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LRP predicts smooth pursuit eye movement onset during the ocular tracking of self-generated movements

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Chen J, Valsecchi M, Gegenfurtner KR. LRP predicts smooth pursuit eye movement onset during the ocular tracking of self-generated movements. *J Neurophysiol* 116: 18–29, 2016. First published March 23, 2016; doi:10.1152/jn.00184.2016.—Several studies have indicated that human observers are very efficient at tracking self-generated hand movements with their gaze, yet it is not clear whether this is simply a by-product of the predictability of self-generated actions or if it results from a deeper coupling of the somatomotor and oculomotor systems. In a first behavioral experiment we compared pursuit performance as observers either followed their own finger or tracked a dot whose motion was externally generated but mimicked their finger motion. We found that even when the dot motion was completely predictable in terms of both onset time and kinematics, pursuit was not identical to that produced as the observers tracked their finger, as evidenced by increased rate of catch-up saccades and by the fact that in the initial phase of the movement gaze was lagging behind the dot, whereas it was ahead of the finger. In a second experiment we recorded EEG in the attempt to find a direct link between the finger motor preparation, indexed by the lateralized readiness potential (LRP) and the latency of smooth pursuit. After taking into account finger movement onset variability, we observed larger LRP amplitudes associated with earlier smooth pursuit onset across trials. The same held across subjects, where average LRP onset correlated with average eye latency. The evidence from both experiments concurs to indicate that a strong coupling exists between the motor systems leading to eye and finger movements and that simple top-down predictive signals are unlikely to support optimal coordination.

anticipatory smooth pursuit; ocular tracking of self-motion; eye-hand coordination; lateralized readiness potential

NEW & NOTEWORTHY

Humans often have to track motion that is generated by themselves, for example, when tracking one's own finger. Here we show, for this task, that brain responses as measured by the lateralized readiness potential (LRP) are correlated with the latency of the accompanying eye movements, even after the contribution of finger motion onset is subtracted. Our results provide the first LRP evidence for a strict eye-hand motor coupling on a trial-by-trial basis.

RESPONDING QUICKLY TO EVENTS in the environment is crucial to an animal's survival. However, some delay from sensation to motor response is unavoidable. To overcome this difficulty, animals often make anticipatory movements (Nijhawan and Wu 2009).

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One example of such anticipatory movements are anticipatory smooth pursuit eye movements. Smooth pursuit eye movements stabilize the image of a moving object in the fovea, increasing visual acuity. Smooth pursuit eye movements are typically initiated with a delay of 100–180 ms relative to the onset of an unpredictable motion (Lisberger and Westbrook 1985; Lisberger et al. 1987). Anticipatory smooth pursuit is often observed when the object's motion is expected. In this case, the latency of pursuit onset can be shortened and the eyes can even start moving before the target (Kowler et al. 2014). Anticipatory smooth pursuit can be induced by the repeated presentation of the same motion trajectory (Kowler and Steinman 1979), by a prior cue indicating the target motion direction (de Hemptinne et al. 2008), by the history of recent trials (Collins and Barnes 2009), or when the target motion is generated by the observers themselves (Steinbach 1969).

The ocular tracking of self-generated movements has been studied since the pioneering work by Steinbach and Held (1968). Observers were asked to track their own hand (e.g., Steinbach and Held 1968) or a visual target on the screen reproducing the hand movement in real time (e.g., Scarchilli and Vercher 1999; Steinbach 1969). For comparison, observers tracked their hand while it was moved by the experimenter or tracked an external moving target. Enhanced performance in the tracking of self-generated motion has been reported in terms of decreased rate of saccades (Mather and Lackner 1980; Steinbach and Held 1968; Steinbach 1969), reduced pursuit latency (i.e., anticipatory smooth pursuit; Gauthier and Hofferer 1976; Scarchilli and Vercher 1999), and reduced delay at reversals (Mather and Lackner 1980; Steinbach 1969; Vercher et al. 1995). The arm motor command as well as proprioception have been proposed to play a role in the coordination of arm and the eye. On one hand, the tracking of active arm motion did not differ from the tracking of passive arm motion, suggesting that proprioception promotes the enhanced performance in self-motion tracking (Mather and Lackner 1980, 1981). On the other hand, Vercher et al. (1996) found that the tracking of the actively self-moved arm was significantly better than the tracking of the passively moved arm or of external movements. Their passive condition was only slightly better (latency 130 ms) than the external condition (150 ms), suggesting only a small contribution of proprioception. Moreover, patients completely deprived of proprioception were still able to start anticipatory smooth pursuit in tracking of self-movements, just like normal subjects (Vercher et al. 1996). Since the patients without proprioception had a smaller pursuit gain than the control subjects, it was argued that the motor command plays a major role in triggering the smooth pursuit, synchronizing the eye with the hand, whereas proprioception might be involved in enhancing the

on-going pursuit of self-motion (Vercher and Gauthier 1992; Vercher et al. 1996). This idea was also supported by model simulations (Lazzari et al. 1997).

Direct evidence supporting the role of the motor command in the execution of anticipatory smooth pursuit, however, is still lacking. In the present study, after replicating the finding of anticipatory smooth pursuit eye movements in response to self-generated finger movements, we combined the measurement of finger movements, eye movements, and event-related potentials (ERPs) to demonstrate the direct link between the motor command for finger movement and ocular tracking. Toward this aim, we took advantage of the lateralized readiness potential (LRP) component, a negative-going potential, which can be observed over the contralateral motor areas before a manual response is produced (for an overview, see Smulders and Miller 2012). The LRP starts shortly (300–500 ms) before the voluntary movements and is assumed to be generated within the primary motor area (e.g., Coles 1989; de Jong et al. 1988). The LRP has been widely used to assess motor preparation and organization (e.g., Hackley and Miller 1995; Low et al. 2002; Miller and Low 2001). Importantly in the context of the present study, the LRP has been found to be related to motor intention and action consequence prediction. Haggard and Eimer (1999) showed that the LRP occurred earlier in trials where participants reported an earlier time for their intention to act and concluded that the LRP was the correlate of action intention. A recent study found that the LRP was stronger if the voluntary action had an effect, relative to the case where no effect followed the action (Hughes and Waszak 2011). The LRP could reflect the underlying mechanism of generating the prediction of voluntary action effect.

Our main finding is that the LRP onset and amplitude are associated with anticipatory pursuit of the finger motion. This demonstrates that the motor system for controlling finger movements and the oculomotor system are closely coupled to achieve optimal eye-hand coordination.

EXPERIMENT 1

Methods

Participants. Ten observers (5 women, mean age 25.2 yr) were recruited for the experiment. All the observers signed written informed consent that agrees with the Declaration of Helsinki and was approved by the local ethics committee. They all had normal or corrected-to-normal vision. All except two were right-handed. All used their right hand to perform the finger motion. The results of the two left-handed observers did not show obvious differences from the others. The author JC was one of the observers.

