PDF hosted at the Radboud Repository of the Radboud University Nijmegen

The following full text is a publisher's version.

For additional information about this publication click this link.
http://hdl.handle.net/2066/92546

Please be advised that this information was generated on 2019-04-15 and may be subject to change.
Behravioral/Systems/Cogntive

Visuomotor Coordination Is Different for Different Directions in Three-Dimensional Space

Julian J. Tramper and C. C. A. M. Gielen
Radboud University Nijmegen, Donders Institute for Brain, Cognition, and Behaviour, Department of Biophysics, 6525 EZ Nijmegen, The Netherlands

In most visuomotor tasks in which subjects have to reach to visual targets or move the hand along a particular trajectory, eye movements have been shown to lead hand movements. Because the dynamics of vergence eye movements is different from that of smooth pursuit and saccades, we have investigated the lead time of gaze relative to the hand for the depth component (vergence) and in the frontal plane (smooth pursuit and saccades) in a tracking task and in a tracing task in which human subjects were instructed to move the finger along a 3D path. For tracking, gaze leads finger position on average by 28 ± 6 ms (mean ± SE) for the components in the frontal plane but lags finger position by 95 ± 39 ms for the depth dimension. For tracing, gaze leads finger position by 151 ± 36 ms for the depth dimension. For the frontal plane, the mean lead time of gaze relative to the hand is 287 ± 13 ms. However, we found that the lead time in the frontal plane was inversely related to the tangential velocity of finger. This inverse relation for movements in the frontal plane could be explained by assuming that gaze leads the finger by a constant distance of ~2.6 cm (range of 1.5–3.6 cm across subjects).

Introduction

Gaze shifts in a natural environment require binocular eye movements with both directional and depth components. When playing tennis, a player has to track the ball with the eyes to estimate its movement direction in 3D space before he/she can hit the ball at the proper position at the proper time. This task requires ball tracking with conjugate (saccadic and smooth pursuit) and disconjugate (vergence) eye movements to adjust fixation to the ball at varying distances relative to the subject.

Almost all studies in eye–hand coordination have been done for movements in a frontal plane, implicitly assuming that the characteristics of eye–hand coordination are identical for all movement directions. Recently, Van Pelt and Medendorp (2008) tested the accuracy of pointing movements to remembered target positions and found that changes in vergence led to errors in memory-guided reaches that were based on the new eye position and on the depth of the remembered target relative to that position. These findings demonstrate that eye position affects hand position in pointing. This result and the finding that directional changes in gaze by saccades are much faster than depth changes in gaze (Chaturvedi and Gisbergen, 1998) raise the question as to whether eye–hand coordination during tracking a moving target or tracing a shape in 3D is similar for the directional and depth components.

When tracking an object moving in the frontal plane, the trajectories of the eye and hand almost superimpose, whereas the eye leads the hand during tracing a complex shape (Gielen et al., 2009). This illustrates that eye–hand coordination is task dependent, in agreement with previous observations that eye–hand coordination changes during learning (Sailer et al., 2005) and that directional and variable errors of the eye and hand change differently according to the task (Sailer et al., 2000).

To investigate any differences between eye–hand coordination in the frontal plane (only conjugate eye movements) and in depth (also requiring vergence eye movements), we have measured 3D eye movements of subjects in two eye–hand coordination tasks. These tasks used stimulus paths in the frontal plane and the same paths rotated along the horizontal axis inducing variations in depth. In the first task, subjects were asked to track a target moving along a curved 3D path with their finger. We investigated whether the observation that gaze almost perfectly follows a target moving in the frontal plane (Fuchs, 1967) also applies to the depth component for targets moving in 3D by presenting the same stimulus path in the frontal and oblique orientation. In the second task, subjects had to move their finger along a curved path in 3D. In this task, each new fixation point is located at a different depth, resulting in combined fast, conjugate saccades and disconjugate vergence eye movements. Based on the different dynamics for gaze changes in direction and in depth (Chaturvedi and Gisbergen, 1998), we expect differences in eye–hand coordination in the frontal plane and for eye–hand movements in 3D space.

Materials and Methods

Subjects. Five human subjects (three males) aged between 23 and 56 years participated in the experiment. All subjects were right-handed and had normal or corrected-to-normal visual acuity. None of the subjects had any known neurological or motor disorder. Furthermore, all subjects had participated in previous eye-tracking experiments with scleral coils.

Received Jan. 28, 2011; revised March 17, 2011; accepted March 31, 2011.

Author contributions: J.J.T. and C.C.A.M.G. designed research; J.J.T. performed research; J.J.T. analyzed data; J.J.T. and C.C.A.M.G. wrote the paper.

We thank Hans Kleijnen, Ger van Lingen, and Stijn Martens for valuable technical assistance. We are grateful to Martha Flanders for stimulating comments and discussions to improve the results and conclusions in this manuscript.

Correspondence should be addressed to Julian J. Tramper, Radboud University Nijmegen, Donders Institute for Brain, Cognition and Behaviour, Department of Biophysics, Geert Grooteplein-Noord 21, 6525 EZ Nijmegen, The Netherlands. E-mail: j.tramper@donders.ru.nl.

