

Target motion direction influence on tracking performance and head tracking strategies in head-unrestrained conditions

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We examined subjects' behavior when they tracked periodic oscillating targets moving along a randomly oriented ramp with the head free to move. This study focuses on the effect of target motion direction on pursuit performance and on head tracking strategies used by human subjects to coordinate eye and head movements. Our analyses revealed that the gaze tracking gain was modulated by both target oscillation frequency and target motion direction. We found that pursuit gain was modulated by the target motion direction: vertical pursuit being less accurate than horizontal pursuit. While gaze tracking was sensitive to target frequency and orientation, head behavior was less modulated by a change of target frequency than by a change of target motion direction. Additionally, subjects had two main strategies for moving their head: They oriented their head to favor rotations around either the head dorsoventral (target motion directions $<20^\circ$) or mediolateral axis (target motion directions $>70^\circ$). In between, the subjects did not choose a consistent rotation axis for identical target motion directions.

Keywords: eye–head coordination, head-free, head-unrestrained, pursuit eye movements

Citation: Daye, P. M., Blohm, G., & Lefevre, P. (2012). Target motion direction influence on tracking performance and head tracking strategies in head-unrestrained conditions. *Journal of Vision*, 12(1):23, 1–12, <http://www.journalofvision.org/content/12/1/23>, doi:10.1167/12.1.23.

Introduction

Humans use combined eye–head movements (called gaze movements, gaze = eye in space = eye in head + head in space) to track moving targets and to keep the object of interest on the fovea. Two categories of movements are used to ensure clear vision while tracking an object: smooth pursuit and saccadic movements. The main purpose of pursuit is to compensate for any gaze–target velocity mismatch while saccades cancel any position error between the moving object and current gaze position. In head-restrained conditions, differences have been reported between horizontal and vertical movements during smooth pursuit. Rottach et al. (1996) reported a smaller gain for the vertical pursuit than for the horizontal pursuit. Similarly, using 2-D target trajectories generated

from Lissajou curves, Kettner, Leung, and Peterson (1996) and Leung and Kettner (1997) showed that the gain of the vertical component of a pursuit movement was smaller than the gain of the horizontal component. To our knowledge, the pursuit system has only been studied for cardinal directions in head-unrestrained conditions (Barnes & Grealy, 1992; Collins & Barnes, 1999; Lanman, Bizzi, & Allum, 1978). Only a few studies addressed the issue of eye–head coordination in two dimensions (Daye, Blohm, & Lefevre, 2010; Goossens & Van Opstal, 1997). Additionally, no study has ever analyzed the influence of target motion direction on pursuit performances in head-unrestrained conditions.

With the head free to move, the central nervous system (CNS) faces several challenges that make the control of head-free movements not a straightforward extension of head-fixed movements. First, it has to account for the

different dynamics of the eyes and head to correctly compute the motor commands and, therefore, to accurately control gaze trajectory. Second, a similar gaze trajectory can be executed by an infinite number of eye and head movements as long as their sum remains identical. Third, with the head free to move, the system must account for the vestibulo-ocular reflex that normally counter-rolls the eye in the orbit to stabilize gaze in space. Fourth, activation and coordination of the neck muscles is a challenging process for the brain. There are more muscles to orient the head–neck mechanical system than its number of degrees of freedom: The system is over-complete (Pellionisz, 1988). This means that several patterns of neck muscle activation can theoretically lead to a similar head trajectory. Finally, one can decide to move one's head faster, slower, or along a different trajectory, but the gaze must remain on the target to ensure a proper tracking of the visual target. Therefore, if gaze and head movements usually have similar trajectories, they can also be controlled independently (Collins & Barnes, 1999).

The present study investigates how the CNS coordinates eye and head movements while tracking a target moving along a randomly oriented straight trajectory with a sinusoidal velocity. A predictive protocol was chosen to generate target movements with a high velocity, hence increasing the contribution of the head during the gaze movement.

First, we confirmed the observations of Collins and Barnes (1999) about the decrease of head and gaze tracking performances with an increase of target frequency, independently of target motion direction. Then, we generalized the previously observed head-restrained pursuit strategies (Kettner et al., 1996; Leung & Kettner, 1997; Rottach et al., 1996) regarding higher ocular tracking performance for horizontal target movement compared to vertical target movement to the head-unrestrained condition. Next, because the same gaze trajectory can be composed of several eye and head contributions, we looked at the influence of target motion direction on gaze and head trajectories. Finally, we analyzed the head tracking strategies used by subjects; did they orient their head to follow target motion direction or to follow a predefined pattern? We found that for oblique target motions the subjects did not use a consistent head axis of rotation for identical target motion directions while they consistently favored dorsoventral rotations for close to horizontal target motion directions and mediolateral for close to vertical target motion directions.

Methods

Experimental setup

Human subjects sat in front of a 1-m distant translucent tangential screen in a completely dark room after giving

informed consent. None of the eight subjects (4 males, 4 females, aged 22–32 years) had any known oculomotor abnormalities. Three subjects (nos. 1 to 3) were completely naive about oculomotor research and five subjects (nos. 4 to 8) were knowledgeable about general oculomotor studies. All procedures were approved by the Université Catholique de Louvain Ethics Committee, in compliance with the Declaration of Helsinki.

The screen spanned ± 40 deg of the horizontal and vertical visual fields. Two laser spots (0.2-deg diameter, red and green) were back-projected onto the screen. A dedicated real-time computer (PXI-8186 RT, National Instruments, Austin, Texas) running LabView (National Instruments, Austin, Texas) controlled the position of the targets (sampled at 1 kHz) via mirror galvanometers (GSI Lumonics, Billerica, LA). Horizontal and vertical eye movements were recorded at 200 Hz by a Chronos head-mounted video eye tracker (Chronos Vision, Berlin, Germany). Any relative movement between the eyes and the Chronos helmet leads to a loss of accuracy of the eye movement recordings and must be avoided. To that goal, a bite bar was mounted onto the Chronos frame to prevent any slippage of the helmet during head movements. Two 3-D optical infrared cameras (Codamotion System, Charnwood Dynamics, Leicestershire, UK) measured (at 200 Hz) the position of a set of six infrared light-emitting diodes (IREDs) mounted onto the Chronos helmet. The position and the orientation of the head were computed offline from the position of the IREDs.

