogram of Latency for Sub01
(A) Pursuit gain

- Black line: Congruent
- Gray line: Incongruent

![Graph showing pursuit gain over time from finger onset (ms).]

(B) Gain difference correlates with latency difference

- X-axis: Congruent - Incongruent Latency (ms)
- Y-axis: Congruent - Incongruent Gain

![Graph showing the correlation between gain difference and latency difference.]

- The dashed line represents the trend of the data.