DOI:10.1523/JNEUROSCI.0486-11.2011

Copyright © 2011 the authors 0270-6474/11/317857-10$15.00/0

The Journal of Neuroscience, May 25, 2011 • 31(21):7857–7866 • 7857
were restrained by a helmet fixed to the chair. Cyclopean eye with the center of the projection area. Head movements to the screen. The height of the chair was adjusted to align the subject’s room (Fig. 1). The subject’s eyes were positioned at a distance of previously in a large magnetic field (Remmel Labs). The three orthogonal for any unintended head movements (see below).

An ired was placed at the tip of the right index finger, oriented toward the diodes (ireds) with an accuracy better than 0.15 mm in all dimensions. At an angle of 30°, to track the position of strobing infrared light-emitting ern Digital) at a sample frequency of 120 Hz. The Optotrak cameras were the inter-pupil distance and 70 cm for the distance to the screen. Were measured before the experiment. Typical distances were 6.5 cm for the distance between the eyes and the distance from the cyclopean eye in previous studies in the literature. For a subject-invariant perception of discrepancies between accommodation and vergence, the subjects had an instruction to move their finger along the shape with a velocity approximatly to depth, elevation, and azimuth, respectively.

Experiments. The experiment started with a calibration trial to calibrate the scleral coils. Subjects were instructed to fixate at 3 × 3 × 3 small spherical targets (radius of 3 mm) with a spacing of 15 cm along each axis, resulting in a total of 27 targets spanning a cube with a volume of 30 × 30 × 30 cm³. Its center was located at \( x = D = 25 \) cm, with \( D \) the distance between the subject’s cyclopean eye and the screen (≈70 cm). During the calibration, the frame of the cube was visible. Targets were sequentially presented from left to right, top to bottom, and front to back, starting at the upper left vertex of the frontal plane. Subjects had to fixate on the target, press a button, and maintain fixation for 1 s for sampling of the coil data.

Stimuli were presented in three blocks. In the first block of eight trials (trials 1–8), stimuli were presented in two different conditions (“tracking” or “tracing”), two different velocities (slow or fast), and two different orientations (frontal or oblique, rotated over 45°). In the tracking condition (trials 1, 3, 5, and 7), subjects were asked to track a dot (diameter of 1.7 cm at \( x = 70 \) cm) moving along an invisible 3D path with their right index finger. In the tracing condition (trials 2, 4, 6, and 8), the entire path (width of 0.8 cm at \( x = 70 \) cm) was visible and subjects were asked to trace the path with their right index finger at approximately the same speed as in the tracking condition. The path was defined by a so-called Cassini shape, given by the following:

\[
\begin{align*}
    x(t) &= a(1 + b \cos 2\omega t) \cos \omega t, \\
    y(t) &= b(1 + b \cos 2\omega t) \sin \omega t,
\end{align*}
\]

with \( D \) the distance between the subject’s cyclopean eye and the screen (70 cm), \( d = 30 \) cm, \( a = 20 \) cm, and \( b = 0.5 \). The dot started at the top and moved along this path in four cycles, with \( \omega = \frac{2\pi}{15} \) or \( \omega = \frac{2\pi}{10} \) rad/s, resulting in a movement duration of 15 s per cycle (slow trials: 1 and 5) or 10 s per cycle (fast trials: 3 and 7). Note that, for the tracing condition, there is no moving stimulus because the complete path is visible. Therefore, in the tracing condition (trials 2, 4, 6, and 8), subjects were instructed to move their finger along the shape with a velocity approximately equal to the velocity in the previous tracking trial. Equation 1 defines the frontal orientation with the path in the \( y-z \) plane (trials 1–4). The oblique orientation was obtained by rotating this path 45° left-handed along the \( z \)-axis (trials 5–8) such that the lower part of the Cassini shape is closer to the subject than the upper part. This transformation from the frontal orientation \((x, y, z)\) to the 45° tilted orientation \((x', y', z')\) is given by the following:

\[
\begin{align*}
    x'(t) &= \frac{x(t) + \sqrt{2} y(t)}{\sqrt[4]{2}}, \\
    y'(t) &= \frac{\sqrt{2} y(t)}{\sqrt[4]{2}}, \\
    z'(t) &= z(t).
\end{align*}
\]

In the second block of four trials (trials 9–12), the shape of the stimuli was given by a helix with four windings, two different orientations (long axis along the \( z \)- or \( x \)-axis) and two different sizes (small or large). All trials in this block were performed in the tracking condition, in which the

and reported that they had no problems in perceiving depth in the presented anaglyph stimuli. One subject (one of the authors) was aware of the purpose of the experiment, whereas the others were naive. All subjects gave informed consent. The experimental procedures were approved by the local Ethics Committee of the Radboud University Nijmegen.

Experimental setup. Subjects were seated in a chair with a high backrest in front of a 2.5 × 2 m² rear-projection screen in a completely darkened room (Fig. 1). The subject’s eyes were positioned at a distance of ≈70 cm to the screen. The height of the chair was adjusted to align the subject’s cyclopean eye with the center of the projection area. Head movements were restrained by a helmet fixed to the chair.