Paradigm

A recording session was composed of eight blocks of twenty-five trials. The paradigm used in this study corresponds to the first part of the paradigm described in Daye et al. (2010). Briefly, after a 500-ms fixation at the center of the screen (initial fixation), the red laser started to move along a randomly oriented straight line with a sinusoidal velocity at a random frequency ($[0.6 \dots 1.2]$ Hz) and random amplitude (peak to peak position $[40 \dots 60]$ deg) for a random duration ($[3000 \dots 3750]$ ms). Parameters were randomized in a continuous fashion (uniform distribution) between the specified boundaries. The target made between 1.8 and 4.5 cycles of motion within the range of duration and frequency used in the paradigm. Around the end of the red target motion, a second green target was briefly presented (duration: 10 ms) at a random position inside a virtual annulus with an inner radius of 15 deg and an outer radius of 30 deg. The trial ended with a fixation at the center of the screen for 500 ms. Subjects were instructed to track the red target with a combined eye–head movement during the pursuit part of the protocol. As soon as they saw the green target, they had to look at its position. We were only interested in the pursuit component of this paradigm; orienting toward the green target was analyzed elsewhere (Daye et al., 2010).

Calibration

The calibration procedure has been described in detail in Daye et al. (2010). In summary, three calibration blocks were performed during a recording session: one at the start of the experiment, one midway through the session, and one after the last experimental block of trials. The calibration procedure allowed the reconstruction of the gaze (i.e., gaze = eye orientation with respect to a space-fixed reference frame) from the IRED position and the eye-in-head orientation measured by the Chronos (Ronsse, White, & Lefevre, 2007). Gaze and head orientations were computed as described in Daye et al. (2010).

Data analysis

Eye and IRED positions were stored on a computer hard drive for offline analysis. All the analysis algorithms were implemented in Matlab (The MathWorks, Natick, MA). Position signals were low-pass filtered (cutoff frequency: 50 Hz) by a zero-phase digital filter. Velocity and acceleration were derived using a central difference algorithm on a ± 10 ms window. Two coordinate systems were used in the analyses. One corresponds to the horizontal and vertical axes of the screen. In the second coordinate system, the movement was decomposed into the direction parallel (X -axis in text and figures) or perpendicular (Y -axis) to the target motion. In this coordinate system, each target moved horizontally and started its movement to the right.

Gaze saccades were detected using a generalized likelihood ratio (GLR) algorithm as in Daye et al. (2010). Every trial was visually inspected; a manual correction of the detection parameters was applied if a saccade was not detected. All the trials were aligned with respect to the onset of the pursuit target movement. We analyzed the data up to the flash presentation or to the pursuit target offset, whichever occurred first.

We defined the smooth gaze velocity (SGV) as the gaze velocity without saccades. To remove a saccade, a linear interpolation replaced the velocity from 20 ms before the gaze saccade onset up to 20 ms after the offset of the gaze saccade using a previously described procedure (de Brouwer, Missal, & Lefevre, 2001). This can be done because we assume that the gaze displacement is the sum of saccadic and smooth tracking commands as has been shown in head-restrained conditions (de Brouwer et al., 2001; de Brouwer, Yuksel, Blohm, Missal, & Lefevre, 2002).

Pursuit parameters

To analyze how subjects combined eye and head movements during head-unrestrained pursuit, we estimated the gain, the frequency (f_{SGV}), and the phase shift between SGV and target velocity. To compute those parameters,

we first fitted a sine wave to SGV. The fit was computed on the last 1.5 periods of pursuit to ensure that subjects were past the initiation phase of pursuit. To evaluate the pursuit gain, we computed the ratio between the amplitude of the velocity fit and the amplitude of target velocity. A second parameter used to evaluate the pursuit performances is the phase difference (or phase shift) between the target and gaze. This is not a simple task because target frequency and mean gaze frequency (estimated with the velocity fit) are closely related (see Equation 7 below) but not strictly equal. Thus, there is no constant time delay (and therefore no constant phase angle) between target and gaze displacements. Therefore, we computed the mean elapsed time between extrema of the target velocity and the corresponding extrema of the gaze fit for the last 1.5 periods of every trial (as a result, we had three extrema). Using this definition, a positive phase corresponds to a lead of gaze with respect to the target while a negative phase corresponds to a lag of gaze with respect to the target. A similar procedure was used on head velocity and head position to compute the equivalent parameters (gain, frequency, and phase shift) for the head movement.

Comparison of linear regression slopes

To compare the slopes of two linear regressions, we used the test detailed in Clogg, Petkova, and Haritou (1995). In summary, the following procedure was followed to test if the slopes of two linear regressions were statistically different:

$$Y_1 = \alpha_1 \cdot X + \beta_1, \quad (1)$$

$$Y_2 = \alpha_2 \cdot X + \beta_2, \quad (2)$$

$$t = \frac{\alpha_1 - \alpha_2}{\sqrt{SEM(\alpha_1)^2 + SEM(\alpha_2)^2}}. \quad (3)$$

Equations 1 and 2 represent the regression equations. β_1 and β_2 are the intercepts of the regressions while α_1 and α_2 are their slopes. X represents the dependent variable while Y_1 and Y_2 represent the independent variables. Equation 3 computes the t value used to test the difference between the slopes α_1 and α_2 . SEM in Equation 3 corresponds to the standard error.

Head rotation strategies

Figure 1A represents four hypothetical configurations of head rotation for different target motion directions (represented by the red lines in Figure 1). The rotation axis of the head is represented by dashed-dotted lines in

