Gaze and retinal-image-stability in two kinds of sequential looking tasks

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Abstract

Eye and head movements used to keep the gaze on target were examined as unrestrained seated subjects performed two tasks: (1) tapping sequences of 3-D targets; and (2) only looking at sequences of 3-D targets. Large differences were observed in the head/eye coordination patterns used in each task. During tapping, the head moved quickly and continuously. Retinal-image speeds were relatively high (up to 5°/s). During looking-only, the head moved more slowly and almost came to rest between gaze-shifts. Retinal image velocities between gaze-shifts were 60-77% lower during looking-only than during tapping. Conclusion: coordinated eye/head patterns are adjusted to satisfy the demands of a particular task. These adjustments affect low-level oculomotor mechanisms between as well as during the gaze shifts, themselves (reported previously) © 1998 Elsevier Science Ltd. All rights reserved.

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1. Introduction

Epelboim et al. [1] reported that the accuracy of gaze-shifts was one of several oculomotor parameters whose value is determined by the purpose of the task within which these gaze-shifts are made. Specifically, seated, free-headed subjects either: (i) tapped a sequence of 3-D targets in a specified order as fast as they could; or (ii) shifted gaze among similar sequences of targets as fast as they could, fixating each target before going on to the next. In the tapping task, subjects looked at each target, but only as accurately as was necessary in order to tap it. In the looking-only task, subjects looked at targets more accurately (gaze-errors were smaller) and did not complete sequences as fast. A subsequent paper (based on the same data) [2] described dynamics of the gaze-shifts made in the two tasks and found that the task's purpose affected the parameters of the so-called, 'main sequence'—an oculomotor construct often assumed to reflect the operation of low-level oculomotor mechanisms. Specifically,

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gaze and eye-in-head peak-speeds of saccades with similar amplitudes were higher and gaze-shift durations were shorter during the tapping task than during the looking-only task.

The present paper uses the same database to describe the performance of the low velocity (i.e. non-saccadic) oculomotor subsystem that maintains gaze between saccadic gaze-shifts under natural conditions, i.e. when the head is not restrained (see [3], for a rationale for assuming only two oculomotor subsystems). The main finding was that gaze-stability, in addition to gaze-accuracy and gaze-shift-dynamics, was adjusted in order to serve the specific purpose of a given task. The reason for studying retinal image motion follows.

Until about 1980 it was generally believed that the goal of intersaccadic low velocity eye movements was to stabilize the image of a visual target on the retina (i.e., minimize its retinal slip velocity). Stable foveal fixation was thought paramount for perceiving a 'phenomenally clear and stable world' [4]. This belief about the stabilizing function of low velocity eye movements had support; Refs. [5,6] reported that retinal slip velocity during fixation was < 10'/s. Such stability however, is only observed when the head is prevented from moving. As soon as the head is freed from artificial

supports, retinal slip velocities increase to as much as 1°/s even when the subject sits or stands as still as possible [7]. Fixation stability worsens when a subject is allowed to move. Steinman et al. [8] asked unrestrained subjects to oscillate the head about its vertical axis while maintaining fixation on a distant target. The mean frequency of head oscillations ranged from 0.5 to 5 Hz with head velocities reaching as much as 100°/s. Under these conditions, mean retinal image velocities were ≈ 4°/s. This result was expected to be detrimental to vision because such relatively high retinal image velocities (2–4 times the velocity observed with the head still) should make it difficult to see clearly. All subjects serving in this experiment reported that except during the fastest head oscillations, vision remained both clear and stable. It even remained clear with the fastest oscillations, where objects in the visual field were perceived to be oscillating slightly. These subjective reports were confirmed in a psychophysical experiment by Steinman et al. [9], who showed that head oscillations of up to 1.3 Hz, which produced retinal image motion of > 2°/s, actually improved contrast sensitivity for low spatial frequencies (< 10 cycles/°). Contrast sensitivity for high spatial frequencies (> 20 cycles/°) was reduced only slightly, i.e. by less than a factor of two of contrast (see [10] for a summary of such effects and their implications for vision).

Other authors [11,12] also looked into the issue of retinal image velocity with the head free. They showed that some non-zero value of retinal image slip during maintained fixation was actually preferred (suggested first in Ref. [7]). Furthermore, this amount of retinal image slip was a relatively stable characteristic of a given subject. Collewijn et al. [11] showed this by having subjects adapt to magnifying spectacles that changed the size of the VOR required to compensate for a given rotation of the head by up to 36%. During the course of this adaptation, which was virtually complete in about 40 min, VOR compensation achieved perfection—retinal image slip was zero, but perfection was not maintained. Adaptation continued until the subject achieved steady state at some non-zero value of retinal image slip. These preferred 'failures' of compensation varied from about 2–8% of the head movement among the subjects studied. The findings described above show that perfect fixation stability is not the goal of oculomotor compensation, nor is fixation stability required for clear vision. Another assumed goal of the oculomotor system's performance, viz. reducing gaze-error as near to zero as possible, is not often achieved and probably not even desired. Epelboim et al. [1] found that gaze-accuracy is one of several oculomotor parameters whose value is determined by the purpose of the task within which eye movements are being made.

The present paper extends this line of research by examining the way in which the purpose of a task affects gaze-stability between gaze-shifts. The main result was that head movement speed and amplitude, as well as VOR-gain was set differently in each task. During tapping, the head moved quickly and continuously, resulting in high retinal-image speeds (up to 5°/s), which did not have adverse effects on tapping performance. In the looking-only task, the head moved more slowly, almost coming to rest when fixation was maintained. Intersaccadic retinal-image speeds were 60–77% lower in the looking-only task than in the tapping task (< 1.5°/s). These new results show that the purpose of a given task plays an important role in the control of eye movements used to maintain gaze on objects of interest. These movements seem likely to be coordinated at the functional level at which head, hand and eye movements are programmed.

2. Method

2.1. Subjects

Four subjects (CE, HC, RS and ZP) participated. All were experienced eye-movement subjects, but had no prior experience with the worktable, the tapping task, or even the specific 3-D looking-only used. The data reported here include the very first attempts of these subjects to perform these tasks.

2.2. Data collection

2.2.1. Apparatus.

Details of the Maryland Revolving-Field Monitor (MRFM), used to record eye movements in this study have been described in detail previously [1,13], so only a very brief description will be given here.