Visual stimuli were rear projected on the screen with an LCD projector (Philips ProScreen 4750) with a refresh rate of 60 Hz. The size of the computer generated image was 123 × 92 cm². A red–green anaglyph stereoscopic system was used to create a red and green copy of the stimulus. Subjects wore anaglyph stereo glasses with red and green filters to ensure that each eye received input from either the red or green stimulus, respectively. The disparity between the red and green images provided the perception of depth. Although the anaglyph stimuli produced discrepancies between accommodation and vergence, the subjects had an accurate percept of stimulus depth (see Figs. 4, 5), in agreement with previous studies in the literature. For a subject-invariant perception of the 3D stimuli, the perspective transformations had to take into account the distance between the eyes and the distance from the cyclopean eye to the screen. Therefore, inter-pupil distance and distance to the screen were measured before the experiment. Typical distances were 6.5 cm for the inter-pupil distance and 70 cm for the distance to the screen.

Finger position was measured with an Optotrak 3020 system (Northern Digital) at a sample frequency of 120 Hz. The Optotrak cameras were located at the upper right corner with respect to the subject, tilted down at an angle of 30°, to track the position of strobing infrared light-emitting diodes (ireds) with an accuracy better than 0.15 mm in all dimensions. An ired was placed at the tip of the right index finger, oriented toward the cameras. In addition, an ired was placed next to the right eye to control for any unintended head movements (see below).

Gaze was measured using scleral coils (Skalar) in both eyes simultaneously in a large magnetic field (Remmel Labs). The three orthogonal components of this magnetic field, with frequencies of 48, 60, and 80 kHz, were produced by a 3 × 3 × 3 m³ cubic frame. The subject’s head was fixated by a helmet in the center of the frame in which the magnetic field is most homogeneous. No instructions were given to the subject regarding eye movements during the experiment. The signals from both coils were filtered by a fourth-order low-pass Bessel filter (3 dB cutoff frequency at 150 Hz) and then sampled at 120 Hz.

To relate finger, gaze, and stimulus position to each other, a right-handed Cartesian coordinate system was defined (Fig. 1). Its origin was located at the subject’s cyclopean eye. The positive x-axis pointed forward, i.e., orthogonal to the screen away from the subject, the positive y-axis upward, and the positive z-axis in horizontal direction to the subject’s right. Note that the \( x, y, \) and \( z \) directions correspond approximatly to depth, elevation, and azimuth, respectively.

Figure 1. Experimental setup. Red-green anaglyph stimuli (123 × 92 cm²) were projected with an LCD projector (Philips ProScreen 4750) on a 2.5 × 2 m² rear-projection screen. The subject was seated in an adjustable chair to align the subject’s cyclopean eye with the center of the projection area, ≈70 cm in front of the screen. Finger movements were measured with an Optotrak 3020 system. A Cartesian coordinate system was defined with its center located at the subject’s cyclopean eye, its \( x \)-axis pointing toward the screen, its \( y \)-axis pointing upward, and its \( z \)-axis pointing in horizontal direction, to the subject’s right.

Visual stimuli were rear projected on the screen with an LCD projector (Philips ProScreen 4750) with a refresh rate of 60 Hz. The size of the computer generated image was 123 × 92 cm². A red–green anaglyph stereoscopic system was used to create a red and green copy of the stimulus. Subjects wore anaglyph stereo glasses with red and green filters to ensure that each eye received input from either the red or green stimulus, respectively. The disparity between the red and green images provided the perception of depth. Although the anaglyph stimuli produced discrepancies between accommodation and vergence, the subjects had an accurate percept of stimulus depth (see Figs. 4, 5), in agreement with previous studies in the literature. For a subject-invariant perception of the 3D stimuli, the perspective transformations had to take into account the distance between the eyes and the distance from the cyclopean eye to the screen. Therefore, inter-pupil distance and distance to the screen were measured before the experiment. Typical distances were 6.5 cm for the inter-pupil distance and 70 cm for the distance to the screen.

Finger position was measured with an Optotrak 3020 system (Northern Digital) at a sample frequency of 120 Hz. The Optotrak cameras were located at the upper right corner with respect to the subject, tilted down at an angle of 30°, to track the position of strobing infrared light-emitting diodes (ireds) with an accuracy better than 0.15 mm in all dimensions. An ired was placed at the tip of the right index finger, oriented toward the cameras. In addition, an ired was placed next to the right eye to control for any unintended head movements (see below).

Gaze was measured using scleral coils (Skalar) in both eyes simultaneously in a large magnetic field (Remmel Labs). The three orthogonal
complete path of the helix was visible. Subjects were asked to follow the shape back-and-forth three times. A helix with the z orientation (trials 9 and 11) had its long axis along the z-axis, and the data points of the helix were defined by the following:

\[
x(t) = \begin{pmatrix} D + r \cos s \\ r \sin s \\ q - \frac{ps}{2\pi} \end{pmatrix}, \quad (0 \leq s \leq 8\pi),
\]

with \(D\) the distance between the subject’s cyclopean eye and the screen (70 cm), \(p = 9\) cm (pitch) and \(q = 18\) cm. Helices with the long axis along the x-axis (trials 10 and 12) were obtained by swapping the x- and z-axis and setting \(q = -12\) cm. For both orientations, the small helix was defined by \(r = 6\) cm (trials 9 and 10) and the large helix by \(r = 10\) cm (trials 11 and 12). In this block, no particular instructions on finger velocity were given. However, it is known that the tracing velocity decreases as curvature increase (Lacquantini et al., 1983). Therefore, the radius of the helix implicitly imposes the finger velocity, resulting in slow trials (trials 9 and 10) and fast trials (trials 11 and 12).