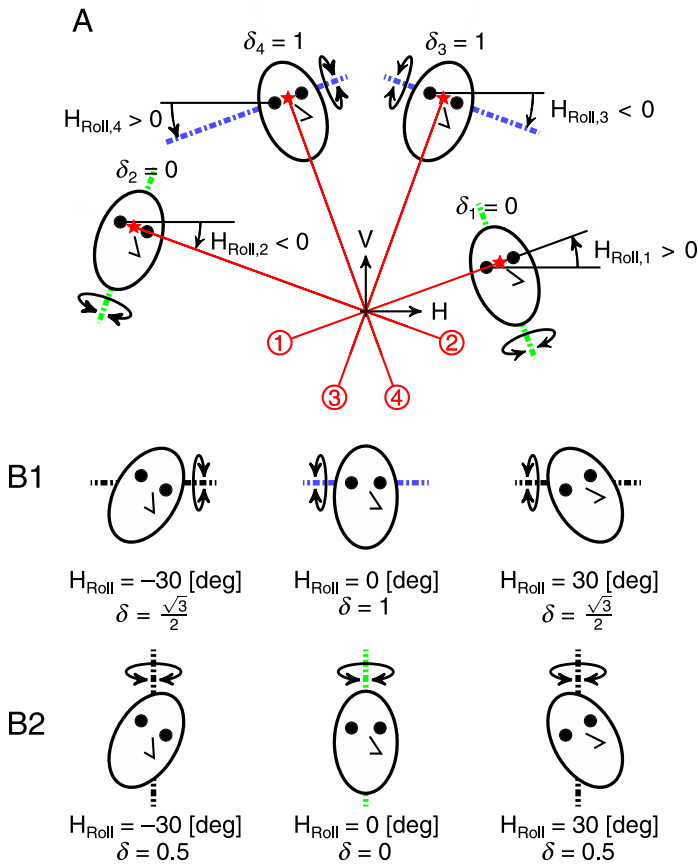


Figure 1. Head configurations during head-unrestrained tracking. This figure represents four theoretical situations related to the strategy of head rotations used by the subjects. The head roll is similar in Situations 1 and 4 and in Situations 2 and 3. Red lines represent the orientation of the target movement. The double-sided black arrows represent the head rotation. Blue dashed-dotted lines represent the mediolateral head rotation axis. Green dashed-dotted lines represent the dorsoventral head rotation axis. Black dashed-dotted lines represent combined head rotation axes. δ_i correspond to the strategy index. Panels (B1) and (B2) represent the value of the strategy index for different head rolls and head rotation axes. See text for more details.

Figure 1. In Situations 1 and 2, subjects slightly inclined their head around the roll axis. Then, they tracked the target with a rotation around the head's dorsoventral axis (represented by green dashed lines in Figure 1). In Situations 3 and 4, subjects rotated their head around the mediolateral axis (represented by blue dashed lines in Figure 1) after a roll of the head to track the target. The roll angle is similar in Situations 1 and 4 ($H_{Roll,1} = H_{Roll,4}$ in Figure 1) and in Situations 2 and 3 ($H_{Roll,2} = H_{Roll,3}$ in Figure 1). Thus, studying the amplitude of the head roll could not discriminate between the two strategies.

To determine the strategy used by subjects, we computed the head velocity vector, $\vec{H}(t)$ (represented by the double-sided black arrows in Figure 1) at each instant. We also computed the vector that linked the two eyeballs

($\vec{E}(t)$). Then, we defined the strategy index as the magnitude of the cross product between the two vectors and called it δ :

$$\delta(t) = \left\| \frac{\vec{E}(t) \times \vec{H}(t)}{\|\vec{E}(t)\| \|\vec{H}(t)\|} \right\|. \quad (4)$$

In Equation 4, $\vec{E}(t) \times \vec{H}(t)$ corresponds to the cross product of $\vec{E}(t)$ and $\vec{H}(t)$ and $\|\vec{X}\|$ corresponds to the magnitude of the vector X . Because this study focused on the maintenance of pursuit, we computed the mean value of $\delta(t)$ during the last period of tracking ($\bar{\delta}$). In Situations 1 and 2 of Figure 1A, the relative distance between the two lines is minimal (ideally $\bar{\delta} = 0$), while in Situations 3 and 4 the distance is larger and close to the maximum (ideally $\bar{\delta} = 1$). Figures 1B1 and 1B2 represent the value of the strategy index as a function of the head roll for head rotations around different axes.

Collected data set

We collected 6533 trials out of which 5748 were valid trials (88%). We removed trials from the analysis if during the pursuit movement IREDs were out of sight for a camera (2%) or if the subject used only saccades or did not track the target (10%).

Results

This study analyzes the strategies used by human subjects to track a periodic target with combined eye-head movements when the orientation of the target trajectory changes. We will start by presenting a typical trial. Then, we will show how target motion direction and frequency influenced pursuit performance. Finally, we will analyze the strategy used by the subjects to move their head.

Typical trials

Figure 2 shows the tracking behavior of a subject (no. 5) for a high-frequency oscillating target (target frequency = 1.12 Hz) with a 27.2-deg amplitude. The gaze movement started with a saccade toward the pursuit target (latency with respect to initiation of target movement = 157 ms). The initial saccade ended close to the target, but gaze velocity did not match target velocity yet. Thus, a second saccade was triggered to cancel the accumulated position error. After the initiation phase (approximately after one cycle of target motion = 1 s), the movement reached a

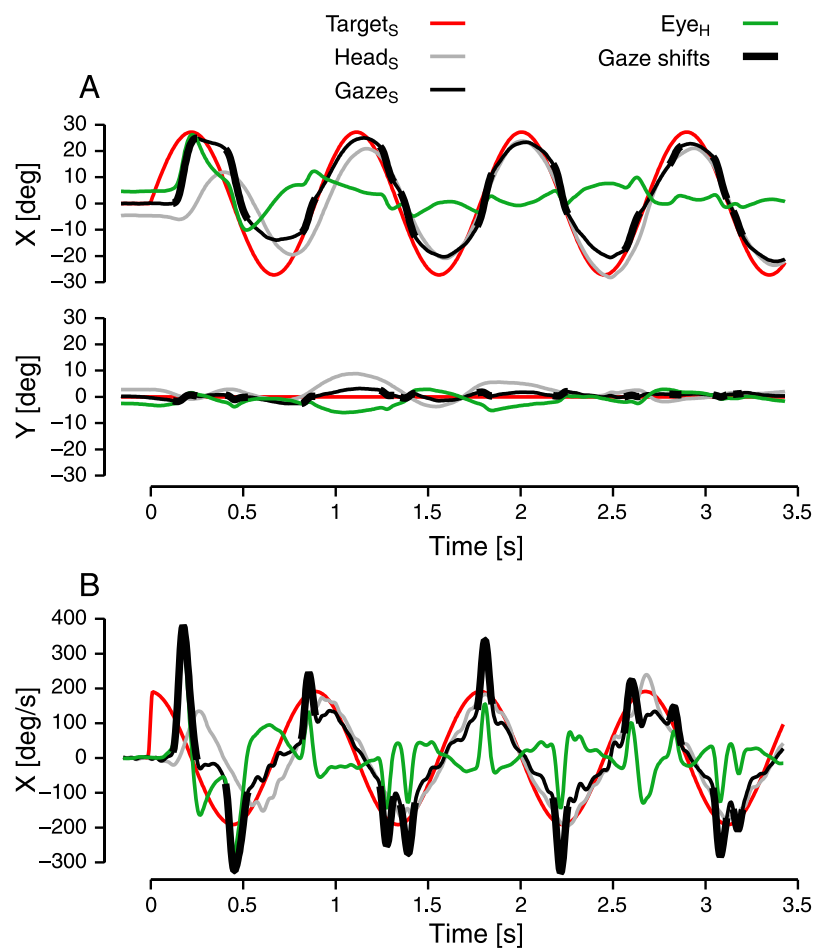


Figure 2. Typical trial. Panel (A) represents the time course of target (red line), gaze (black line), eye-in-head (green line), and head (gray line) positions. X represents the direction parallel to target motion. Y represents the direction perpendicular to target motion. Panel (B) represents target, gaze, eye-in-head, and head velocities along the target trajectory ($\dot{X}$) as a function of time. Same color convention as in (A). Thick black lines represent gaze saccades. Time origin is the initiation of the target movement.

steady-state regime. After the initiation phase, the gaze velocity remained smaller than the velocity of the target for the rest of the trial. As a result, several saccades were triggered to compensate for the position error induced by the slower gaze pursuit component. It can also be observed in Figure 2 that the head started its movement later and more slowly compared to the target. After a cycle of target motion (around 1 s), the head movement was in a stationary regime. During the rest of the trial, the head velocity was close to target velocity, but the head lagged behind by 25.9 ms.