Finger tracking task. The observers were asked to place their right index finger in the center of a flat screen and to move the finger against the screen (Fig. 1). The Zebris marker attached to the index finger nail was part of the Zebris motion capture system and also served as the tracking target. In a viewing distance of 40 cm, the Zebris marker was 1.4 deg in diameter; the finger was around 2 deg in width. The room was illuminated, so observers could clearly see the marker, the fingers, and the right arm. Observers mainly recruited their elbow and shoulder joints to move the finger in the task. In each trial, a 50-ms sound signal prompted the observers to start

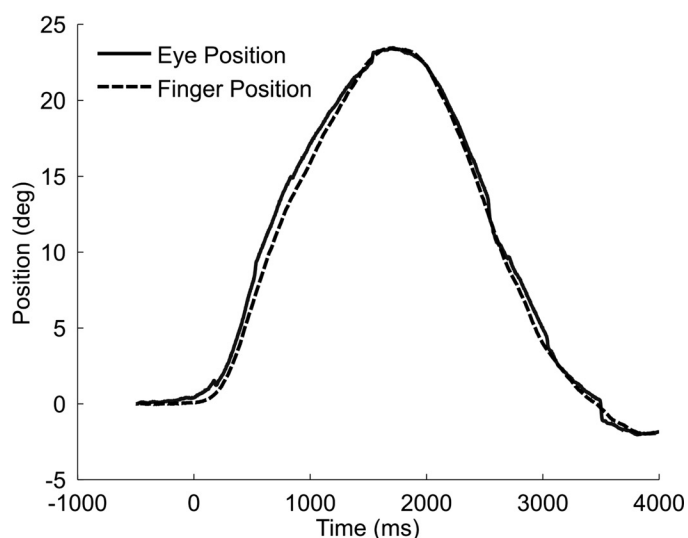
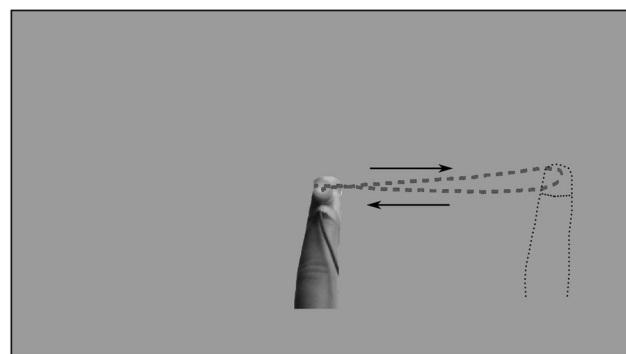


Fig. 1. A sample trial. Subjects moved the finger against a screen while tracking the marker attached to the fingernail with their gaze. The marker was part of the motion capture system for localizing the finger positions. In each trial, subjects started by moving their finger to either the left or the right side of the screen. They were required to turn back to the center in the second half of the movement.

moving the finger either to the left or to the right while tracking the finger with their gaze. After a certain distance of movement (13.1 cm on average), which was decided by the observers, they were required to return to the starting point. The observers 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 to balance the left and the right direction. There were no further constraints on the task. After the observers finished the movement, they had to leave the finger at the center and keep fixating the finger until another audio cue indicated the end of the trial. The observers practiced for about 10 trials to get familiar with the procedure before the experimental session began (120 trials). A short break was administered every 30 trials. The eye tracker was recalibrated after each break.

Control tasks. The control tasks took place in the same room under the same illumination. In the control tasks, the observers were asked to track a moving dot on the screen with their gaze, with their hands resting on the desk. The dot motion trajectories were a selection from each observer's finger movements recorded in the finger tracking task. After the observers finished the finger tracking task, we processed the motion position recordings to get the start, turn, and end point of the position

track. The turning point was defined by the peak in the position. The start and end points were obtained by searching back and forward, respectively, from the turning point until the displacement in the overall direction of motion between consecutive samples dropped below 0.5 pixel, corresponding to a speed of 2.6 deg/s. The part from the starting point to the end point was cut out to be replayed. All the trials were visually checked and discarded if the procedure did not lead to a reasonable segmentation (1.6%). The motions (sampled at 100 Hz in the finger tracking) were adapted to the screen refresh rate at 120 Hz by linear interpolation between two nearby samples.

In the control tasks, at the beginning of each trial, observers were presented with a fixation spot in the center of the screen. The fixation spot was a green bull's eye, with an outer radius of 1 deg and an inner radius of 0.15 deg. The observers were asked to fixate the spot and press a button to start the trial. After the button press, a drift-correction of the eye-tracking system was performed. If the drift correction was successful, the inner radius of the fixation spot would expand to 0.25 deg, which would serve as the pursuit target. After a fixed duration of 1 s, the target began to move either to the left or to the right. The observers were required to track the pursuit target as closely as possible.

We manipulated the predictability of the dot motion in three control conditions. In the unpredictable condition, the trials were randomized and thus the motion direction was completely unpredictable. In the predictable direction condition, we grouped the trials by motion direction. Half of the observers first underwent the left motion trials and subsequently the right motion trials, and vice versa for the other half of the observers. In the predictable trace condition, two representative movement traces (one left moving, one right moving) were picked and presented to the observer repeatedly in all trials. The representative traces were picked so that they had similar moving duration, amplitude, and starting speed as the averaged trace of each observer. In the predictable trace condition, therefore, the observers were able to predict the moving direction as well as the whole movement kinematic. The random direction condition and the predictable direction condition had 118 trials, on average, because we excluded the motion trajectories if we could not obtain a good segmentation (1.6%). The predictable trace condition had 120 trials (60 left moving, 60 right moving).

Finger movement recording. The position of the finger was tracked at 100 Hz by a Zebris ultrasound motion capture system (Zebris Medical, Isny im Allgäu, Germany) controlled through a custom-made MATLAB toolbox (The MathWorks, Natick, MA). The Zebris marker was fixed on the fingernail. The nominal resolution of the system is below 0.1 mm. The nominal accuracy is less than 1 mm with a measurement distance of 1 m in the current setup. The time stamp of the position data was given by the host computer in MATLAB.

Eye movement recording. Eye movements were recorded at 500 Hz using an EyeLink II head-mounted eye tracker (SR Research, Mississauga, ON, Canada). A chin rest was used to limit the head movements. Analyses were all based on the right eye movements.

Data analysis. To detect the finger movement onset, we first selected a rough estimate, which was the first sample of the first series of at least five consecutive samples in which the

finger moved in the direction of the overall motion. We subsequently selected epochs of 800 ms centered on the first estimate to use for the final onset detections for both the finger movements and the eye movements. Saccades were removed from the eye tracks before further processing. The final onset detection was obtained by the method described by Schütz et al. (2007). The position signals were low-pass filtered below 30 Hz. Velocity signals were calculated by digital differentiation of the position data and were low-pass filtered below 10 Hz. Regression lines with 80-ms length were fitted to the velocity trace. All regression lines with $R^2 < 0.7$ or a slope $< 10^\circ/s^2$ were discarded. The one with the highest R^2 value in the remaining lines was selected. The intercept of this line with the time axis was defined as the movement onset. Individual trials were visually checked and discarded if the procedure did not lead to reasonable estimations ($< 10\%$). The exact same procedure was applied to both the finger movement (dot movement) onset detection and the eye movement onset detection in all the conditions in *experiment 1*. The eye movement latency was defined as the eye movement onset time relative to the onset of the finger movement (or the dot movement in the control trials) in each trial. As a result, negative latencies indicate anticipatory eye movements. In the analyses, the Bonferroni correction was used for multiple comparisons.

Results

The observers were able to balance the two movement directions (left trials: 49.9% on average, ranging from 45% to 55% across subjects). The mean absolute speed of the finger movement over the whole trial was 17.9 deg/s, ranging from 8.7 to 32.3 deg/s. The mean movement length before turning back was 18.7 deg (13.1 cm), ranging from 11.3 to 24.6 deg.