The last block of eight trials (trials 13–20) was identical to the first block, except that the stimulus shape was given by a Limaçon shape instead of a Cassini shape. The Limaçon shape in the frontal orientation (trials 13–16) was defined as follows:

\[
x(t) = \begin{pmatrix} D - d \\ r \sin \omega t + \frac{u}{2} \sin 2\omega t \\ \frac{u}{2} + v \cos \omega t + \frac{u}{2} \cos 2\omega t \end{pmatrix}, \quad (4)
\]

with \(D\) the distance between the subject’s cyclopean eye and the screen (70 cm), \(d = 30\) cm, \(u = 20\) cm, and \(v = 10\) cm. The oblique orientation (trials 17–20) was obtained by rotating this path 45° left-handed about the z-axis (Eq. 2).

Each experiment took –40 min including the application of eye coils and infrared markers (8 min), instructions (2 min), calibration (3 min), first block with trials 1–8 (10 min), second block with trials 9–12 (5 min), third block with trials 13–20 (10 min), and removing of eye coils and markers (2 min).

Data calibration. The Optotrak system measures the 3D coordinates of the markers in Optotrak coordinates. The transformation into the laboratory coordinates [i.e., the same coordinate system defined for the stimuli (see Fig. 1)] involves a rigid body transformation, which translates the origin of the Optotrak coordinate system to the origin of the laboratory coordinate system and rotates the Optotrak coordinate axes to align with the laboratory coordinate axes. A procedure described by Challen (1995) was used to determine the rigid body transformation parameters (i.e., a rotation matrix and a translation vector).

Precise mapping of gaze position requires calibration of the eye coils. Commonly, a neural network is trained to obtain a proper mapping of gaze to hand position. Precisely, let \(y_h\) be the position of the hand for the specific gaze position \(y_g\) and let \(y_h = f(y_g)\). In addition, let \(y_h = (x, y, z)\) be the hand position in 3D space. Assume that the subject is in a fixed position with respect to the camera system. Then, for each gaze position \(y_g\), the corresponding hand position \(y_h\) can be determined. However, this mapping is not perfect due to various factors such as calibration errors, head movements, or occlusions. To account for these errors, a regression model is used:

\[
y_h = f(y_g)\]

The regression model is typically learned using a training set of gaze and hand positions. Once the model is trained, it can be used to predict the hand position for any given gaze position. This is particularly useful in applications such as virtual reality or augmented reality, where precise mapping of gaze to hand position is required.
If we assume a constant fixation time between saccades, the saccadic lead time equals half the fixation time (i.e., \( \tau_{\text{fix}} = \frac{1}{2} t_{\text{fix}} \)), because this corresponds to the time shift that gives the best overlap between gaze and finger position (Fig. 3a, dashed line). Similarly, if there would be one single fixation with a duration \( t^1_{\text{fix}} \) its corresponding individual saccadic lead time \( t^1_{\text{sac}} \) would be equal to \( \frac{1}{2} t_{\text{fix}} \). In general, fixation times are not constant. To find an average saccadic lead time \( \tau_{\text{sac}} \) of a trial, each individual saccadic lead time \( t^i_{\text{sac}} \) should be weighted according to the corresponding fixation time \( t^i_{\text{fix}} \), resulting in the following:

\[
\tau_{\text{sac}} = \frac{\sum t^i_{\text{sac}} t^i_{\text{fix}}}{\sum t^i_{\text{fix}}} = \frac{1}{2} \sum t^i_{\text{fix}},
\]

which simplifies to \( \tau_{\text{sac}} = \frac{1}{2} t_{\text{fix}} \) if all fixations have the same duration \( t_{\text{fix}} \).

Next, we extend the model by assuming an additional lead time \( \tau_0 \) (Fig. 3b). Thus, each saccade at time \( t \) brings gaze to a new position that is equal to the gaze position at time \( t + t_{\text{fix}} + \tau_0 \). This implies that gaze jumps to a new position before the finger has reached the previous gaze position.

Figure 3b shows that, in this model, the total lead time \( \tau_{\text{tot}} \) is equal to the saccadic lead time plus \( \tau_0 \). We will call \( \tau_0 \) the primary lead time.

The model described above gives us the total lead time but is insufficient to quantify the contribution of the saccadic and primary lead time.

**Effect of finger velocity on primary lead time.** The analyses described in the previous section provide the total lead time of gaze relative to finger position and its two components: a saccadic lead time, which is a function of the fixation times between saccades, and a primary lead time. Although the primary lead time is independent of fixation time, it may depend on finger velocity (Gielen et al., 2009). Therefore, we propose two hypotheses regarding the effect of finger velocity on the gaze–finger lead time. Our null hypothesis is that the primary lead time is constant and independent of finger velocity. Alternatively, we hypothesize that gaze leads the finger by a constant distance. Therefore, we plotted the primary lead time as a function of mean tangential finger velocity.