Gaze and head peak velocities

With the set of parameters used in the paradigm (see [Methods](#) section), the target reached peak velocities comprised between 92 (percentile 5) and 196 deg/s (percentile 95) with a maximum value of 224 deg/s.

The range of observed peak head velocity was between 50 (percentile 5) and 166 deg/s (percentile 95) with a maximum value of 251 deg/s.

Head and gaze tracking performance

For horizontal movements, target frequency has been reported to play a key role in the performance of gaze tracking but with less impact on the head behavior (see Figure 2 of Collins & Barnes, 1999). To compare our data with previous ones, we started by analyzing the change of pursuit parameters (amplitude, frequency, and phase shift) as a function of the target oscillation frequency for gaze and head trajectories. The analyses use linear fits because they are a good approximation over the range of observed frequencies.

We first looked at the relationships between gaze (g_G) and head (g_H) gains and target frequency (f_T ; see [Methods](#)

section for the computation of the gains). Linear regressions provided the following results:

$$g_G = (-0.73 \pm 0.01) * f_T + (1.27 \pm 0.01),$$

$$\text{vaf} = 0.404, P < 0.001, \quad (5)$$

$$g_H = (-0.13 \pm 0.02) * f_T + (0.85 \pm 0.02),$$

$$\text{vaf} = 0.011, P < 0.001. \quad (6)$$

As previously reported, there was a strong influence of target frequency on the gaze tracking gain and a smaller (but statistically significant) effect on the gain of the head movement (compare vaf of both regressions). A *t*-test, as expressed in the [Methods](#) section, confirmed the steeper slope of the gaze regression (thus the bigger effect of target frequency on the gaze movement) compared to the slope of the head regression (one-tailed *t*-test, $t(14) = 10.42, P < 0.001$).

A second critical parameter of the movement is the frequency of the gaze and the head movements. A difference in frequency between target and gaze quickly leads to large tracking errors. Concurrently, a frequency difference between target and head movements leads to an increase of eye movements to ensure an accurate gaze tracking. Linear regressions between target frequency (f_T) and gaze (f_G) and head (f_H) frequencies resulted in the following equations:

$$f_G = (0.994 \pm 0.001) * f_T + (0.003 \pm 0.002),$$

$$\text{vaf} = 0.984, P < 0.001, \quad (7)$$

$$f_H = (0.991 \pm 0.002) * f_T + (0.005 \pm 0.002),$$

$$\text{vaf} = 0.975, P < 0.001. \quad (8)$$

[Equations 7](#) and [8](#) demonstrate the very strong relationship between gaze (head) and target oscillation frequencies. A *t*-test did not show a statistical difference between the two regression slopes (two-tailed *t*-test, $t(14) = 0.31, P = 0.76$).

The last parameter we used to quantify the global performance of the tracking system was the phase difference between gaze and target movements and between head and target movements. The phase represents the mean lag (negative phase) or lead (positive phase) of the gaze (head) with respect to the target (see [Methods](#) section). Linear regressions between target frequency (f_T) and head (ϕ_H) and gaze (ϕ_G) phases resulted in

$$\phi_G = -(0.051 \pm 0.001) * f_T + (0.031 \pm 0.001),$$

$$\text{vaf} = 0.248, P < 0.001, \quad (9)$$

$$\phi_H = -(0.096 \pm 0.003) * f_T + (0.082 \pm 0.002),$$

$$\text{vaf} = 0.181, P < 0.001. \quad (10)$$

The head phase appears to be more sensitive than the gaze phase to target frequency. A *t*-test shows that the slope for the gaze phase was shallower than the slope for the head phase (one-tailed *t*-test, $t(14) = 2.50, P < 0.05$). This result points toward a bigger effect of target frequency on the head phase than on the gaze phase.

At this stage, we confirmed that the frequency of an oscillating target is a critical parameter that determines the tracking performance of a periodic moving target in head-unrestrained conditions. However, the variability of the gains as a function of target oscillation frequency appeared to be larger compared to previous observations for horizontal movements. Therefore, we investigated if the orientation of the moving target had an influence on head and gaze pursuit gains. [Figure 3](#) represents the gain of gaze pursuit (upper row) and the gain of head pursuit (lower row) along the direction of target motion as a function of the orientation of the pursuit target. Because of the symmetry of the pursuit target motion direction around the horizontal axis, we computed the orientation in [Figure 3](#) as $O_T = O_{T \bmod \pi}$ (mod represents the modulo operator). We observed a modulation of both gaze and head pursuit gains when the orientation of the target was modified. To quantify this observation, we computed a non-linear fit between target motion direction and the gaze and head gains. Non-linear regressions resulted in

$$g_G = (0.113 \pm 0.007) * \cos[2\pi * (0.0055 \pm 0.0001) * O_T]$$

$$+ (0.617 \pm 0.005),$$

$$\text{vaf} = 0.164, P < 0.001, \quad (11)$$

$$g_H = (0.078 \pm 0.008) * \cos[2\pi * (0.0052 \pm 0.0002) * O_T]$$

$$+ (0.732 \pm 0.006),$$

$$\text{vaf} = 0.060, P < 0.001. \quad (12)$$

O_T in [Equations 11](#) and [12](#) represents target motion direction. Regressions ([Equations 11](#) and [12](#)) showed that the gain of the head movement is less sensitive to a change of the orientation than the gain of gaze movement (compare both the amplitude of the cosine regressions and the vafs of [Equations 11](#) and [12](#)). However, the frequency parameter of both fits ([Equations 11](#) and [12](#)) is similar. Those observations can be seen as evidence that both gaze and head share, at least partially, a common drive that modulates their response as a function of the orientation of the target.