The MRFM consists of three subsystems (Fig. 1):

(1) The revolving field monitor/sensor coil subsystem (RFM) records angular positions of the eyes and head. This system consists of two major parts: (i) a machine that produces three mutually perpendicular magnetic fields that revolve at different frequencies (976, 1952 and 3904 Hz) inside the RFM chamber; and (ii) sensor-coils that when placed inside the chamber, carry an induced current that is dependent on the spatial orientation of the sensor-coils. Each revolving field is produced by two sets of five-element, ac-current-carrying coils in a 'cube-surface coil' arrangement [14]. The magnetic field is spatially homogeneous throughout a large fraction (≈ 1 cubic meter) of the volume inside its cubical frame. When a sensor coil is placed inside the RFM chamber, ac-current is induced in the coil by the revolving magnetic fields. The total ac-current induced in each sensor-coil immersed in this field is a superposi-
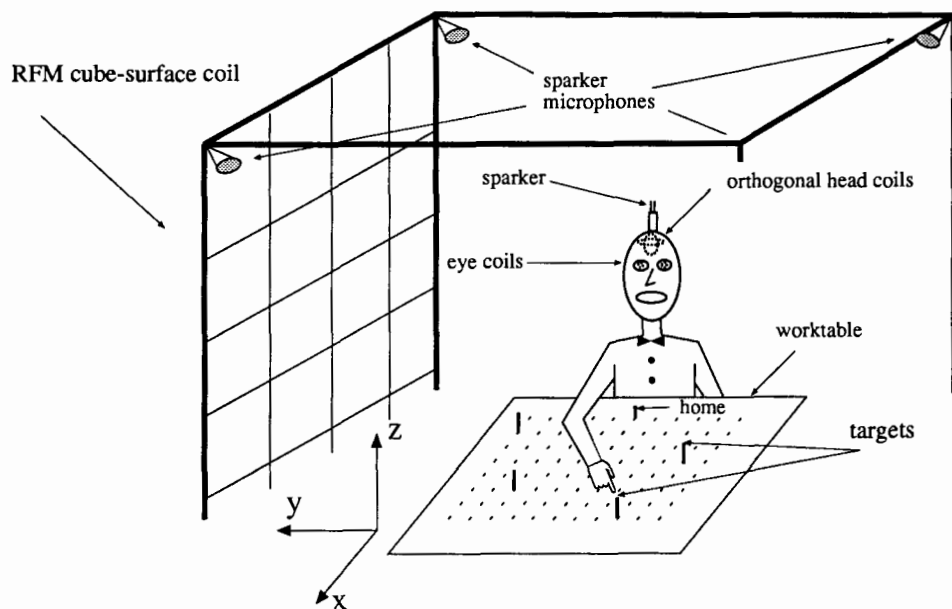
Fig. 1. The MRFM apparatus (see text for explanation).

tion of three sinusoids, each having a different frequency and amplitude. The precision of angle measurement of the RFM is better than 1′ with linearity better than 0.01%. Data are acquired at 976 Hz. Successive pairs of samples are averaged and then outputted and stored at 488 Hz (effective bandwidth = 244 Hz).

Sensor coils embedded in a silicone annulus (SKALAR-DELFT), held on each eye by suction, measured horizontal and vertical eye rotations. A head coil apparatus, consisting of two approximately orthogonal sensor coils, measured roll, pitch and yaw angles of the head.

(2) The sparker tracking system (STS) is used to track 3-D translations of the head by detecting the arrival time of acoustic signals generated by a 'sparker' mounted on the subject's head. The precision of this distance measurement is < 0.2 mm with an accuracy of 1 mm, where precision is the standard deviation of a large sample of position samples of a stationary sparker and accuracy is the comparison of the mean of this sample with respect to measured physical coordinates of the worktable (see below).

(3) The worktable serves as a platform for the targets. Its flat surface contains a grid of 154 (11 rows and 14 columns, 4.5 cm apart) wells with microswitches at the bottom. The area of the table used for targets was 58.5 cm wide and 45 cm deep. The field of view of the table varied depending on the head distance.

Rods topped with LEDs of different colors placed in some of the wells served as targets. When the subject tapped a target, a micro-switch recorded this event (accuracy = 2 ms). A target without a LED, in a well

near the subject, was the 'home' position (Fig. 1). The top of the home target was the origin of the worktable coordinate-system (see Fig. 1 for the definitions of the axes of this coordinate system).

MRFM data were collected in discrete 'bursts', each containing the 12 signals produced by the three subsystems (RFM, STS and the worktable). For each second, 488 RFM bursts were stored. New sparker data were stored on every eighth RFM burst (61 Hz) and intermediate sparker values were interpolated linearly.

2.3. Data analyses

General procedures for handling MRFM data have also been described previously [1,13], so only a very brief description will be given here. Only analyses developed specifically for the present study will be described in detail.

2.3.1. Calibrations

Three calibrations were performed: (1) sparkers of two different heights were placed in 18 locations on the worktable to calibrate sparker-space; (2) the locations of the sighting centers of the right and left eye of each subject were estimated psychophysically with the head located and held by a bite-board; and (3) the orientations of the eye sensor-coils relative to the lines-of-sight were recorded at the start of each experimental session by having the subject fixate an image of his pupil in a mirror placed parallel to the y-axis of the worktable. This was carried out separately for each eye.

2.3.1.1. Definition of the instantaneous line-of-sight (gaze) unit vector. The line-of-sight was defined as the

line parallel to the worktable x-axis that passed through the on-bite-board sighting-center position (determined previously) while the subject fixated the mirror image of his pupil with his head in a known bite-board position during the mirror trial of a given session. The line-of-sight was assumed to be fixed relative to the subject's eye. Thus, once the line-of-sight was known (defined) for a given orientation and spatial location of the eye (henceforth the eye's configuration) the line-of-sight can be found for any arbitrary configuration of the eye, as long as all translations and rotations that moved the eye from the known line-of-sight configuration to the new arbitrary configuration could be determined. Inasmuch as the line-of-sight unit vector indicated gaze direction (eye-in-space), the line-of-sight unit vector at an arbitrary RFM burst, i, will referred to as the 'gaze unit vector' and denoted by G_i.

2.3.1.2. Definition of instantaneous target vectors.

The target vector for a given target and eye was defined as the vector from the sighting center of the eye to the target location, both defined in table coordinates (see Fig. 2).