If the latter hypothesis is true, the primary lead time \( \tau_0 \) is equal to lead distance \( \Delta z \) divided by the mean tangential finger velocity, and, therefore, the primary lead time \( \tau_0 \) as obtained from the cross-correlation should decrease for higher tangential finger velocities. We applied three different methods to obtain an estimate for \( \Delta z \). The mean lead distance was obtained by fitting \( \tau_0 = \frac{\Delta z}{v} \) for each subject by variation of \( \Delta z \) (method I).

We used the bootstrap method (\( n = 100 \)) to compute the SD. In a second approach, we calculated \( \Delta z = v \tau_0 \) for each trial, which gives the mean lead distance and SD for each subject and for all data (method II). In addition, we determined the lead distance directly for every trial as the mean distance between gaze and finger position at each saccade onset (method III). We used a two-sample \( t \) test at the 5% significance level to test for significant differences between the lead distance distribution obtained by methods I and II and a Mann–Whitney \( U \) test at the 95% significance level to test for significant differences between methods I and III and between methods II and III.

**Results**

**Behavior during tracking**

Figure 4a shows a quasi 3D view of stimulus (dashed line), gaze (gray line), and finger position (solid black line) for subject S5 tracking a target moving along the oblique Cassini shape. The dashed line is hard to distinguish from the solid line because of the almost perfect tracking by the subject. Figure 4b–d shows the corresponding frontal, top, and side views, respectively, for one repetition of the stimulus. In the tracking condition, gaze follows the moving target quite well by smooth pursuit in three dimensions. Gaze and finger trajectories deviate more from the stimulus path in the depth direction (\( x \)) than in the frontal direction (\( y \) and \( z \); Fig. 4, compare b, c). In addition, gaze occasionally deviates from the target during blinks and small saccades. Data in Figure 4 are representative for all subjects.

Figure 4e–g shows the corresponding time traces of stimulus (dashed line), gaze (gray line), and finger position (solid black line) for the \( x \), \( y \), and \( z \) components, respectively. The time traces show that gaze is superimposed almost perfectly on hand position in the \( y \) and \( z \) directions. In the \( z \) direction (depth; Fig. 4e), the noise is larger than in the \( y \) and \( z \) directions as a result of small errors in measurement and calculation of vergence (see Materials and Methods). These results demonstrate that subjects are able to perceive the anaglyph stimuli correctly and that they have an accurate percept of the position of the moving target in 3D. In addition, the time traces show that gaze leads finger position by a small amount of time. This will be quantified in more detail later.

**Behavior during tracing**

Figure 5a shows a quasi 3D view of stimulus (dashed line), gaze (gray line), and finger position (solid black line) of the same subject (S5) for tracing the very same shape as in Figure 4. Figure 5b–d shows the corresponding frontal, top, and side views, respectively. For tracing, the azimuth and elevation components of gaze move along the completely visible shape by a sequence of saccades. During a saccade, gaze deviates from the stimulus path as a result of transient divergence (Fig. 5c,e). This divergence originates from an asymmetry between abducting and adducting saccadic eye movements. Because the abducting eye has a higher acceleration in a horizontal saccade and is on-target somewhat earlier than the adducting eye, the binocular fixation point shows an outward-looping trajectory in depth during a saccade (Collewijn et al., 1997). In the \( x \) direction (depth), these deviations can be as large as 5 cm for large saccades and are disproportionately
The fingers are shifted by interpolated by a cubic spline (dashed line). Maximum overlap between this dashed line and finger position occurs when finger position is shifted by a time maximum overlap between gaze and finger position, which corresponds to the time of the peak of the cross-covariance function.

**Figure 3.** Schematic illustration of the analysis to calculate lead time of gaze relative to hand. a. Graphical representation of one directional component of gaze position (gray line) and finger position (solid black line) while tracing a circle in the frontal (y–z) plane at a constant velocity. \( \tau_y \) is the subject’s fixation time between saccades, which is constant in this example. In that case, maximum overlap between gaze and finger position, which corresponds to the time of the peak of the cross-covariance function between gaze and hand position, occurs when finger position is shifted by a time \( \tau_y \), indicated by the dashed line. b. Same as a, but now gaze position leads hand position by an additional time \( \tau_0 \). Maximum overlap occurs when finger position is shifted by a time \( \tau_{ext} = \tau_y + \tau_0 \) toward the left (dashed line). c. Same as b, but the saccade onsets (gray dots) are interpolated by a cubic spline (dashed line). Maximum overlap between this dashed line and finger position occurs when finger position is shifted by \( \tau = \tau_0 \).

**Figure 4.** Stimulus (dashed line), gaze (gray line), and finger position (solid black line) of subject S5 tracking the oblique Cassini shape. Data of one cycle are shown. (a) Quasi 3D view (a), frontal view (b), top view (c), and side view (d). e–g show the corresponding time traces for x, y, and z direction, respectively.