Finally, to test if the frequency had an impact on the modulation of the gains with target motion direction, we divided the data into three frequency bins ($f_T < 0.75$ Hz, $0.75 \leq f_T < 1.05$ Hz, and $f_T \geq 1.05$ Hz). For each frequency bin, we computed the mean gaze and head pursuit gains for different target motion directions (bins of 5 deg). The lower row of [Figure 3](#) shows that the head

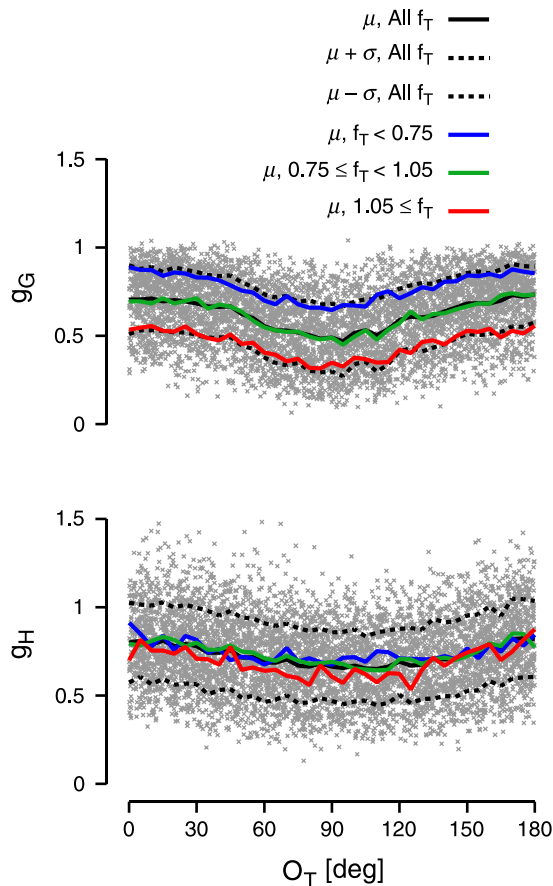


Figure 3. Head and gaze gains as a function of target motion direction. The upper (lower) row represents the gaze (head) pursuit gains as a function of the orientation of the moving target. Solid black lines represent the mean gaze (head) pursuit gain for 5-deg target motion direction bins. The dashed black line represents the standard deviation around the mean of the gaze (head) pursuit gain for 5-deg target motion direction bins. Solid blue lines represent the gaze (head) pursuit gain as a function of the target motion direction for trials with a target frequency smaller than 0.75 Hz. Solid green lines represent the mean gaze (head) pursuit gain as a function of the target motion direction for trials with a target oscillation frequency comprised between 0.75 and 1.05 Hz. Red solid lines represent the mean gaze (head) pursuit gain as a function of target motion direction for trials with target frequencies larger than 1.05 Hz.

pursuit gain was insensitive to the target oscillation frequency (color curves are superimposed). In contrast, the upper row of Figure 3 shows that both target motion direction and target oscillation frequency influenced the gain of the gaze tracking system (color curves are separate).

Head tracking strategies

Target motion direction also influenced the strategy used to control head and gaze movements. Figures 4A–4D show a spatial representation (horizontal–vertical, not

normalized) of the target, head, and gaze trajectories for three different orientations of the pursuit target. To study the stationary phase of the movement, the last 1.5 periods of the movements were represented in Figure 4. Figure 4A shows an oscillating target with a larger horizontal than vertical component (horizontal target amplitude = 22.42 deg, vertical target amplitude = 5.38 deg). The gaze trajectory orientation was very similar to the orientation of the moving target. The head displacement was slightly tilted toward horizontal compared to target trajectory. Figure 4B shows a trial with a larger vertical than horizontal component (horizontal target amplitude = 6.00 deg, vertical target amplitude = 20.80 deg). As for the preceding example, gaze and target trajectories had very similar orientations. However, in this situation, the head movement was tilted more vertically with almost no horizontal displacement. Figure 4C shows a trial in which horizontal and vertical components of the pursuit target had similar amplitudes (horizontal target amplitude = 16.65 deg, vertical target amplitude = 16.13 deg). As for the trial in Figure 4A, gaze and target trajectories had a

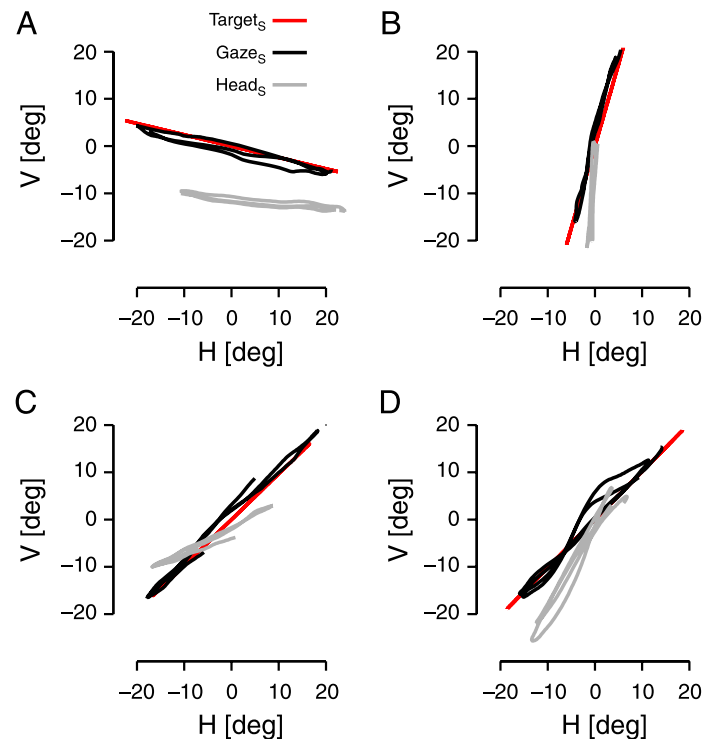


Figure 4. Typical head and gaze spatial trajectories for different target motion directions. Panels (A)–(D) represent the spatial displacement (horizontal–vertical, not normalized) of the target (red lines), the gaze (black lines), and the head (gray lines) for the last 1.5 periods of target motion. Panel (A) represents a target moving mainly horizontally (Subject no. 7). Panel (B) represents a trial where the target moved mainly vertically (Subject no. 4). Panels (C) and (D) represent two trials with similar target trajectories but with very different head movement strategies (C: Subject no. 6, D: Subject no. 1).

very similar orientation. However, the head trajectory remained less steep than the orientation of the target and was biased toward the horizontal. Finally, Figure 4D shows another trial in which horizontal and vertical components of the pursuit target again had similar amplitudes (horizontal target amplitude = 18.55 deg, vertical target amplitude = 18.87 deg). In contrast to the head trajectory in Figure 4C, the head trajectory of Figure 4D was tilted more vertically compared to the orientation of the target, as in Figure 4B.