Anticipatory smooth pursuit of finger movements. In finger tracking, after the onset of audio cue, observers overall moved the finger at 416 ms and moved the eye at 396 ms. Across 10 observers, finger response times and eye response times were highly correlated ($r = 0.99$, $P < 0.001$). The variability of finger/eye response times were also highly correlated ($r = 0.97$, $P < 0.001$). A cumulative frequency plot of the eye latencies in all conditions are shown in Fig. 2. In the analysis, median latency was calculated for each individual subject. The mean of all subjects' latencies was used as the overall averaged latency. In the finger tracking task, the eye latency was on average -19.4 (SD 17.8) ms relative to the finger. In comparison, in the unpredictable condition of the dot replay tracking the pursuit latency was 110.3 (20.0) ms. In the predictable direction condition and the predictable trace condition, the pursuit latencies were comparable with those in the finger tracking condition, 2.1 (38.5) and -7.7 (41.9) ms, respectively. Repeated-measures ANOVAs over latencies revealed significant differences between four conditions [$F(3, 27) = 46.4$, $P < 0.001$], with the finger condition and the predictable conditions having shorter latency than the unpredictable condition (all $P < 0.001$). Repeated-measures ANOVAs over the standard deviations also revealed significant differences [$F(3, 27) = 9.6$, $P < 0.001$]. Finger tracking showed less variance than the predictable direction and predictable trace conditions (marginally significant, $P = 0.077$ and $P = 0.065$, respectively). Random direction condition had less variance than the predictable direction and predictable trace conditions ($P = 0.016$ and

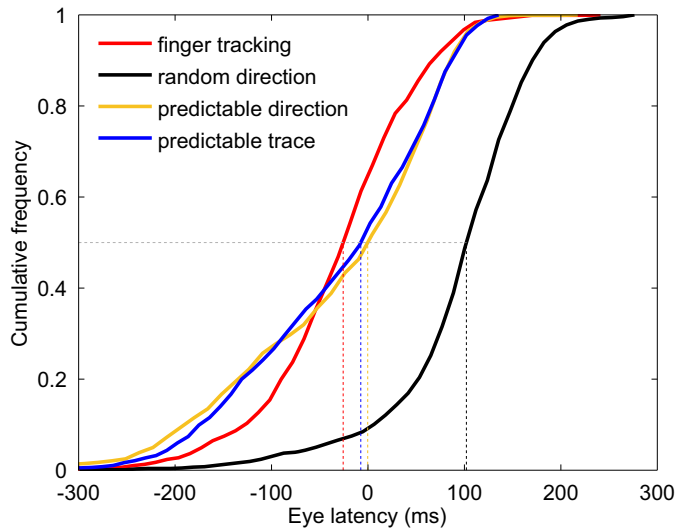


Fig. 2. Cumulative frequency plot of eye latencies in all trials of 10 observers. The averaged latency of all subjects was as follows: finger tracking, -19 ms; random direction, 110 ms; predictable direction, 2 ms; and predictable trace, -8 ms. The standard deviation (indicated by the slope) of finger tracking latencies (17.8 ms) was as low as that in the random direction condition (20.0 ms), both of which were smaller than the in two predictable conditions (38.5 and 41.9 ms). Dotted lines indicate the 0.5 cumulative frequency (median) in each condition.

$P = 0.037$, respectively). Finger tracking did not differ from the random direction condition in variance ($P = 1.0$). The eye latency distributions of the predictable direction condition (skewness = -0.78 , kurtosis = 3.00) and the predictable trace condition (skewness = -0.56 , kurtosis = 2.51) were similar, but they differed from the distribution of the finger tracking condition (skewness = -0.44 , kurtosis = 3.72). Note that in all the dot tracking conditions, a sound cue was presented at 1 s before the appearance of the tracking target. As a result, the tracking target was temporally predictable, which explains the relative low pursuit latencies in the control conditions.

Tracking the finger with considerably fewer saccades. The rate of saccades is an important index of smooth pursuit performance. We measured the saccade rate for all the condi-

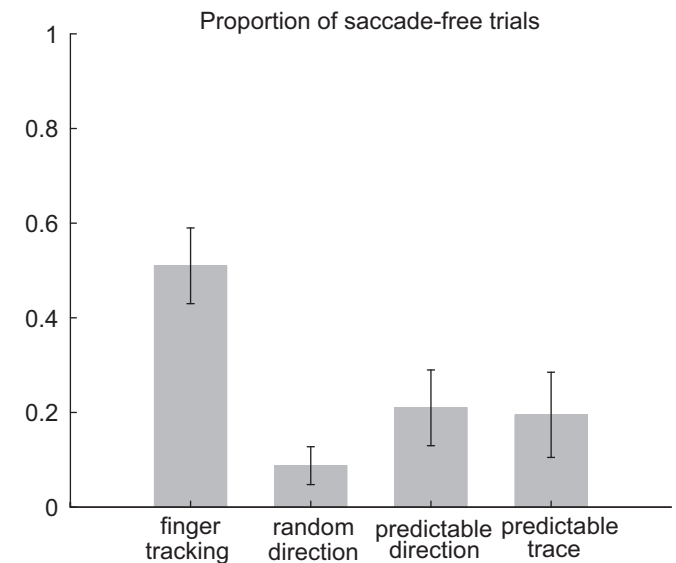
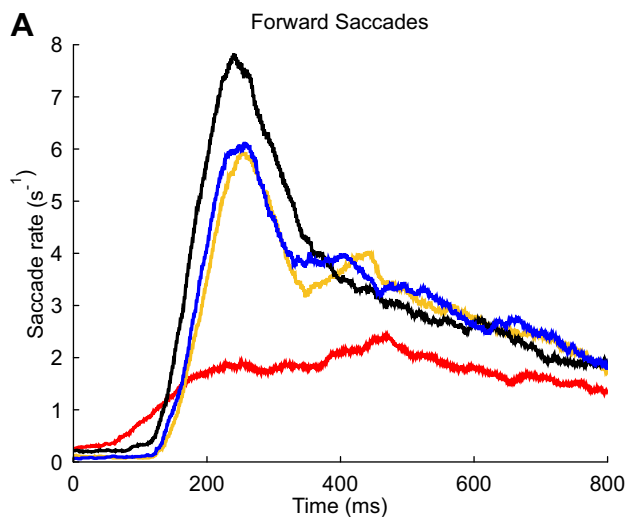


Fig. 4. Proportion of trials without any saccade in the 100 - to 400 -ms range during pursuit. Fewer saccades occurred in the finger tracking condition. Values are averages; error bars represent \pm SE.

tions time-locked to the motion onset. Finger tracking showed very few catch-up saccades (Fig. 3). This was especially evident in the initial period of the pursuit. In the time window of 100 – 400 ms, 51% of all the trials did not have any saccade in the finger tracking condition. In contrast, only 9% of the trials were saccade free in the unpredictable condition and around 20% trials were free of saccades in the two predictable conditions (Fig. 4). An arcsine transformation was applied to the proportion data to normalize the data and to stabilize variance (e.g., Theeuwes 1994). Repeated-measures ANOVA revealed significant differences between the four conditions [$F(3, 27) = 20.4$, $P < 0.001$]. Pairwise comparison showed that the finger tracking condition had a greater percentage of saccade-free trials than any other condition (all $P < 0.02$). The other comparisons did not reach significance (all $P > 0.10$).

The eyes led the finger during pursuit. Figure 5 shows the position error, which is the difference between eye and pursuit

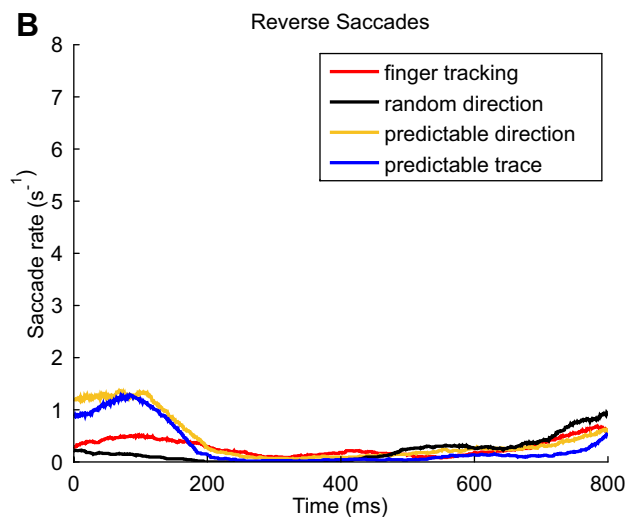


Fig. 3. Moving average of saccade rate in each condition (100 -ms window). *A*: the rate of forward saccades moving the eye forward to catch up with the target. *B*: the rate of reverse saccade moving the eye back to the target. Finger tracking (red line) was associated with fewer saccades, especially in the initial phase of tracking.