**Lead times in gaze–finger coordination**

As explained in Materials and Methods, the time of the peak of the cross-covariance between gaze and finger position gives a measure of the mean lead time of gaze relative to finger position. Figure 6a shows the mean lead time of gaze relative to the finger (corresponding to time of peak of the cross-covariance function) in the y and z direction (top panel) and depth (x) direction (bottom panel). Data of all subjects are shown, but only trials with the Cassini and Limaçon stimulus shapes are included (no helices). Squares and circles in Figure 6a represent the lead times for the frontal and oblique stimulus orientations, respectively. The lead times shown here represent the total lead time (Fig. 3b). The lead times of gaze relative to the finger for the components in the frontal plane are not significantly different for the frontal and oblique stimulus orientations. This means that any depth components in the path do not affect the lead times for the components of gaze and hand in the frontal plane. We also tested whether lead times in the y and z direction (top panel) were different for Cassini and Limaçon shapes with the frontal orientation (squares) versus the shapes with the oblique orientation (circles). We did not find a significant difference (Mann–Whitney U test, \( p = 0.34 \)).

When saccades are involved in eye–hand coordination like in tracing, the time of the peak of the cross-covariance function depends on the fixation time between saccades and may depend on...
the velocity of tracing. To investigate this in detail, Figure 6b shows the same data as in Figure 6a, but lead times of trials with the helices as stimulus shape are included as well. Different gray symbols refer to data from different subjects. For the y and z directions (frontal plane), there is a significant correlation between lead time and tangential finger velocity ($r = -0.72, p < 0.01$) (Fig. 6b, top). This correlation is not significant in depth ($p = 0.91$) (Fig. 6b, bottom). Thus, a lower tracing velocity of the finger results in a larger lead time of gaze with respect to finger for the frontal plane but not for the depth direction. The mean ± SE gaze–finger lead time is $287 \pm 13$ ms ($n = 84$) in the frontal plane and $151 \pm 36$ ms ($n = 28$) in depth (Fig. 7). The difference between the lead times in the frontal plane and depth is significant ($p < 0.01$).

These results for tracing are different from the results obtained for tracking. For tracking, we calculated the lead time of gaze relative to finger position, of target relative to gaze position, and of target relative to finger position, in the frontal and the depth direction (Fig. 8). We subdivided the lead times in the frontal plane into trials for shapes in the frontal orientation (Fig. 8, squares) and in the oblique orientation (circles). Because we did not find a significant difference between frontal and oblique stimulus orientation (Mann–Whitney $U$ test, $p > 0.1$) for all three lead times, data for both stimulus orientations were pooled. We calculated the correlation between the lead time of gaze relative to finger and mean tangential finger velocity for the frontal and depth directions. For both directions, this correlation was small and did not appear to be significant ($r = -0.12, p = 0.37$ for the frontal direction and $r = -0.35, p = 0.22$ for the depth direction). We also calculated the lead times averaged over all trials and subjects for the frontal and the depth direction. In the tracking condition, gaze and finger lag behind the moving target. For gaze, the mean ± SE delay is $51 \pm 4$ ms ($n = 60$) in the frontal plane and $140 \pm 57$ ms ($n = 14$) in depth. For the finger, the mean ± SE delay is $80 \pm 4$ ms ($n = 60$) in the frontal direction and $67 \pm 22$ ms ($n = 14$) in depth. As a result, gaze leads the finger on average by $28 \pm 6$ ms ($n = 60$) in the frontal plane but lags behind the finger by $95 \pm 39$ ms ($n = 14$) in depth. The mean lead times of gaze relative to the finger in the tracking condition are significantly different from the mean lead times in the tracing condition ($p < 0.01$) both for the frontal and depth components (Fig. 7). In Discussion, we will further elaborate on these findings.

**Effect of saccades on gaze–finger timing**

In the previous section, we have shown that the lead time between gaze and finger position for tracking is on average 287 ms in the frontal direction (Fig. 7) and that this lead time varies with tangential finger velocity in the frontal plane (Fig. 6b, top). Moreover, the mean lead time for the frontal direction is significantly different from the value for depth (151 ms) (Fig. 7). In this section, we will investigate the effect of saccades on the relative timing of gaze and finger position.

As illustrated in Figure 3, we hypothesize that the lead time of gaze relative to the finger in the frontal direction in the tracing condition is a combination of a saccadic lead time and a primary lead time. To test this hypothesis, we interpolated all saccade onsets with a cubic spline, as illustrated in Figure 3c. Next, we calculated the mean gaze–finger lead time from the cross-covariance between the spline function and finger position for the frontal direction. The results are shown by the symbols in Figure 6c. Different symbols refer to data from different subjects. Figure 6c gives the primary lead time as a function of tangential finger velocity in the frontal plane. The mean ± SE value for the primary lead time is $166 \pm 12$ ms, which is significantly smaller (Mann–Whitney $U$ test, $p < 0.01$) than the total mean lead time (287 ms) (Fig. 6b, top) of gaze relative to finger in the tracing condition. The correlation between primary lead time and finger velocity is significant ($r = -0.61, p < 0.01$).
In the previous section, we found that the gaze–finger lead time in depth is 151 ± 36 ms (mean ± SE), which is significantly different from the total lead time of 287 ± 13 ms in the frontal direction (Fig. 7, first two bars). However, after correction for the saccadic lead time, the mean primary lead time in the frontal direction is 166 ± 12 ms, which is not significantly different from the mean lead time in depth (Mann–Whitney U test, 9 = 0.71).