From the examples of Figures 4A–4D, it appears that mean gaze orientation was similar to target motion direction, but that mean head orientation was closer to a cardinal direction than the target motion direction. To quantify this observation, we computed the angle between the target motion direction and the mean orientation of the gaze and head trajectories. We found a similar pattern for each quadrant ([0...90 deg], [90...180 deg], [180...270 deg], and [270...360 deg]). Therefore, we pooled the data of the four quadrants together. Figure 5A shows the difference between the target and the head orientations ($O_T - O_H$) as a function of the orientation of the target. Then, we computed the mean of the difference between target and head orientations for 2.5-deg bins and represented it with the black solid line (SD: dashed black lines).

Figure 5A shows a clear influence of target motion direction on the difference between target and head orientation. When the orientation of the target was smaller than 30 deg, the more the target was tilted vertically, the larger the difference between the head orientation and the target motion direction. In contrast, when the orientation of the target was larger than 60 deg, the more the target was tilted vertically, the smaller the difference between the head orientation and the target motion direction. Finally, a transition between those two situations appeared when the target motion direction was between 30 and 60 deg.

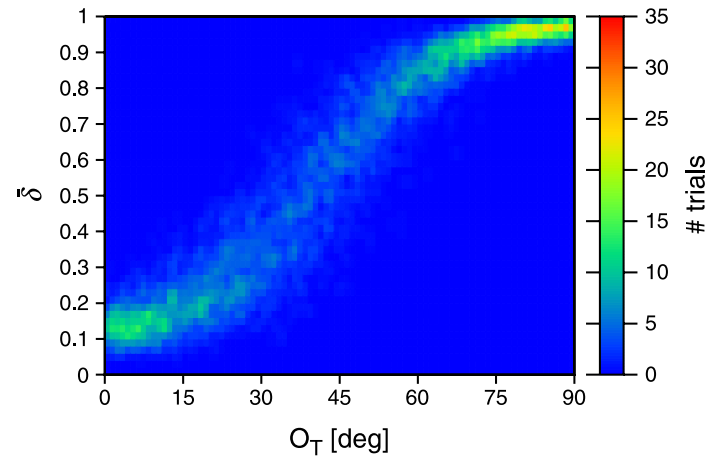
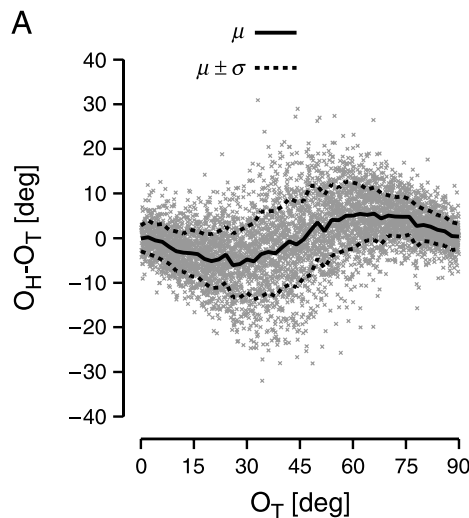


Figure 6. Head rotation strategies. This figure represents the distribution of the strategy index $\bar{\delta}$ as a function of the target motion direction (O_T). The color scale represents the number of trials in each bin.

The same analysis was conducted on the gaze trajectory. We represented in Figure 5B the difference between gaze and target motion directions as a function of target motion direction. We computed the mean (solid line) and the standard deviation (dashed lines) for bins of 2.5 deg. Comparing Figures 5A and 5B, one can see that the gaze orientation was less sensitive to the orientation of the target movement than the orientation of the head, even if more variability was present when the target motion direction was between 30 and 60 deg.

As explained in the Methods section, the head roll cannot be used to dissociate vertical and horizontal head movement strategies. Thus, to study the different head tracking behaviors when the target motion direction changed, we computed the strategy index $\bar{\delta}$ for every trial

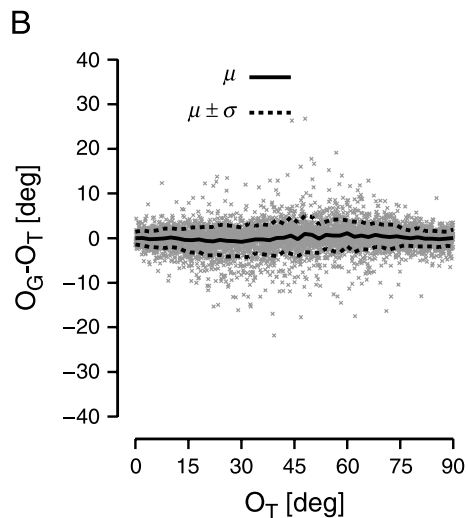


Figure 5. Head and gaze movements as a function of target motion direction. Panel (A) represents the mean relative head orientation ($O_H - O_T$) as a function of the target motion direction (O_T). Panel (B) represents the mean relative gaze orientation ($O_G - O_T$) as a function of the target motion direction. Solid and dashed lines correspond to the mean values and SD, respectively.

Subject no.	$O_{T,A}$ (deg)	$O_{T,M}$ (deg)
1	24	68
2	22	72
3	20	70
4	20	72
5	22	72
6	16	70
7	24	66
8	24	70
All	22	69

Table 1. Upper limit of target motion direction corresponding to $\bar{\delta} < 0.3$ ($O_{T,A}$) for each subject separately. Lower limit of target motion direction corresponding to $\bar{\delta} > 0.89$ ($O_{T,M}$) for each subject separately. The limits were computed using one-tailed *t*-tests.

(see [Methods](#) section). Small values of $\bar{\delta}$ correspond to head rotations around an axis orthogonal to the horizontal semicircular canal plane. Large (up to 1) values of $\bar{\delta}$ correspond to head rotations around an axis parallel to the interaural axis. Theoretically, if subjects switched abruptly from a horizontal to a vertical head rotation strategy, $\bar{\delta}$ with respect to the orientation of the target should represent a staircase function.

The distribution of $\bar{\delta}$ as a function of the target motion direction is represented in [Figure 6](#). [Figure 6](#) shows that two areas of high density emerged as a function of the target motion direction. For target motion directions smaller than 30 deg, subjects used a head movement strategy that promoted rotations around the dorsoventral axis of the head (mean($\bar{\delta}(O_T \leq 30 \text{ deg})$) = 0.22). For target motion directions larger than 60 deg, [Figure 6](#) shows that subjects used head rotations around the mediolateral axis of the head (mean($\bar{\delta}(O_T \geq 60 \text{ deg})$) = 0.92). Similar to the results in [Figure 5A](#), a transition zone was present between the two behaviors in [Figure 6](#). Those areas are represented by a less dense concentration of the data in [Figure 6](#), pointing toward a less defined strategy in which the subjects chose from among a wide range of combined head rotations.