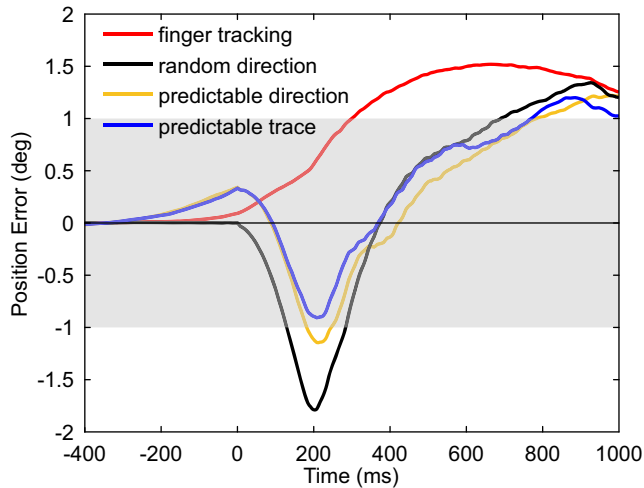


Fig. 5. Position error (gaze position minus target position) in each condition. The finger tracking condition was unique, with the eye always leading the finger during pursuit. *Time 0* was the finger/dot motion onset. The gray-shaded area indicates the width of the finger (~ 2 deg).

target positions, the pursuit target being the finger or the dot. *Time 0* was the start of the target motion. Position errors were calculated by subtracting the absolute distance to the center of the pursuit target from that of the eye. The values are positive in the first half of the movements before turning (1,151 ms on average, ranging from 715 to 1,577 ms), indicating that the eyes were leading. Variance in the turning time and the fact that motion speed was not constant made it difficult to interpret the position error in the later part of pursuit. Therefore, in this part of the results we only emphasize the initial phase of pursuit (< 500 ms). On average, the eye was always leading the finger in the finger tracking condition, contrary to what we observed in the unpredictable control condition and the two predictable control conditions. In the unpredictable condition, the eye lagged behind in the initial open-loop phase and then caught up with the target mainly by means of saccades. In the predictable conditions, the anticipatory movements enabled the eye to be slightly ahead of the finger before the motion started. The eye, however, lagged behind in the open-loop phase of the pursuit, and saccades were again needed to catch up with the finger motion.

The eyes turned exactly at the same time as the finger. The task required observers to reverse the motion of the finger and return to the center before the end of the trial. We individuated the turning point of the finger and the eye as the point where the displacement reached its peak (Fig. 6). In the finger tracking, the eyes turned together with the finger without delay [-3.3 ms; not significantly different from 0, $t(9) = 0.53$, $P = 0.61$]. Repeated-measures ANOVA revealed a significant difference between the four conditions [$F(3, 27) = 6.96$, $P < 0.02$]. Pairwise comparison showed that the finger tracking condition had significantly less delay than the random direction condition ($P < 0.001$) and the predictable direction condition ($P < 0.01$). The other comparisons did not reach significance (all $P > 0.18$). Because the trace itself was not predictable in the predictable direction condition, it is reasonable that it had a higher delay than the finger tracking. There was a general tendency of decreasing delay with increased predictability (from random direction to predictable direction to predictable trace). Note that the delay found in this study was smaller than

typical pursuit delays observed in other studies (~ 100 ms; Carl and Gellman 1987; Lisberger and Westbrook 1995). This is most likely due to the fact that the target began to slow down before turning, making the turning points roughly predictable in all the trials.

Discussion

We observed better ocular tracking of self-motion compared with the tracking of externally driven dot movements with identical trajectories. Tracking performance was enhanced in terms of reduced pursuit latency, reduced rate of saccades, both backward catch-up saccades in the early phase of motion (Fig. 3B) and forward saccades in the later phase (Fig. 3A), and reduced delay at reversal. This largely confirmed the findings of earlier studies showing more accurate ocular tracking of self-generated motion relative to tracking of external motion (Mather and Lackner 1980; Ross and Santos 2014) or tracking of passive movements (Steinbach 1969; Steinbach and Held 1968; Vercher et al. 1995, 1996). As a novel manipulation in our paradigm, we varied the predictability of the dot motion in the control conditions. We found that even in the very predictable control condition (the predictable trace condition), the tracking performance was not as good as in the finger tracking condition. Part of the decreased performance with externally triggered motion might be due to the fact that observers may have some residual uncertainty concerning the timing of the motion onset in the control conditions, despite the audio cue presented 1 s before onset. The one advantage of finger tracking would thus indicate that the brain is able to coordinate the hand and eye movement in real time. Another observation is that the eye led the finger in the finger tracking (Fig. 5), whereas the eye first lagged behind and then caught up with the target mainly by means of saccades in all the control conditions. These novel observations further suggest that finger tracking is unique and that a nonvisual prediction mechanism dominates the pursuit in finger tracking.

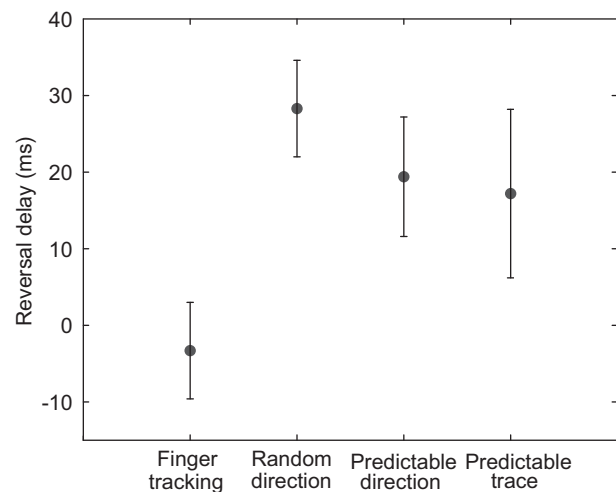


Fig. 6. Reversal delay in each condition (turning time of eye minus turning time of finger). The finger tracking had no delay (-3 ms). The delay was larger in the 3 control conditions (28, 19, and 17 ms, respectively). Values are averages; error bars represent \pm SE.

EXPERIMENT 2

We observed anticipatory smooth pursuit during ocular tracking of self-generated hand movements in *experiment 1*. Because it is well known that lateralized readiness potentials (LRPs) are elicited before the onset of hand movement, in *experiment 2* we aimed to find out whether there is a direct link between LRPs and anticipatory smooth pursuit during self-motion tracking. Measuring LRPs required modifying the setup to a certain extent. Specifically, LRPs are typically measured by a subtraction method (de Jong et al. 1988) that requires comparison of ERPs elicited by the left-hand movements and ERPs elicited by the right-hand movements. Therefore, we asked subjects to use the left hand when they decided to move to the left and to use the right hand when they decided to move to the right. Hand movements, eye movements, and EEGs were simultaneously recorded.

Methods

Participants. Twelve observers (6 women, mean age 26.5 yr) were recruited for the study. All the observers signed written informed consent that agrees with the Declaration of Helsinki and was approved by the local ethics committee. They all were right-handed, had normal or corrected-to-normal vision, and were naive to the purpose of the study. None of them participated in *experiment 1*.

Experimental setup. The observers were seated on a chair before a table in a lighted room. A chin rest at the edge of the table was used to limit head movements. A wooden board was fixed vertically on the table to serve as a platform for the observers on which to place and move their fingers. In the center of the platform, a black dot (diameter 0.1 deg) was drawn as a fixation spot. The platform was 40 cm away from the eyes. Behind the platform was the eye tracker camera. We opted for the remote solution because we wanted to avoid use of a head-mounted system while recording ERPs, but positioning the eye tracker above the fixation point produced relatively more noisy data in *experiment 2*. The Zebris motion capture system was placed at the left side of the desk, about 60 cm away from the platform. During the experiment, all three recording systems (motion capture, eye tracker, and EEG recording) were synchronized through a digital trigger generated by an independent device (NI-6009; National Instruments, Austin, TX).