2.3.1.3. Definition of the instantaneous eye-in-head unit vector.

The eye-in-head vector, or the orientation of the eye with respect to the head, was defined using the Helmholtz coordinate system. The coordinate axes of the Helmholtz system were defined during the mirror trials and were fixed to the head as it moved. The initial Helmholtz axes were defined as follows. The Helmholtz y-axis unit vector (Y_{H0}) is a unit vector that lies along the line joining the sighting centers of the two eyes and points from the left eye to the right eye. The Helmholtz x-axis unit vector (X_{H0}) is obtained by Gram–Schmidt orthogonalization of the y-axis unit vector and the worktable coordinate system x-axis (which is equal to

the line-of-sight unit vector during the mirror trials). Finally, the z-axis unit vector (Z_{H0}) is obtained from the cross product of X_{H0} and Y_{H0} Once the axes of the Helmholtz coordinate system are defined on the bite-board, Helmholtz coordinate axes at an arbitrary RFM burst, i, (X_{Hi}, Y_{Hi} and Z_{Hi}) can be obtained using head angles and sighting center positions for that burst.

The eye-in-head unit vector, E_i is obtained for an arbitrary RFM burst, i, by converting the gaze unit vector, G_i defined above, into the Helmholtz coordinate system whose axes at burst i are X_{Hi}, Y_{Hi} and Z_{Hi}.

2.3.1.4. Definition of the instantaneous head unit vector.

The head unit vector, H_i, at an arbitrary RFM burst, i, was defined as the x-axis of the Helmholtz coordinate system, X_{Hi}, calculated for that burst.

2.3.1.5. Definition of the retinal image vector.

In order to calculate the motion of the target image on the retina, it was necessary to define a unit vector that indicated the position of the target with respect to the eye. An eye-fixed coordinate system was defined for this purpose. Its axes at an arbitrary RFM burst, i, were defined as follows. Y_{ei} was set to the Helmholtz y-axis, Y_{Hi}. X_{ei} was obtained by the Gram–Schmidt orthogonalization of the Y_{ei} and the instantaneous gaze unit vector, G_i. Finally, Z_{ei} was the cross product of X_{ei} and Y_{ei}. Once the coordinate axes at RFM burst i were calculated, the coordinates of the target vector for the target of interest, T, were converted into the eye coordinate system to get target vector in eye coordinates, T_{ei} from which the target image unit vector is calculated as:

$$I_i = T_{ei} / \| T_{ei} \|.$$

2.3.1.6. Calculating 'instantaneous' gaze, eye-in-head, head and retinal image speeds.

The calculation was the same for gaze, eye-in-head, head and retinal-image speeds, using the appropriate unit vectors, G, E, H or I, respectively. Given two unit vectors at RFM bursts i and j (u_i and u_j), the angle between them can be calculated using their dot product:

$$\alpha = arccos(u_i \cdot u_j) \tag{1}$$

Given *alpha* in radians, instantaneous speed for the interval between bursts i and j, in degrees/s, is:

$$vel = \frac{\alpha}{j-i} \frac{180}{\pi} 488 \tag{2}$$

where 488 bursts/s is the RFM sampling frequency. Note that the speed obtained in this manner is a scalar quantity and as such, does not carry any information about the direction of motion.

The interval for calculating 'instantaneous speed' for slow control velocities in prior research ranged from 50 ms to the entire inter-saccadic interval, which could last
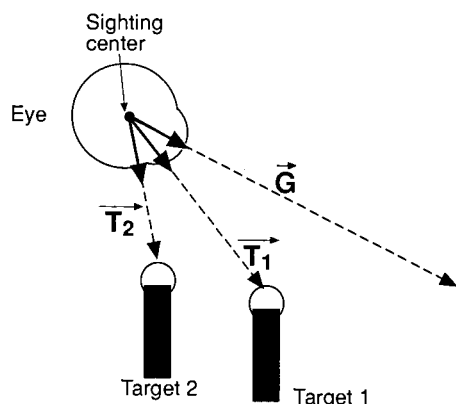

Fig. 2. Definition of target (T) and gaze (G) vectors. When the eye rotates, G changes, but T1 and T2 are unchanged, because the sighting center is assumed to be fixed in the head and unaffected by eye movements. T1 and T2 change when the sighting center translates, which occurs when the head either translates or rotates.

as much as several seconds. Smaller intervals were usually used to estimate the amount of image motion on the retina [7]. Longer intervals were usually used for calculating direction and velocity of sustained drifts [15]. In the present experiment, inter-saccadic intervals were fairly short, usually less than 1 s in the tapping task and speeds of gaze, eye and head movements throughout inter-saccadic intervals were usually quite variable. These facts lead to the decision to use a 40 ms sampling frequency for gaze, eye, head and retinal image speeds between gaze-shifts. Using intervals greater than 40 ms, but less than 100 ms resulted in approximately the same values for gaze, head, eye-in-head and retinal image speeds as when using 40 ms intervals. Smaller intervals produced slightly higher values, but were more variable and more susceptible to noise.

2.3.1.7. Saccade detection and calculation of mean speeds during a single fixation period. Detecting all saccades present in the data was difficult. During tapping, gaze speeds were typically fast between saccades and differentiating between fast slow control and small saccades was very difficult in this condition. Even picking out saccades manually by using a mouse while analog records were displayed, was difficult because one had to work on several very different levels of scale, i.e. large scale to see gaze-shifts between targets, which could be larger than 50° and very small scale to see very small saccades, which could be smaller than 1/2°, that occasionally occurred when fixation was maintained on a single target and were embedded in what could be relatively fast slow control gaze movements (sometimes greater than 10°/s).

Fortunately, it was not necessary to detect the smallest saccades in the analyses used in the present report because inter-saccadic speeds were always measured during a 120 ms window of maximum retinal image stability. The particular 120 ms interval was selected using a sliding window technique with step-size of 10 ms. The exact procedure was as follows:

1. Find a period of time during which gaze remains near a given target in the sequence. This was easy, because the two gaze-shifts that took the gaze to the target and away from the target were large enough to be detected easily.
2. Calculate instantaneous retinal-image speeds for each RFM burst within this period.
3. Calculate the mean of the instantaneous retinal-image speeds for each 120 ms window within this period, starting at the beginning of the period and moving in 10 ms steps. For example, for a period that lasted 620 ms, 50 mean retinal-image speeds were calculated: the first is for a window that started at the beginning of the period ($t = 0$) and lasted 120 ms; the second for a window that started at $t = 10$ ms; the third for $t = 20$ ms, etc., until the last mean retinal-image speed was calculated for the window that started at $t = 500$ ms and ended at the end of the period.
4. Select the window that produces the lowest mean retinal-image speed (maximal image stability) and use this window in all future analyses.