To compare the strategy of each subject in our study, we computed the distribution of $\bar{\delta}$ as a function of the target motion direction separately for each subject. As expressed in the previous paragraph, three subsets of data can be observed in [Figure 6](#), depending on the strategy used to track the target with the head. To compare the behavior between subjects, we first computed the upper limit of the target motion direction ($O_{T,A}$) for which $\bar{\delta}$ was smaller than 0.3 using one-tailed *t*-tests ($P < 0.05$). Second, we computed the first target motion orientation ($O_{T,M}$) for which $\bar{\delta}$ was larger than 0.89 using one-tailed *t*-tests ($P < 0.05$). The lower boundary (0.3) was estimated using the mean value plus two times the standard error of the head strategy index (all subjects pooled together) for target motion directions smaller than 20 deg. The higher boundary (0.89) was computed using the mean value minus two times the standard error of the head strategy index (all subjects pooled together) for target motion directions larger than 70 deg. [Table 1](#) shows the two computed transition orientations ($O_{T,M}$ and $O_{T,A}$) for each subject and for all data pooled across subjects. As shown in [Table 1](#), the behavior was consistent across subjects. All of them started to significantly use combined rotations for target motion directions bigger than approximately 20 deg or smaller than approximately 70 deg. Finally, to test if subjects used a consistent head rotation axis during oblique movements, we computed the variance of the head strategy index for bins (width: 2 deg) of target motion orientations. A small variance corresponds to head rotations around a specific axis chosen consistently by subjects, whereas a large one arises when subjects choose different axes on each trial for the same target motion direction. We also computed the mean of the variances computed for each 2-deg bin of target motion direction for the three areas defined by [Table 1](#) for each subject: dorsoventral rotations for $0 \leq O_T < O_{T,A}$, combined rotations for $O_{T,A} \leq O_T \leq O_{T,M}$, and mediolateral rotations for $O_{T,M} < O_T \leq 90$. Those values are presented in columns two to four of [Table 2](#). Finally, we used two-tailed *t*-tests to see if the population of variances of either

Subject no.	$\mu(\sigma^2(\text{DV}))$	$\mu(\sigma^2(\text{COMB}))$	$\mu(\sigma^2(\text{ML}))$	$t(\text{DV, COMB})$	$t(\text{ML, COMB})$
1	$1.75 * 10^{-3}$	$6.73 * 10^{-3}$	$0.42 * 10^{-3}$	$P < 0.01$	$P < 0.01$
2	$3.76 * 10^{-3}$	$13.77 * 10^{-3}$	$0.83 * 10^{-3}$	$P < 0.01$	$P < 0.01$
3	$3.74 * 10^{-3}$	$6.51 * 10^{-3}$	$0.47 * 10^{-3}$	$P < 0.01$	$P < 0.01$
4	$4.80 * 10^{-3}$	$14.76 * 10^{-3}$	$0.60 * 10^{-3}$	$P < 0.01$	$P < 0.01$
5	$2.78 * 10^{-3}$	$6.18 * 10^{-3}$	$0.38 * 10^{-3}$	$P < 0.01$	$P < 0.01$
6	$2.70 * 10^{-3}$	$9.96 * 10^{-3}$	$0.38 * 10^{-3}$	$P < 0.01$	$P < 0.01$
7	$4.09 * 10^{-3}$	$10.00 * 10^{-3}$	$0.69 * 10^{-3}$	$P = 0.011$	$P < 0.01$
8	$2.63 * 10^{-3}$	$12.02 * 10^{-3}$	$1.07 * 10^{-3}$	$P < 0.01$	$P < 0.01$
All	$4.74 * 10^{-3}$	$13.53 * 10^{-3}$	$1.56 * 10^{-3}$	$P < 0.01$	$P < 0.01$

Table 2. Columns two to four present the mean variance for the three head rotation areas for each subject. DV: dorsoventral rotations ($0 \leq O_T < O_{T,A}$); COMB: combined rotations ($O_{T,A} \leq O_T \leq O_{T,M}$); ML: mediolateral rotations ($O_{T,M} < O_T \leq 90$); μ corresponds to the mean operator; σ corresponds to the variance operator. The fifth column represents the *P*-values resulting from a two-tailed *t*-test comparing DV and COMB. The last column represents the *P*-values resulting from a two-tailed *t*-test comparing ML and COMB.

dorsoventral or mediolateral rotations was significantly different from the population of variances of the combined rotations. The P -values of the t -tests are presented in the fifth and sixth columns of Table 2. Table 2 shows that there is a significant increase of the variance of the strategy index for the combined rotations compared to either dorsoventral or mediolateral rotations. The broader distribution of $\bar{\delta}$ values for oblique target angles is indicative of a failure to choose a consistent head rotation axis for similar target motion directions.

Discussion

In this study, we examined how humans coordinate eye and head movements during the tracking of a periodic target moving along a randomly oriented ramp. We confirmed the high sensitivity of gaze and head tracking performances (gain, frequency, and phase) to target oscillation frequency. We demonstrated that the motion direction of the target modulated the gain of both head and gaze movements. Analyzing the relative orientation of head and gaze trajectories with respect to the orientation of the moving target, we showed that gaze orientation always matched target motion direction, but when the target was within ~ 20 deg of a cardinal direction, subjects promoted rotation around the dorsoventral axis of the head (target motion direction smaller than 20 deg) or the mediolateral axis of the head (target motion direction bigger than 70 deg).

Gaze and head tracking behavior

We found that when subjects were asked to pursue a periodically oscillating target in two dimensions with the head free to move, the CNS efficiently combined gaze saccades and head-unrestrained tracking to ensure that the target remained close to the fovea. Because the velocity of the target reached large values (226 deg/s for a target oscillating at 1.2 Hz with an amplitude of 30 deg), sometimes close to three times the velocity saturation (around 80 deg/s) in head-restrained conditions described by Meyer, Lasker, and Robinson (1985), we assumed that subjects had to use combined eye–head movements instead of eye-only movements to increase the range of accessible velocity and thus accurately track the periodic target.