Procedure. In *experiment 2*, the observers were required to use the left finger when they chose to move to the left and the right finger when moving to the right. In the beginning of each trial, the observers had to put their two index fingers in the center of the platform. The observers were asked to fixate on the fixation spot in between the two fingers. After the computer program found that the two fingers were at the center, it executed a drift correction for the eye recording. If the drift correction was successful, an audio cue with a duration of 200 ms was presented. The frequency of the audio cue (400 vs. 800 Hz) indicated the two conditions (fix vs. pursuit), with the meaning counterbalanced across observers. After the audio cue, the observer was required to start to move either the left finger to the left or the right finger to the right. Depending on the trial type, the observer either kept fixating the fixation spot or tracked the moving finger. As in the *experiment 1*, the observers were required to make smooth movements and to balance the two directions. There were no further constraints

for the movements. After the observer finished the movement, a sound cue of 200 Hz signaled the end of the trial. Observers conducted 240 trials in total, with 120 fix trials and 120 pursuit trials pseudorandomly interleaved. The finger movements, eye movements, and EEG signals were recorded in all trials.

Finger movement recording and analysis. Both the right and left finger positions were recorded at 100 Hz. Each finger had a marker attached, whose position was monitored by the Zebris system. The same method described in *experiment 1* was used to detect the finger movement onset. Individual trials were visually checked and adjusted if the procedure did not lead to reasonable estimations of the pursuit onset (14.8%). For example, the algorithm sometimes missed the original onset and selected the returning phase of the motion. In rare cases, an uneven acceleration in the initial phase of motion lead to an extrapolated onset that was not plausible given the eye movement trace.

Eye movement recording and analysis. Eye movements were recorded at 1,000 Hz by an EyeLink 1000 desktop-mounted eye tracker (SR Research). The right eye was tracked. The calibration was based on three horizontal predefined locations on the platform. As described in *Procedure*, in the beginning of each trial, the eyes were fixating on the fixation spot in the center of the platform, which was located in between the two fingers. In most of the trials (93.3%) in the pursuit condition, the observers executed a small saccade to the finger that was about to move. In this case, the initial saccade was strictly necessary to move the eyes from the center fixation spot to one of the two fingers, and the onset of the pursuit immediately followed the saccade. The onset of this saccade, therefore, was defined as the eye movement latency in these trials. In other trials without this catch-up saccade, the same method used in detection of the finger movement onset was used to detect the eye movement onset.

EEG recording and analysis. EEG was recorded from 32 scalp sites according to the international 10–20 system (FP1, FP2, F3, F4, C3, C4, P3, P4, O1, O2, F7, F8, T7, T8, P7, P8, Fz, Cz, Pz, FC1, FC2, CP1, CP2, FC5, FC6, CP5, CP6, TP9, TP10, HLeo, Veo, HReo). A BrainAmp amplifier (Brain Products, Munich, Germany) digitized the data at a sampling rate of 1,000 Hz. The ground electrode was placed at the AFz location, and the reference electrode was placed at the Cz location. The electrooculogram (EOG) was captured by three electrodes (HLeo, Veo, and HReo). The HLeo and HReo electrodes were placed at the right and left of the outer canthi to record horizontal EOG. The Veo electrode was placed below the right eye to record vertical EOG. EEG data were stored and analyzed offline with EEGLAB toolbox functions (Delorme and Makeig 2004) and customized scripts in MATLAB. Data were re-referenced to the average offline. Separate EEG epochs of individual trials were extracted. All the trials with EEG voltages exceeding the range $[-80, 80] \mu\text{V}$ were excluded. A baseline correction was applied based on a duration of $[-300, -100]$ ms locked on the audio cue onset. In the analysis of LRPs, the EEG data were low-pass filtered below 8 Hz (e.g., Everaert et al. 2014). To obtain LRPs, a subtraction procedure was used as described by de Jong et al. (1988):

$$\text{LRPs} = (C3-C4)_{\text{right hand}} - (C3-C4)_{\text{left hand}} \quad (1)$$

Lateralized potentials from other pairs of electrode channels (e.g., FC1/FC2, CP1/CP2, etc.) were calculated using the same

procedure. Because eye movements introduce artifacts in the EEG signals, in the pursuit condition we only examined the EEGs before the eyes started to move. In the fix condition, we only included the trials that did not have any saccade and that remained within a radius of 0.5 deg at the center (70%).

Given the noisy nature of ERP signals, even average LRP traces for single observers can have complex profiles, making the computation of latency impossible with the raw data. Jackknifing is an analysis technique that is widely established in ERP research as a way to circumvent this problem (Kiesel et al. 2008; Luck et al. 2009; Miller et al. 1998; Ulrich and Miller 2001). In jackknifing, each observer's latency score is estimated as the averaged data of the remaining subjects. Therefore, the technique estimates the contributions of each individual observer to the grand mean. Whereas jackknifing makes the computation of LRP latency a treatable problem, it also produces estimates that are biased in two ways. First of all, the variance is underestimated to an extent that depends on the sample size [$1/(n - 1)^2$ times the variance of the real latency, with n being the sample size; Ulrich and Miller 2001]; intuitively, removing one trace from the pool average has a progressively smaller effect as the pool size increases. Second, because the specific observer's data do not contribute to the estimate (while all other observers' data do), the jackknifed estimate of latency for one observer is negatively related to the actual latency (Smulders 2010; Stahl and Gibbons 2004).

We performed a linear mixed-models analysis to find out whether LRPs predict eye movement latencies on a single-trial basis (Winter 2013). This analysis was done using R 3.1.1 (R Core Team 2014) and the R package lme4 (Bates et al. 2013). Visual inspection of residual plots did not reveal any obvious deviations from normality. However, the data violated homoscedasticity with unequal residual variances. We therefore applied the Box-Cox transformation on the eye latencies (Box and Cox 1964; van Albada and Robinson 2007). After the transformation, the residual variances became equal.

Results

Observers were generally able to follow the instructions to either track the finger in the pursuit condition or to maintain fixation in the center in the fix condition. Trials in which they failed to do so were excluded from analysis (8.8%). On average, observers started to move the finger 558 ms and the eyes 519 ms after the onset of the audio cue. That is, observers generally moved the eyes slightly before they moved the finger (see Fig. 7 for individual subjects' finger onset and eye onset). The eye latency relative to the finger movement onset differed between observers, ranging from -196 to 72 ms. Despite this large inter-individual difference, we were able to demonstrate that eye and finger movements were coupled. For each observer, we calculated the correlation between the finger response times and eye response times locked to the audio cue onset across trials. The correlations were all highly significant (ranging from 0.47 to 0.80, all $P < 0.01$). Especially high correlations (0.79, 0.73, 0.64) were found for the observers who moved the eyes much earlier than the finger (-196 , -110 , -128 ms). Across observers, finger response times were correlated with eye response times ($r = 0.78$, $P = 0.002$; Fig. 7). Moreover, the variabilities of finger and eye response times were correlated ($r = 0.92$, $P < 0.001$). These results show that

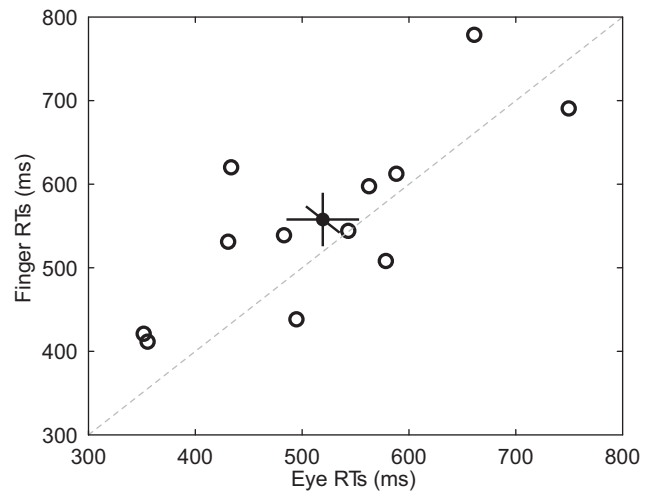


Fig. 7. Eye reaction times (RTs) and finger RTs relative to the sound cue. Open circles indicate individual observers. Filled circle is the average value (eye RT, 519 ms; finger RT, 558 ms); error bars represent \pm SE.

observers did co-plan and co-execute the finger and eye movements in the task. Excluding the first catch-up saccade, which moved gaze onto the pursuit finger, saccade rate was as low as that in finger tracking of *experiment 1*. For example, in the window [200, 400] ms after finger onset, *experiment 2* yielded a saccade rate of 2.7 per second, compared with 2.0 per second in the finger tracking condition of *experiment 1*. In comparison, the control conditions in *experiment 1* showed much higher saccade rates (5.7, 4.6, and 4.8 for random direction, predictable direction, and predictable trace conditions, respectively).