It is possible for the selected 120 ms window to contain a saccade, but this is very unlikely, because it would mean that a window with a saccade resulted in the lowest mean retinal image speed, lower than all windows within the given period, that did not contain saccades. Inasmuch as saccadic latency is usually longer than 120 ms, it is almost certain that a saccade free window with maximum image stability would be available in every interval between the larger saccades. Over 100 windows of 120 ms selected using the above procedure were examined using large scale magnification and none contained saccades.

2.4. Procedure

Subjects performed two tasks. In the tapping task (TAP), subjects tapped sequences of targets located on the worktable. Targets were rods (extending 2.3 cm above the surface of the worktable) topped with colored LEDs. In the other task (LOOK-ONLY), subjects looked at a sequence of targets on the worktable, without tapping them. Tapping and looking-only trials were run during separate sessions on separate days.

Target sequences contained two, four or six targets. Target-order was indicated by the colors of their LEDs, namely, yellow, green, red, flashing-yellow, flashing-green and flashing-red. The flashing LEDs flickered at 10 Hz. The order of colors was the same for the all sequences, i.e. the two-target sequence started with yellow and ended with green and the four-target sequence started with yellow and ended with flashing yellow. Target-order stayed the same throughout the study. During some sessions, the subjects tapped or looked at targets in any order they chose, required only to look at each target exactly once and to end the sequence on the home target.

Each randomly-generated target configuration was tested in a block of ten trials. The subject kept his eyes closed before each block while the experimenter placed the targets in locations selected by the computer. Configurations were selected so that no two targets were placed in adjoining wells. When the experimenter indicated that the configuration was prepared, the subject placed his right index finger on the home target and began the trial when ready, by pressing a button held in his left hand. He then opened his eyes and performed the looking or tapping sequence. The trial length was set to 4 s (for two targets), 6 s (four targets) or 9 s (six targets). At the end of each tapping sequence, the

subject pressed the home target and closed his eyes. At the end of each looking-only sequence, he looked at the home target and closed his eyes. Eyes were kept closed at all times when not performing a sequence.

The experiments took place in a well-lit room, with clear views of the walls and MRFM frame around the worktable. Viewing was binocular. The subject was seated and the head and torso were free to move.

The subject was instructed to remain seated and perform as quickly as possible in the specified order. They were not instructed on when or how to search for the next target in the sequence. Details of the subjects' searching strategies were reported earlier [1]. No instructions were given as to how to move head, eyes, or arm.

The diameter of the LEDs on top of the targets was 5 mm. The visual angle subtended by the LED depended on the location of the target and the position of the subject's head, which moved throughout the trial. The visual angles subtended by the LEDs during the experiments ranged from 1/4° to 3/4°.

3. Results

3.1. Gaze and head movement patterns

Fig. 3a shows subject CE's typical gaze and head movements during a 3-s segment of a tapping trial. HC, ZP and RS's performances were similar. The top row of Fig. 3a shows horizontal (left) and vertical (right) gaze-angles (solid lines) and target-angles (dashed lines) plotted as a function of time. Horizontal gaze-angle is defined as the angle between the line of-sight vector and the worktable $x–z$ plane, henceforth called the 'vertical plane' (see Fig. 1a). Vertical gaze-angle is defined as the angle between the line-of-sight vector and the worktable $x–y$ plane, henceforth called the 'horizontal plane'.

Target-angle traces show movements of target vectors (T; see Method and Fig. 2). Target angles for three targets, labeled T1, T2 and T3 are shown in Fig. 3a.

A target vector for a given eye and target is defined as the vector from that sighting center of the eye (a point within the eye from which the line-of-sight originates) and that target. Horizontal and vertical target-angles are defined as angles between the target vector and the vertical and horizontal planes, respectively. When the line-of-sight of an eye is pointing exactly at a given target, the horizontal and vertical gaze-angles for that eye will coincide with horizontal and vertical target-angles for that eye and target (the gaze traces will fall on the target traces). Changes in target-angle traces are caused by the translations of the eye's sighting center, which is fixed within the head and translates with it, not by movements of the targets themselves (see

Fig. 2). The targets remained stationary throughout the trial. For example, the 20° rightward (down on the graph) movement of the horizontal component of target vector T2, occurred because the sighting center translated to the left by about 15 cm (bottom panel of Fig. 3a) and the distance between the sighting center and T2 is approximately 40 cm. The direction of the gaze vector does not affect the target vector, because the target vector is defined with respect to the sighting center, fixed in the head and the target, which is stationary in space.

All gaze and target-angle traces in Fig. 3a (and in all subsequent analog records) are shown only for the right eye. Traces for the left eye followed the same pattern.

The graphs in the middle row of Fig. 3a show horizontal (left) and vertical (right) head angles for the same time interval as the gaze-angles. Horizontal and vertical head angles are the angles between the head vector (defined in Section 2) and the vertical and horizontal planes, respectively. The bottom row of Fig. 3a shows the translations of the sighting center of the right eye in worktable coordinates. Horizontal translations along the worktable y-axis (left to right from the point of view of the subject) are shown on the left. Translations along the worktable z-axis (up and down) are shown on the right. Torsional (roll) head angles and head translations along the worktable x-axis (near to far), were also measured and used in the calculations, but they are not shown because they add little to the following discussion.

Gaze traces in Fig. 3a contain gaze-shifts that take the line-of-sight from one target to the next, as well as much smaller gaze-shifts that move the line-of-sight within the locale of the target. Periods during which the line-of-sight remained near the same target are defined as 'looking episodes' [1]. About 30% of looking episodes in the tapping task contained small gaze-shifts, about 75% of these small gaze-shifts were corrective, i.e. they brought the line-of-sight closer to the target of interest. Three looking episodes are indicated with brackets in the top row of Fig. 3a.