The difference between total lead time (Fig. 6b) and primary lead time (Fig. 6c) corresponds to the saccadic lead time (method I). Table 1 shows the saccadic lead time in milliseconds. Values are given as mean ± SD over all tracing trials. The saccadic lead time for the five subjects ranges from 93 to 142 ms. Figure 9 shows the histograms of the fixation times for all trials per subject (S1–S5), as well as the distribution of fixation times for all subjects. The solid and dashed lines in each histogram indicate the median and mean value, respectively. The median fixation times for the five subjects range from 233 to 267 ms. As explained in Materials and Methods, the saccadic lead time is related to the length of the fixations in a trial (Eq. 6). As a check for consistency, we have also calculated the saccadic lead time from the individual fixations in each trial according to Equation 5 (Table 1, method II). For this method, the saccadic lead time for the five subjects ranged from 119 to 169 ms, which is larger than the corresponding lead times found by method I. This difference is significant (Mann–Whitney U test, 9 = 0.71) for subjects S2, S4, and S5 and for all subjects pooled. We will give an explanation for this difference in Discussion.

The general notion in the literature is that gaze leads finger position in time. Our null hypothesis was that this lead time should be constant and independent of velocity of the finger, yet, after correction for the saccadic lead time, we still find a significant negative correlation between the gaze–finger lead time and mean finger velocity. The data in Figure 6c suggest an inverse relationship between lead time and tangential finger velocity. This inverse relationship is qualitatively in agreement with the hypothesis that gaze leads finger position by a constant displacement. This predicts \( \tau_v = \frac{\Delta S}{\nu} \), where \( \tau_v \) is the primary lead time, \( \Delta S \) is the mean lead distance of gaze relative to finger position, and \( \nu \) is the tangential finger velocity.

To test the hypothesis that gaze leads the finger by a constant displacement, we fitted the relation \( \tau_v = \frac{\Delta S}{\nu} \) to the data in Figure 6c by varying \( \Delta S \). The best fit over all subjects for the primary lead time is shown by the solid line in Figure 6c and corresponds to a mean ± SD lead distance of 2.6 ± 0.1 cm. Fits for each subject separately reveal that the range of lead distances is between 1.5 and 3.5 cm (Table 2, method I).

Another method to determine the mean lead distance of gaze relative to finger is to calculate \( \Delta S = \nu \tau_v \) using the primary lead time and the mean tangential velocity of each trial. The results
demonstrate that the mean ± SD lead distance of gaze relative to finger position in the frontal plane for the tracing condition is 2.6 ± 1.4 cm with a range between 1.7 and 3.6 cm for all subjects (Table 2, method II). For subjects S2, S4, and S5 and for the pooled dataset, the lead distance found by this method is close to the value obtained by the best fit to the data (method I) and is not significantly different from the value obtained by the best fit.

Alternatively, the lead distance is obtained directly by calculating the distance between gaze and finger position at each saccade onset for all tracing trials. The median lead distance obtained by this method has a range between 2.2 and 3.9 cm (Table 2, method III). Compared with method II, method III gives significant differences for subjects S2 and S3 and for the pooled dataset. Compared with the value obtained by the best fit (method I), method III yields significantly different results for the mean lead distance for all subjects, except subject S5. The median values obtained by method III are smaller (range of 2.2–3.9 cm) than the mean values (range of 2.9–4.2 cm; see Discussion). The analyses indicate that not lead time, but lead distance, is approximately constant, resulting a lead time that is inversely proportional to the finger velocity.

Discussion

The dynamics of saccades and smooth pursuit, which are involved in the control of gaze in the frontal plane, are very different from that of the vergence system. This led us to suggest that the lead time of gaze relative to the finger is different in the frontal plane and in depth. Our results revealed that the lead time of gaze relative to the finger was not constant for tracing but inversely related to tangential velocity of the hand. The lead time is relatively large (~500 ms) for small velocities and decreases to ~200 ms for finger velocities of ~30 cm/s (Fig. 6b). After correction for a saccadic lead time, the remaining lead time still decreases inversely with finger velocity (Fig. 6c). Our results can be explained by assuming that gaze leads finger position by a constant distance of ~2.6 cm.

The lead time of gaze relative to the finger was obtained from the cross-covariance between gaze and finger position. Because the lead time of gaze varied with tangential velocity and because the tangential velocity varied along the Cassini and Limaçon shapes, the peak of the cross-covariance reflects the mean lead time over a range of velocities in a trial.

For tracing, the gaze–finger lead time has two components: a saccadic and a primary lead time. The saccadic lead time reflects the contribution of saccades to the total lead time and therefore depends on the fixation time between saccades. We estimated the saccadic lead time by taking the difference between total lead time and primary lead time (method I) and from the individual fixation times according to Equation 5 (method II). The values found by method II are larger than for method II (Table 1). This difference can be explained by considering Figure 3a. In this figure, the fixation end points (or saccade onsets) are located exactly at the finger position curve (black line). However, in general, the fixation end points will not perfectly superimpose on the finger position trace because of measurement errors, motor noise, and limited pointing accuracy of the subject. As a consequence, the fixation duration of a particular fixation will be slightly shorter or longer compared with the hypothetical situation in Figure 3a. Assuming that the difference between the measured and hypothetical fixation time is ±ε with equal probability, Equation 5 becomes

$$\tau_{\text{frac}} = \frac{1}{2} \sum (t_{\text{fix}}^i - \epsilon)^2 + Ne^2$$

with $N$ the number of fixations. This equation shows that the saccadic lead time estimated from detected fixations is biased toward larger values (because of the term $Ne^2$). However, the noise does not affect the value of the saccadic lead time obtained by cross-covariance (method I). Thus, methods I and II give the same results only if the fixation end points exactly superimpose on the finger position (Fig. 3a) or on the finger position shifted in time (Fig. 3c). If not, method II will yield systematically larger saccadic lead times than method I.