Our primary interest was to investigate the link between LRPs and the eye movement latency. Figure 8 shows the LRPs at FC1/FC2, C3/C4, and CP1/CP2 sites in both the fix condition and the pursuit condition for all subjects. The LRPs were quite similar between the two conditions in the time window before -150 ms. After -150 ms, the eyes started to move in some trials ($>20\%$), thus contaminating the LRPs with EOG artifacts, resulting in large lateralized potentials in the pursuit condition. Therefore, care was taken to avoid the artifacts. ERPs were analyzed only in the time window preceding any overt eye movement. The analysis was threefold. First, we split the pursuit trials into "early pursuit" and "late pursuit" based on the median of the eye movement latencies for each observer. We found that the early pursuit trials showed stronger LRPs than the late pursuit trials in the time window before any explicit movement started. Second, on a trial-by-trial basis, we constructed a linear mixed model to show that the LRP amplitude predicted the eye movement latency on a single-trial basis. Third, across subjects, we found that the eye movement latencies were correlated with the LRP latencies.

Stronger LRPs in early pursuit trials. For each observer, the eye movement latencies relative to the finger onset resembled a normal distribution. We aimed to find whether the trial-to-trial variance of the eye latency was related to the LRPs. To avoid the artifacts from eye movements, the 100-ms time window before the earliest eye movement was selected for LRPs analysis (Fig. 9, shaded window). The time window was customized to each observer, because observers had different eye movement latency distributions. Trials that had any saccade in the fixation period were removed. Trials that had

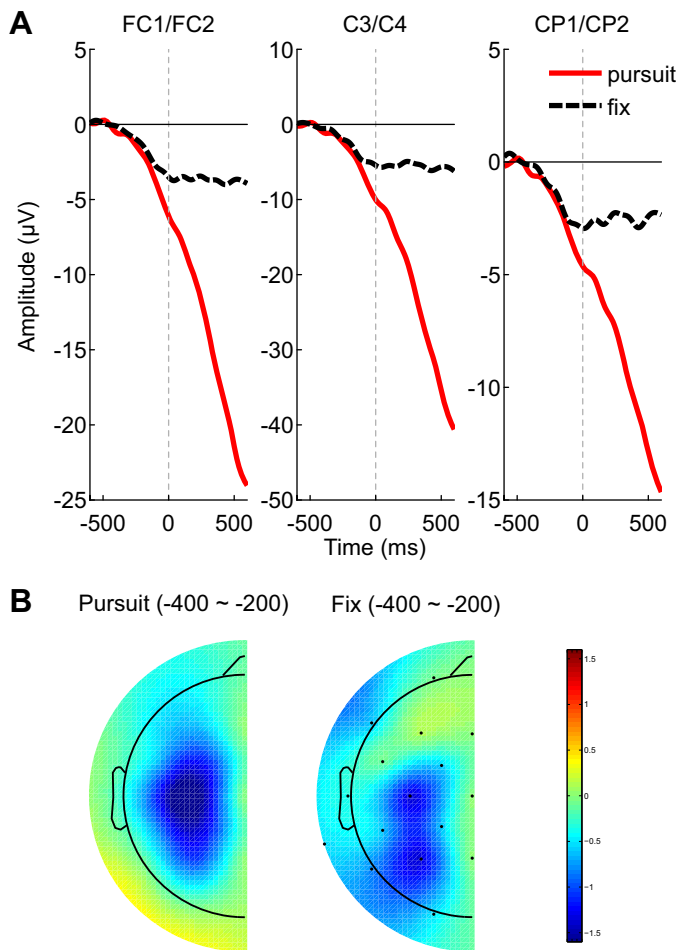


Fig. 8. A: LRP at 3 pairs of channels (FC1/FC2, C3/C4, and CP1/CP2) for both pursuit and fix conditions. *Time 0* was the onset of finger movements. The large lateralized potential in the pursuit condition after motion onset is due to eye movement artifacts. The LRP started at around 400 ms before finger motion onset. The LRP of the pursuit vs. fix condition did not differ until around -150 ms, where the pursuit had started in 20% of trials. B: topographic map of the lateralized potentials in fix vs. pursuit condition, plotted at the left half of the topographic figure, with the right half left out.

latencies outside 1.5 SD range were also excluded (20.8% removed in total). We split the remaining trials (95 trials, on average, ranging from 72 to 107 for each subject) by the median latency into early pursuit trials and late pursuit trials. We were therefore able to compare the LRPs between the early pursuit and the late pursuit trials. Figure 9 illustrates the median split procedure in *subject 1*.

Figure 10 shows the lateralized potentials at each pair of channels for early pursuit and late pursuit trials. *Time 0* was the earliest eye movement onset. Before any eye movement started, the lateralized potentials were stronger overall in the early pursuit trials than in the late pursuit trials. A 3×2 ANOVA over the lateralized potentials in the window of $[-100, 0]$ ms on the three pairs of channels between the two conditions found a significant main effect of the two conditions [$F(1,11) = 5.07$, $P < 0.05$]. The stronger LRP in the early pursuit trials suggests that the motor preparation activities were probably available to the eye movement system.

Microsaccades did not contaminate the result. We looked for microsaccades in the time window in which we measured LRP

(shaded window in Figs. 9 and 10), with an algorithm using a velocity threshold of 6 SD and a minimum duration requirement of 6 samples (Engbert and Kliegl 2003). Microsaccades were rare. In all subjects, 8 trials in early pursuit and 11 trials in late pursuit contained microsaccades. Excluding these trials did not change the result.

An alternative explanation was that the finger movement metrics (speed, amplitude, etc.) may be different between early pursuit trials and late pursuit trials, which could explain the stronger LRPs in the early pursuit trials. However, the finger movement speed did not differ between the two conditions in any aspect, including the average speed of the initial 200 ms [early vs. late pursuit trials: 11.7 vs. 11.1 deg/s, $t(11) = 1.22$, $P = 0.25$], the average speed of movements before reversal [16.1 vs. 16.4 deg/s, $t(11) = -1.26$, $P = 0.24$], and the peak speed of movements before reversal [33.9 vs. 34.2 deg/s, $t(11) = -0.12$, $P = 0.91$]. The movement length was different in two groups of trials [14.0 vs. 14.5 deg, $t(11) = -3.44$, $P < 0.01$], but the early pursuit trials had a shorter movement length, which is unlikely to be the reason for larger LRPs. Therefore, the stronger lateralized potentials in the early pursuit trials cannot be explained by the finger movement itself.