The head rotated and translated briskly and continuously throughout the trial. Head rotations, as well as head translations, caused the sighting centers of the eyes to translate. In order to compensate for sighting center translations, gaze moved smoothly during looking episodes. These smooth eye movements were used in combination with occasional saccades to track the target, which moved with respect to the eye, as the sighting center of the eye translated. These tracking movements reduced retinal image velocity considerably, but did not eliminate it completely. Mean retinal image velocities during looking episodes in the tapping task were 2.5–5°/s depending on the subject. These values are similar to those observed in prior head-free experiments, in which subjects moved the head actively as
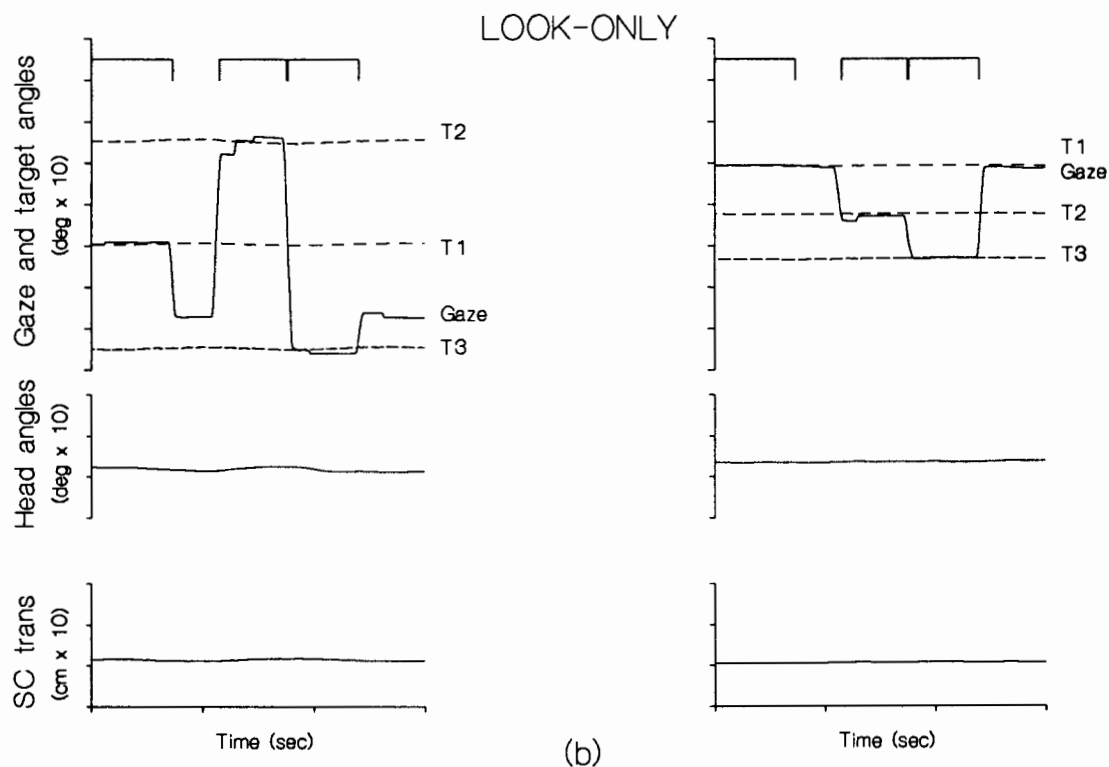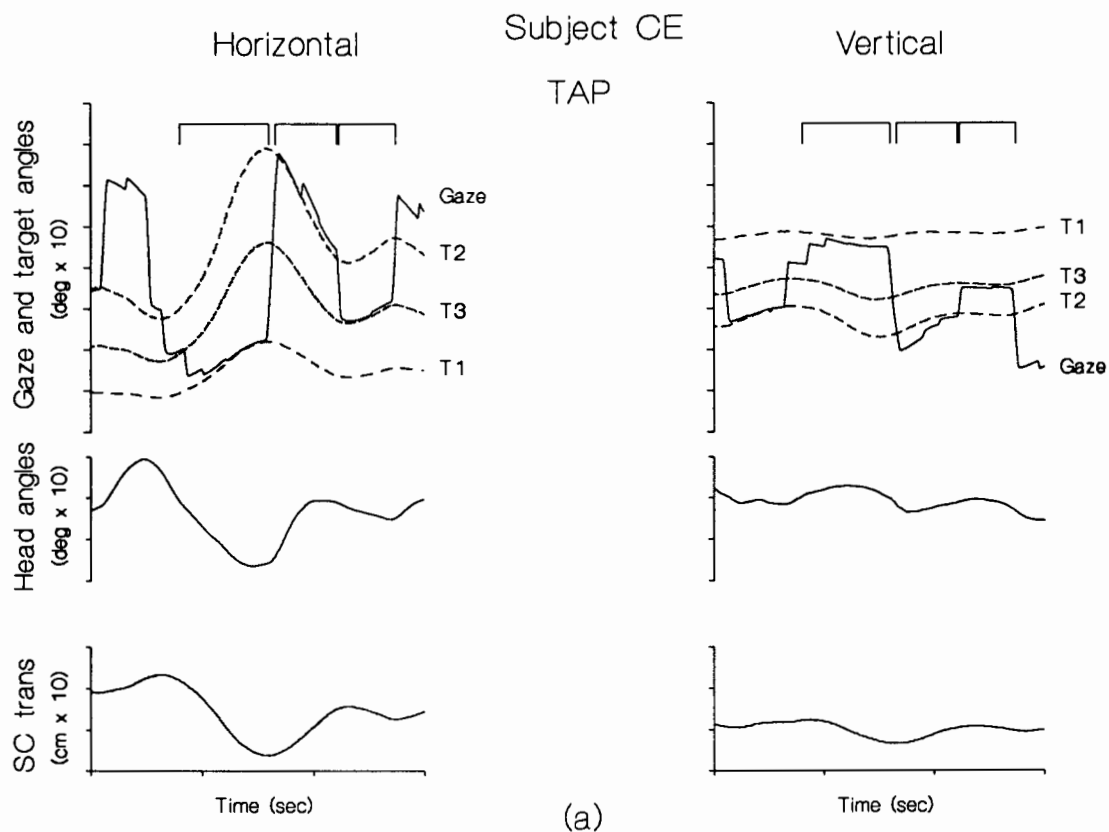
Analog records for subject CE during 3 s segments of a tapping trial (a) and a looking-only trial (b). Horizontal components are show left. Vertical components are shown on the right. The layout is the same for (a) and (b). The top row shows gaze (solid lines) ar angles (dashed lines) for right eye plotted as a function of time. Brackets above the graph show episodes during which CE was looking f the three targets whose traces are shown. The second row shows head angles as a function of time. The bottom row shows translatio sighting center of the right eye as a function of time (see the text for definitions and a full explanation).

they attempted to maintain fixation on a distant target [8].

Fig. 3b shows gaze, target and head angles, as well as sighting center translations, for subject CE in a 3-s segment of a typical looking-only trial. The patterns of gaze and head movements in Fig. 3b are typical for CE, as well as for subjects HC and RS. Subject ZP made larger head movements in the looking-only task than the other subjects and his performance will be discussed in some detail later.