The distribution of measured fixation times (Fig. 9) reveals a sharp peak for values <250 ms with a mean value exceeding 250
might imply a more rapid sequence of saccades with shorter intervals. If so, the inverse correlation between lead time of gaze and finger velocity might be an artifact of the inverse correlation between finger velocity and fixation time. To investigate this in more detail, we calculated the correlation between finger velocity and fixation duration for each subject. This correlation appeared to be small (range of 0 to 0.3). In addition, we did not find a significant correlation between mean fixation interval and mean finger velocity (\( p > 0.3 \)). Finally, the mean finger velocity was not significantly correlated to the number of saccades per second. Therefore, we conclude that our result of an inverse relation between lead time and tangential hand velocity is not an artifact of a hidden correlation between hand velocity and saccade frequency.

The results in Figure 7 show that the mean lead times for tracking of gaze relative to the finger (28 and 95 ms for the frontal plane and depth, respectively) are much smaller than the corresponding lead times for tracing. In addition, Figure 5 shows that gaze position deviates from the stimulus shape more for depth than for direction in the tracing condition. This is not attributable to an erroneous percept of stimulus depth. The almost perfect match between stimulus position, gaze, and finger position for tracking indicates that subjects perceive the anaglyph stimulus quite well. Because the complete stimulus is visible in the tracing condition, it is highly unlikely that the percept of the stimulus path is inferior in the tracing condition. The less accurate match between stimulus path and gaze position in depth is in agreement with previous studies (Admiraal et al., 2003, 2004), which have shown that fixation accuracy on targets is less when visual information is available on target position relative to the environment, especially for the depth component. Moreover, Gonzalez et al. (1998) reported that the perceived depth of random dot stereograms is not affected by vergence, which suggests that imperfections of gaze in depth do not affect the accuracy of pointing in depth.

After correction for the saccadic lead time, we found a mean primary lead time of gaze relative to the finger in the frontal plane, which is close to the lead time for depth (166 and 151 ms, respectively). This might suggest that the underlying mechanisms may be similar. This is not true because the lead time of gaze varies with tangential finger velocity in the frontal plane but not for depth. Moreover, the different results for tracking (i.e., a lead time of gaze of 28 ms in the frontal plane but a lag of 95 ms in depth) suggest different mechanisms for tracking in the frontal plane and in depth.

Our results clearly demonstrate differences in the coordination of gaze and finger position for the frontal plane and depth. There is some evidence from the literature supporting this result. For example, several studies have demonstrated that direction and depth are processed separately as independent variables during updating across eye movements (Ghez et al., 1997; Henriques et al., 1998; Van Pelt and Medendorp, 2008). Moreover, there is evidence that target depth and direction are processed in functionally distinct visuomotor channels (Flanders et al., 1992; DeAngelis, 2000; Cumming and DeAngelis, 2001; Vindras et al., 2005). Another difference is that gaze leads finger position in the tracking condition by 28 ms in the frontal plane but lags behind the finger in depth by 95 ms. Although the lag between target and gaze depends on the predictability of the moving target (Collewijn and Tammers, 1984), it seems highly unlikely that anticipation or predictability would be different for the frontal plane and for depth. It is also highly unlikely that the velocity of the moving target or the finger velocity (typically \( <30 \text{ cm/s} \), corresponding to \( \sim 15^\circ/\text{s} \) in this study) is too fast for the vergence

For all subjects, the mean value exceeds the median value. This can be attributed to the fact that fixation times can only be positive. Therefore, any outliers correspond to large positive values, which implies that the mean value is biased toward larger values. This positive bias also affects the median value but to a smaller extent.

Another consideration is that finger velocity and saccade interval might be related. For example, a higher movement velocity...
system to track. This follows from results by Erkelens et al. (1989), who showed that errors between gaze and a moving target are <1° in the depth direction for movement velocities in the range between 10 and 40°/s. Therefore, we conclude that the different lead time of gaze relative to the finger for the frontal plane and for depth reflects differences in the dynamics of visuomotor control for version and vergence.

The results of our study suggest that feedforward and (internal) feedback transformations, which are thought to be part of the servo-control system for eye–hand coordination (Wolpert et al., 1995), should not only deal with time delays in internal and sensory feedback loops but also with spatial aspects. The latter seems obvious, but our study is the first to demonstrate that the visuomotor transformations generate a constant lead of gaze in space by ~2.6 cm. This distance is relatively small and may be a compromise between a distance that which is small enough to have a sharp percept of target and finger position and long enough for planning the finger trajectory. If the aim is to lead the finger such that both the target and finger position are sharply represented on the retina, then it might be retinal eccentricity rather than distance in space that is relevant. In that case, the distance of 2.6 cm, which corresponds to ~2° in our study, will become smaller or larger if the distance of the stimulus shape is nearer or farther away, respectively.

References