Larger LRP associated with early pursuit latencies in individual trials. We constructed a linear mixed model to use the LRP signals to predict the eye movement latencies on a single-trial basis. The LRP amplitude averaged at the FC1/C3/CP1 channels at the time window of $[-200, -100]$ ms relative to the finger onset was selected. To avoid eye movement artifacts, trials for which the eyes moved before -100 ms were removed. *Observer 2* was thus removed because only 5 trials were left. The remaining 11 observers had, on average, 71 trials, ranging from 42 to 106. We employed a model comparison approach to compare the full model against a null model. In the full model, the LRP signal was included as the fixed effect. As random effects we had intercepts as well as slopes

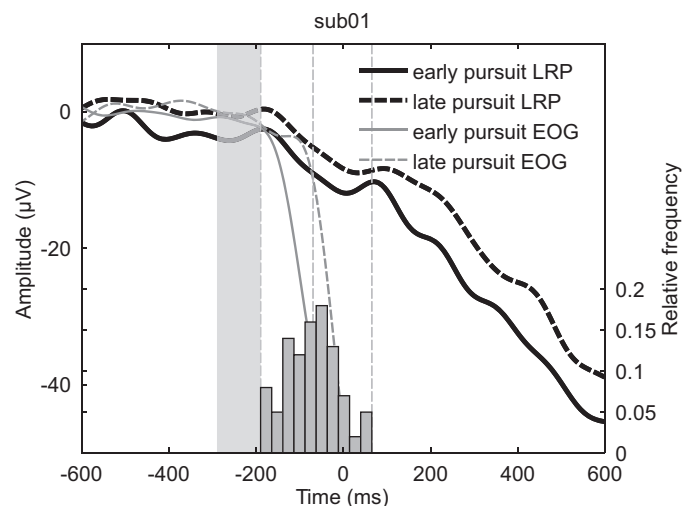


Fig. 9. Median split procedure in an example observer. The bar plot shows the histogram of eye latencies. Trials were split based on the median eye latency into early pursuit and late pursuit. Individual EEG traces were aligned to finger motion onset (*time 0*). The corresponding LRPs (black lines) were computed as the potential difference between electrodes C3 and C4. The EOG signals (gray lines) were computed as the potential difference between left horizontal and right horizontal EOG electrodes. The 100-ms shaded window before the earliest eye onset, which is before the EOG artifacts come into place, was used for analysis.

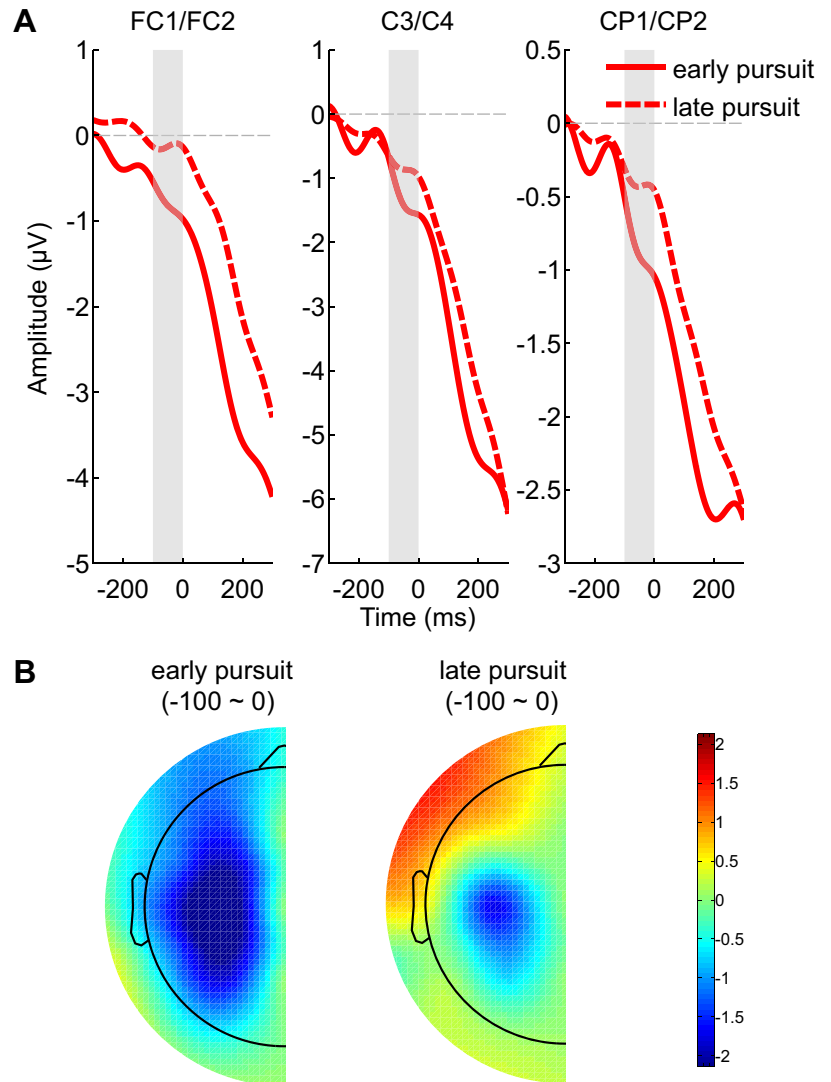


Fig. 10. *A*: lateralized potentials at each pair of channels for early pursuit trials (solid line) as well as late pursuit trials (dashed line). *Time 0* was the earliest onset of eye movements within each observer, which corresponded to around -200 ms in the case of the example observer represented in Fig. 9. Before any overt movements, early pursuit trials showed stronger lateralized potentials. *B*: topographic map of the lateralized potentials in early vs. late pursuit, plotted at the left half of the topographic figure, with the right half left out. The lateralized potentials were stronger in early pursuit trials.

for individual subjects. In the null model, the fixed effect (LRP signals) was removed, with all the random effects remaining. Comparison of the full model against the null model showed that the full model was significantly better [$\chi^2(1) = 4.45$, $P = 0.035$]; that is, the LRP signal was a significant predictor of the eye movement latency.

Earlier LRP was associated with earlier pursuit latencies across observers. Individual observers had different eye movement latencies (from -196 to 72 ms). To find out whether LRPs correlated with eye movement latency at the observer level, we employed a jackknifing approach to obtain LRP latencies. For each observer, the LRP latency was obtained from the fix condition, because the EOG artifacts cannot be disentangled from the real LRPs in the pursuit condition. The LRP latency estimations were thus based on the fix condition. To further avoid artifacts from small eye movements in the fix condition, trials with any saccade or with the eye positions away from the center for more than 0.5 deg were removed (29.4%). We correlated the LRP latencies with the eye latencies in the pursuit condition, since obviously no eye latencies were available from the fix condition. A high correlation was

found between the jackknifed LRP latency and the eye movement latency across 12 observers ($r = -0.71$, $P < 0.01$; Fig. 11). One subject (Fig. 11, *top left* data point) appeared to be an outlier. The result remained the same after this subject was excluded ($r = -0.69$, $P < 0.01$). Note that given the reversal in the correlation, the results show that the earlier the LRP latency, the earlier the eyes started to move for individual observers.

An alternative explanation for the across-subject correlation may be that the observers who tend to pursue early also tend to make some small eye movements even in the fix condition. This is unlikely because we excluded the trials with saccades or where the eyes deviated away from the center in excess of 0.5 deg. Furthermore, we subtracted the averaged eye position of left-moving trials from the averaged position of right-moving trials in the 300-ms time window before the finger onset. The eye position difference was very small, ranging from -0.07 to 0.04 deg. The amount of eye movements did not correlate with the LRP onset across subjects ($P > 0.10$). We therefore concluded that the observed correlation was not a result of eye movement artifacts in the fix condition.