In contrast to their behavior during tapping, all subjects except ZP kept the head relatively still when they were only looking at the targets. During looking episodes (labeled with brackets above the graphs in Fig. 3b) the head was almost stationary, the sighting center did not move relative to the target and gaze was quite stable at each target position. This was also the case in the tapping task; $\approx 20\%$ of looking episodes contained small gaze-shifts, $\approx 75\%$ of which were corrective. Corrective gaze-shifts usually occurred at the very start of each looking episode (within the first 200–300 ms) and gaze remained relatively stable throughout the rest of the looking episode. Mean retinal image velocities were $< 1.5°/s$, which was much lower than retinal image velocities observed during tapping.

Although the head moved much more during tapping than during looking-only, large head movements were also observed occasionally in the looking-only task. Fig. 4 shows ZP's gaze, target and head angles, as well as sighting center translations. ZP's tapping gaze patterns were similar to those of CE (compare Fig. 3a and Fig. 4a), as well as to those of the other two subjects. That is, his head rotated and translated throughout the tapping sequence while smooth gaze movements, together with occasional saccades, were used to keep the line-of-sight on the target between the gaze-shifts. However, unlike CE and the other two subjects, ZP tended to make substantial head movements when he was only looking at the targets. In the example shown in Fig. 4b, there are three large (10–15°) horizontal head movements. These head movements were associated with large saccades that had horizontal components of 35–50°. In all three gaze-shifts shown in Fig. 4b, the head started moving at, or after, the onset of the gaze-shift and became relatively stationary within 300 ms after its offset. Compare ZP's looking-only pattern of discrete head movements, followed by relative head stability to ZP's tapping pattern, shown in Fig. 4a. The graphs contain four large gaze-shifts, each consisting of a head movement and a saccade with a large (35–50°) horizontal component. However, in contrast to the pattern in the looking-only example, in which the head did not start moving until after the saccade started (Fig. 4b), in the tapping example, the head was already moving when the saccade started and did not stop moving after the saccade ended. This difference in the head/eye

timing pattern between the two tasks was observed in all subjects, whenever a large head-movement was made during looking-only. In other words, head movements made during looking-only were discrete: they started with the head at rest at the same time, or after the saccade started and ended with the head relatively stationary very soon after the saccade ended. Head movements made during tapping however, were continuous—they were not separated by periods of relative head stability. The continuous head movement pattern used during tapping helped the subjects perform the tapping task faster. They did not have to take the time to stabilize the head between gaze-shifts. However, they may have sacrificed visual clarity and stability by speeding up. These fast head movements were not fully compensated resulting in rather fast retinal-image slip.

## 3.2. Summary of head, gaze, eye-in-head and retinal image velocities

Fig. 5 compares mean head, gaze, eye-in-head and retinal image velocities during looking episodes for looking-only and tapping. Looking episodes were sorted into two types: (i) sequence episodes, during which the subject looked at the correct target in the sequence; and (ii) search episodes, during which the subjects looked at a target out-of-sequence, presumably as part of a search pattern used to locate the next target in the sequence (see [1]). All velocities shown in Fig. 5 were computed for the 'steady-state' part of the looking episode, which was defined as a 120 ms interval, within the looking episode, during which mean retinal image velocity was at its lowest value (see Section 2).

All analyses of velocities during looking episodes that follow were averaged over trials with different numbers of targets and over different repetitions in a block and were taken from trials in which the experimenter, rather than the subject, specified the order of the targets in the sequence. There were small effects of repetition, number of targets and target-order on the velocities reported here, but these difference can be accounted for by small correlations between velocity during the maximum-stability window and the duration of the entire looking episode. The biggest, most robust and most interesting effects on velocities were produced by the differences in the tasks (tap vs. look-only) and by the type of looking episode (sequence vs. search) within each task.