In the first part of the study, we showed that *both* the frequency and the orientation of the target modulated the performance of gaze and head movements. Our analyses extended the observations of Collins and Barnes (1999) about head-unrestrained tracking of horizontal oscillating target to a condition where the target did not move only horizontally but explored a large range of possible target motion direction from horizontal to vertical directions. We found the same relationship between gaze pursuit

gain, head pursuit gain, and target frequency as Collins and Barnes. However, our data revealed more variability of both gaze and head pursuit gains for a given frequency bin than the variability observed by them. Figure 3 demonstrated that the larger variability came from the larger range of orientations of the moving target in our experiments. As previously observed in head-restrained situations (Kettner et al., 1996; Leung & Kettner, 1997; Rottach et al., 1996), the gain of pursuit was smaller when the target moved vertically than when the target moved horizontally. Therefore, it appears that the variability of the gain as a function of the target motion direction is not a property of eye-only movements but is also present during head-unrestrained tracking. Finally, our regression analyses pointed toward a less sensitive gain of the head movement with respect to the orientation and the frequency of the target than the sensitivity of the gaze movement to the same parameters.

Our results are the generalization of observations previously made in head-restrained conditions to head-unrestrained conditions. Those new results are important because the control of head-free movements is not a straightforward extension of head-fixed movements for the CNS. As noted in the second paragraph of the Introduction section, several factors must be taken into account to control accurately the gaze trajectory when the head is free to move compared to head-fixed conditions.

Finally, we think that the observation of a similar behavior both in head-restrained and head-unrestrained conditions is supplementary evidence that the CNS controls gaze and head trajectories instead of the eye and the head separately.

Head movement strategies

To our knowledge, this paper is the first to study the strategies used by humans to control head trajectory when the target moves obliquely. Figures 4, 5, and 6 demonstrate the existence of two extreme behaviors; in the first one, head rotations were mainly performed around the dorsoventral axis of the head (small values of $\bar{\delta}$, with target motion directions between 0 and 20 deg). In the second one, the head movements were mainly performed around the mediolateral axis of the head (large values of $\bar{\delta}$, with target motion directions between 70 and 90 deg). Because the distribution between 20 and 70 deg is less dense, this means that subjects did not use a consistent strategy. Importantly, individual subjects had a behavior consistent with those observations. We showed that all subjects used dorsoventral rotations for target motion directions smaller than approximately 20 deg. They used mediolateral rotations for target motion directions larger than 70 deg. Finally, we showed that, if the strategy was well defined below 20 deg and above 70 deg, no clear strategies were used by the subjects for combined rotations. For a similar target motion direction, they did not use a similar combination of dorsoventral and mediolateral rotations.

We think that the observed two strategies can be explained by two facts. First, horizontal and vertical head rotations are very different biomechanically. Head rotations around the dorsoventral axis of the head are carried out around the first cervical vertebra through the full range of motion (35–45 deg). However, head rotations around the mediolateral axis of the head imply a bending of the spine for downward rotations larger than 10–15 deg and for upward rotations larger than 25 deg (Hislop & Montgomery, 2007). Second, authors have shown that neck muscles in the cat can be divided into two pools: The activity of the first group does not change as a function of the head posture, whereas the activity of the second pool is correlated with the head posture (Thomson, Loeb, & Richmond, 1994, 1996). Therefore, it seems reasonable to first modify the head posture (through a change of head roll) by changing the activity of the second pool of muscles. Then, a set of muscles similar to the set activated for horizontal head rotations can be activated to track the target with the head. This is consistent with the assumption that a common drive, correlated with the gaze displacement, is sent to both eye and head but that the head receives, in addition, an independent drive related to an independent goal.

Linked to the strategies used by the subject to move their head, the discharge of either the horizontal or the posterior and the anterior semicircular canals (SCC) are maximized. To test if the strategy selected by the subjects is linked or not to the discharge of a particular set of canals, our experiment could be reproduced with monkeys while plugging either the horizontal or the vertical and the anterior canals. If they do not use the same strategy as control monkeys, this would prove that the orientation of the head during head tracking is linked to the optimal discharge of the canals. If they use the same strategy, this would show that it is the set of muscles activated that determines the strategy used by the subjects to track a target.

Dimensionality of the tracking movement

If the movement along a horizontal (vertical) straight line is unidimensional, our paradigm could be thought to generate one-dimensional eye–head movements because the target is moving along a straight line, even if its orientation changed. We believe that our results, linked to the anatomy, show that our paradigm generated two-dimensional eye movements. For pursuit movements, Krauzlis and Lisberger (1996) have shown that the activity of Purkinje cells in the flocculus is modulated by the direction of the pursuit signal. Therefore, to generate an oblique eye movement, even along a straight line, the discharge of different neural populations must be synchronized to ensure accurate tracking whatever the orientation of the linear trajectory. A similar division exists for the control of head movements. The nucleus reticularis gigantocellularis (NRG) and the nucleus reticularis pontis caudalis (NRPC) contain excitatory and inhibitory burst

neurons that discharge during horizontal head rotations (Peterson, Pitts, Fukushima, & Mackel, 1978). Finally, the Forel's field of H (FFH) and the interstitial nucleus of Cajal discharge during vertical head rotations (Fukushima, van der Hoeft-van Halen, & Peterson, 1978; Isa, Itouji, Nakao, & Sasaki, 1988; Isa, Itouji, & Sasaki, 1988). Thus, as for the control of the eye movement, a synchronization of different populations of neurons is necessary to generate an oblique head movement.

The head strategy analysis proves that the head orientation is changed to promote rotations around either the head dorsoventral axis or mediolateral axis. Nevertheless, as shown by Figure 5, there is a difference between the mean orientation of the head trajectory and the target motion direction. This difference is not present for the orientation of the mean gaze trajectory. Therefore, eye-in-head movements have both horizontal and vertical components (horizontal/vertical with respect to the head orientation). As a conclusion, the movement generated by the subjects during this experiment is not unidimensional.

Conclusion

We demonstrated that the gain of gaze tracking was modulated by the orientation and the frequency of the moving target. We also showed that those two parameters (frequency and orientation) of the moving target had less influence on the gain of the head movement during the experiment. In addition, subjects used two strategies to control head trajectory with a bias toward rotations either around the dorsoventral or the mediolateral axis of the head. Those results are supplementary evidence that the CNS is controlling gaze and head trajectory instead of eye and head separately.

Acknowledgments

Support for this work was provided by Fonds National de la Recherche Scientifique, Action de Recherche Concertée (Belgium). This paper presents research results of the Belgian Network Dynamical Systems, Control and Optimization, funded by the Interuniversity Attraction Poles Programmes, initiated by the Belgian State, Science Policy Office. This work has been supported by NSERC (Canada), ORF (Canada), CFI (Canada) and the Botterell Foundation (Queen's University, Kingston, ON, Canada). One of the authors (PMD) was supported in part by the intramural research program of the National Eye Institute, NIH, DHHS.

Commercial relationships: none.
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