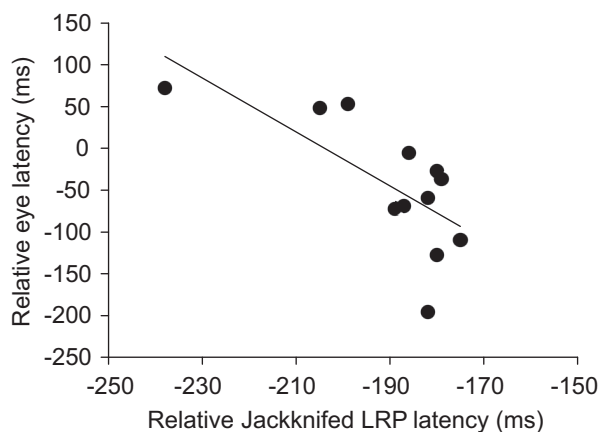


Fig. 11. Jackknifed LRP latency was correlated with eye latency across observers. Because the jackknifed latency is negatively related to each subject's real latency (see EXPERIMENT 2, *Methods*), the negative correlation in the plot indicates that the earlier the LRP onset was for one subject, the earlier this subject moved the eye.

Discussion

Our results suggest that LRPs are correlated with smooth pursuit latencies while the finger onset is kept fixed. An alternative explanation of the correlation could be that the observed LRPs are contaminated by pursuit-related signals before the start of pursuit. This explanation is unlikely for the following reasons. First, it cannot explain the result of cross-subject correlation between the LRP onset and the eye latency. For this analysis, the LRP onset was obtained in the fix condition where no explicit eye movements were executed, and thus no pursuit-related signals could contaminate the LRPs. Second, previous studies generally failed to find lateralized potentials before the start of eye movements (van der Lubbe et al. 2000, 2006). For example, van der Lubbe et al. (2006) examined saccade-locked lateralized EEG activity. They did not find any lateralized potentials in the time intervals from 1,000 to 40 ms before saccade onset and observed only an insignificant weak effect from 40 to 0 ms before saccade onset. Therefore, it seems that EEG technique is not sensitive enough to capture eye movement preparation signals. Note that when we compared LRPs between trials, the trials were aligned to the finger movement onset, and the earliest eye onset was only used to exclude possible eye movement artifacts in the epochs. We chose not to align our epochs to the onset of eye movements, as previous studies did, so the eye movement preparation signals we observed are estimated very conservatively.

The source of variation in the LRPs across trials and across subjects is not completely clear. The larger LRPs in the early pursuit trials relative to the late pursuit trials were not associated with the speed or amplitude of the finger movement per se. Most likely, the variance of LRPs across trials may reflect the well-documented spontaneous fluctuations in neural activity (Buzsáki 2006). Whatever the origin of the inter-trial variation, stronger LRPs are associated with stronger predictive signals to the oculomotor system, leading to an earlier pursuit onset. As for the variance of LRPs across subjects, it may reflect the individual differences in the central response organization and the execution of motor responses (Osman and Moore 1993). The correlation of LRP amplitude and eye latency across

subjects suggests that the central body and oculomotor system are closely tied.

GENERAL DISCUSSION

Finger tracking is a classical paradigm in the investigation of eye-hand coordination, the most common finding being that ocular tracking of self-motion is enhanced compared with the tracking of externally driven motion (Mather and Lackner 1980; Ross and Santos 2014; Steinbach, 1969; Steinbach and Held 1968; Vercher et al. 1995, 1996). In the present study we replicate the classical finding, showing that finger tracking is better in terms of both reduced saccade rate and decreased latency, and we extend it by demonstrating that ocular tracking of externally driven motion is not quite as good as finger tracking, even when the motion is completely predictable in terms of both onset time and kinematics. Furthermore, by measuring ERPs associated with the generation of hand motor commands (LRPs), we were able to prove the interdependence of the neural processes leading to finger and eye movements.

We know from previous literature that smooth pursuit control is influenced by nonvisual information. For example, smooth pursuit can be initiated if observers try to track the hand in darkness (e.g., Berryhill et al. 2006; Gauthier and Hofferer 1976; Jordan 1970). In fact, we found that gaze is ahead of the finger during tracking, which highlights the importance of nonvisual inputs during this process. However, we presently show that not all forms of top-down controls trigger pursuit eye movements in the same way. Finger tracking is unique, because even extremely predictable tracking stimuli do not initiate smooth pursuit as efficiently.

The neural bases of eye-hand coordination have been previously examined in primate lesion studies and in humans both with patient studies and through neuroimaging. Consistently, the evidence points to a role of the cerebellum in eye-hand coordination. Impaired coordination has been observed in patients with cerebellar lesions (Sailer et al. 2005), and cerebellar lesions degrade the tracking of hand movements in monkeys (Vercher and Gauthier 1988), as evidenced by increased pursuit latency and saccade rate. Functional MRI studies in healthy humans also found enhanced activities in the cerebellum during the execution of coordinated eye-hand movements (Miall et al. 2000, 2001). The cerebellum is likely part of a coordination control system that synchronizes the arm motor system and the oculomotor system. Another neural signature of eye-hand coordination was evidenced in studies showing that smooth pursuit eye movement modulates the excitability of the arm motor cortex, as estimated by transcranial magnetic stimulation (TMS) and motor evoked potentials (Hiraoka et al. 2014; Maioli et al. 2007). Evidently, smooth pursuit eye movements trigger the common coordination system that produces a covert manual tracking plan in the arm motor cortex.

Our second experiment shows that this strict eye-hand motor coupling acts on a trial-by-trial level. We recorded EEG while observers performed the finger tracking task. We analyzed our data at the level of single trials, aggregating subsamples of trials as well as the subject level. At all three levels the LRPs were predictive of pursuit latencies.

The LRP has been extensively documented as related to response activation for arm movements. It is generally assumed that it is generated in the primary motor cortex (e.g.,

Coles 1989; de Jong et al. 1988). Indeed, the lateralization is reversed for foot movements (Leuthold and Jentzsch 2002) due to the fact that the foot representation in the primary motor cortex is uncrossed. As for eye movements, studies failed to find cortical lateralized potentials before the start of saccades (van der Lubbe et al. 2000, 2006). Also, to our knowledge, this is the first study to examine the EEG during pursuit eye movements. When we had five observers track a visual target on the screen moving either to the left or to the right, we failed to observe any cortical lateralized potentials before the start of smooth pursuit eye movement. Therefore, oculomotor activity per se is not represented by the LRP. However, in the current experiment we found that the LRP is strongly predictive of the start of the smooth pursuit eye movements. This explains why the smooth pursuit of self-motion has less lag and fewer saccades compared with the pursuit of external motion, as we observed in *experiment 1* and previous studies (Gauthier and Hofferer 1976; Mather and Lackner 1980; Ross and Santos 2014; Scarchilli and Vercher 1999; Steinbach 1969; Steinbach and Held 1968; Vercher et al. 1995).

In the present study we observed a correlation between LRP and the pursuit latency in coordinated eye-hand movements. This study does not deal with the underlying causal relationship. On the one hand, it is likely that the motor command signal was fed to the oculomotor system via the cerebellum. On the other hand, it is also possible that a command control signal (e.g., signals from the cerebellum, or attention) triggers the hand movements and the smooth pursuit eye movements.

Conclusion

In the present study we examined the ocular tracking of intentional finger movements as well as external dot movements with identical trajectories. Enhanced performances in the pursuit of self-motion were observed, in terms of reduced pursuit latency and decreased rate of saccades, as well as reduced delay at reversal. Furthermore, by measuring EEG, we found that the LRPs of the finger movements were predictive of the onset of pursuit at a single-trial as well as cross-subject level while the finger movement onset was kept fixed. This result provides the first direct evidence supporting the notion that preparatory signals within the arm motor cortex are shared with the oculomotor system.

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DISCLOSURES

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

AUTHOR CONTRIBUTIONS

J.C., M.V., and K.R.G. conception and design of research; J.C. performed experiments; J.C. and M.V. 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.

ENDNOTE

At the request of the author(s), readers are herein alerted to the fact that additional materials related to this manuscript may be found at: <http://dx.doi.org/10.5281/zenodo.48651>. These materials are not a part of this manuscript and have not undergone peer review by the American Physiological Society (APS). APS and the journal editors take no responsibility for these materials, for the Web site address, or for any links to or from it.

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