As seen in Fig. 5, the head moved much faster during tapping than during looking-only, requiring the eye to move faster in the opposite direction within its orbit in order to compensate for the translation and rotation of the head to keep the retinal image of the visual scene from moving too fast for effective vision [10]. Eye-in-head moved substantially faster than the head during tapping, because the eye had to compensate the head's
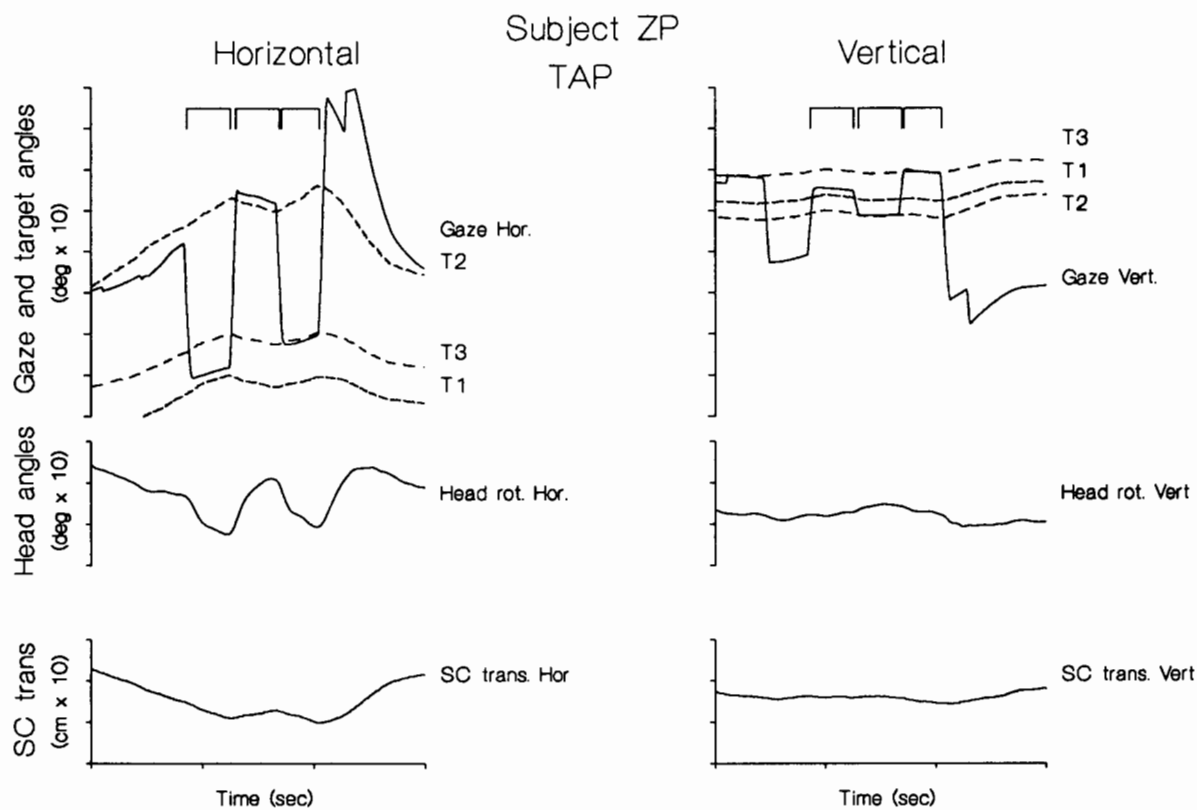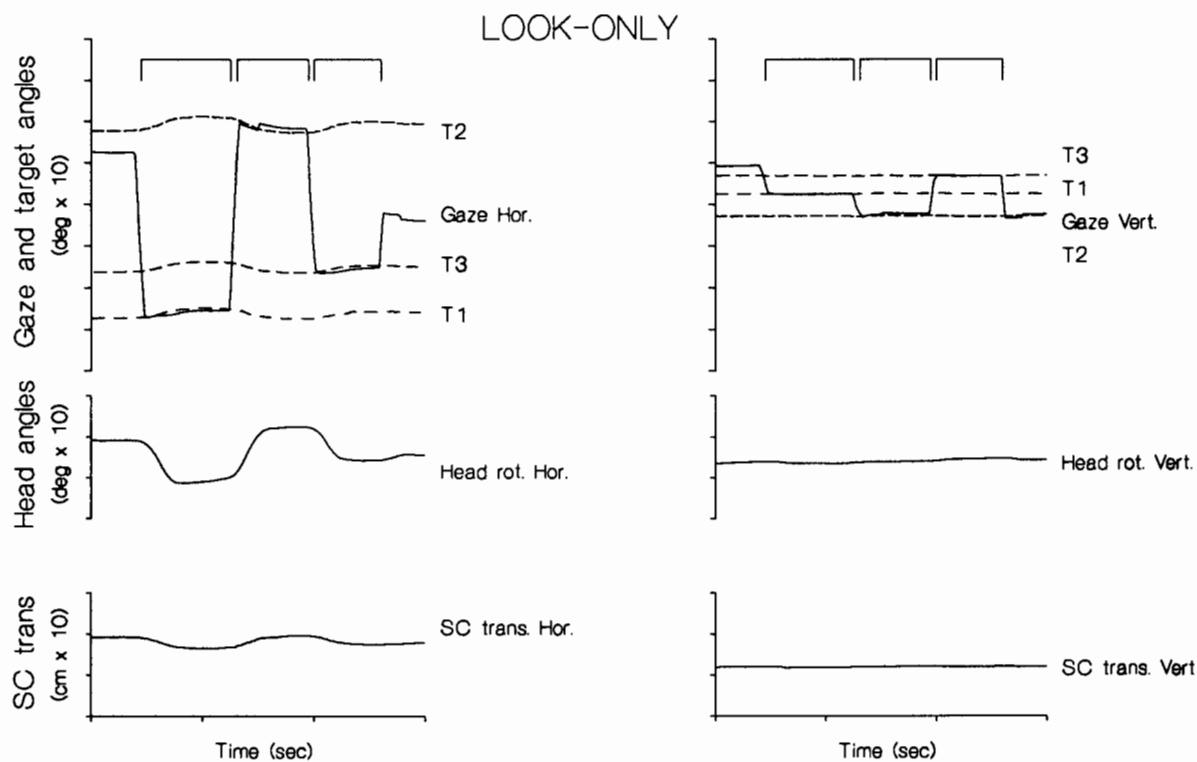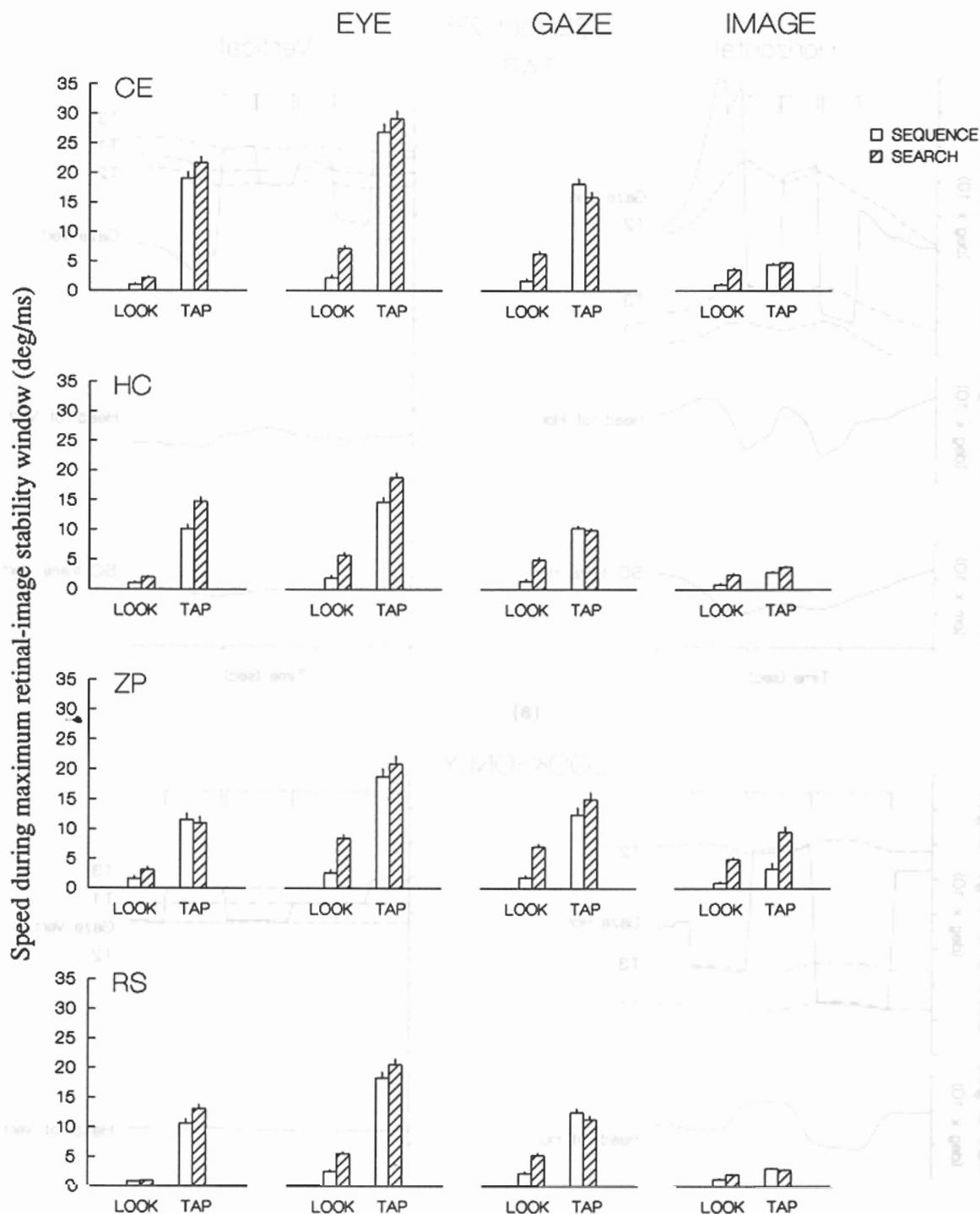
4. Analog records for subject ZP during 3-s segments of a tapping trial (a) and a looking only trial (b). The layout is the same as in Fig.

Fig. 5. Mean head (column 1), eye-in-head (column 2), gaze (column 3) and retinal image (column 4) speeds calculated during a 120 ms window [of] maximum retinal-image stability (see text). Rows show data for individual subjects (subject's initials are labeled in the upper left). Means for [sequ]ence episodes are shown with open bars. Means for search episodes are shown with filled bars. Error bars show 1 S.E.. Each open bar is based [on 6]82–1370 sequence episodes. Each filled bar is based on 93–358 search episodes.

[tra]nslations, as well as rotations and the head tended to [tra]nslate rapidly during the tapping task. Differences in [hea]d velocity and perhaps in the degree of compensation [for] head movement, resulted in much faster average [min]imal retinal image velocities during tapping (up to [...°/]s) than during looking-only (< 1.5°/s).

Within the looking-only task, compensation for head movements was more complete for sequence than for search episodes, resulting in higher retinal image velocities during search episodes. This difference in retinal image velocity persisted even when head velocity was similar for sequence and search episodes, as it was for subject ZP.

During tapping, the head rotated almost equally fast during sequence and search episodes, despite the fact that the arm and torso were not moving towards the target during search episodes. This means that although search was a separate process that had similar properties in the two tasks, search was not actually independent of the task itself. The pattern of head movements during looking episodes was influenced by the purpose of each particular looking episode, but the greatest influence was exerted by the purpose of the overall task.

4. Discussion

The results show clearly that excellent retinal-image stabilization was not common during an active, purposeful task that resembled tasks performed in everyday life. The oculomotor system sacrificed image-stability in order to achieve speedy performance. This strategy makes sense once we recall the finding that some non-zero, amount of retinal-image motion enhances contrast sensitivity at low spatial frequencies. These are the frequencies used to detect relatively large objects in the visual environment [9,10]. Successful tapping did not require resolving fine details. The LED targets subtended from $1/4°$ to $3/4°$ as the subject moved about to reach and to tap them. Once a high degree of visual acuity was not required, cognitive and motor resources were not allocated to minimize retinal-image motion in the presence of rapid head and torso movements, which were needed to tap target sequences quickly. It is also possible that translational movements of the head and movements of the arm provided additional depth information, making resolving details of the visual scene less important.

In the looking-only task a higher degree of image-stability became desirable for some reason. Possibly high level of image-stability was part of the subjects' interpretation of what it means to 'look at' something. To achieve this stability, subjects employed a different eye-head strategy. They limited movement of the head and torso and perhaps raised the 'gain' of the low velocity compensatory subsystem. Subjects were not aware of making these adjustments. They were too busy, fulfilling the demands of each task, which implies that the purpose of a given task automatically sets parameters that will be optimal for its performance (Refs. [1,2] came to the same conclusion about other oculomotor performance characteristics, viz. gaze-shift dynamics and the effective use of search and memory).

These findings offer additional support to a hypothesis proposed by Epelboim et al. [2] to explain task-dependent differences in gaze-shift-dynamics. They proposed that the parameters of gaze-shifts were adjusted as part of a global adjustment to the eye-head coordination patterns, affecting both the gaze-shifts themselves and the low velocity eye movements between the gaze-shifts. We now know that the low velocity eye movements were affected by this task-dependent adjustment, as had been predicted. It seems likely that the global adjustment was determined by trading-off retinal-image-stability and bodily movement requirements between gaze-shifts and not by the need to make the gaze-shifts faster. The components of each task, e.g. finding each target and preparing motor programs for gaze-shifts and arm movements, used information collected during the relatively long intervals between the gaze-shifts (400–800 ms), rather than during the much briefer gaze-shifts (< 100 ms). During these inter-gaze-shift intervals the task-dependent differences in motor performance characteristics, head as well as eye, were striking, much larger than the differences observed during the gaze-shifts, themselves [2].

Acknowledgements

References

[1] Epelboim J, Steinman RM, Kowler E, Edwards M, Pizlo Z, Erkelens CJ, Collewijn H. The function of visual search and memory in sequential looking tasks. Vis Res 1995;35:3401–22.

[2] Epelboim J, Steinman RM, Kowler E, Pizlo Z, Erkelens CJ, Collewijn H. Gaze-shift dynamics in two kinds of sequential looking tasks. Vis Res 1997;37:2597–607.

[3] Steinman RM, Kowler E, Collewijn H. New directions for oculomotor research. Vis Res 1990;30:1845–64.

[4] Steinman RM. The role of eye movements in maintaining a phenomenally clear and stable visual world. In: Monty RA, Senders JW, editors. Eye Movements and Psychological Processes. Hillsdale, NJ: Lawrence Erlbaum Associates, 1976:121–54.

[5] Nachmias J. Two dimensional motion of the retinal image during maintained fixation. J Opt Soc Am 1959;49:901–8.

[6] Nachmias J. Determiners of drift of the eye during maintained fixation. J Opt Soc Am 1961;51:761–6.

[7] Skavenski AA, Hansen RM, Steinman RM, Winterson B. Quality of retinal image stabilization during small natural and artificial rotations in man. Vis Res 1979;19:678–83.

[8] Steinman RM, Collewijn H. Binocular retinal image motion during active head rotation. Vis Res 1980;20:415–29.

[9] Steinman RM, Levinson JZ, Collewijn H, Van der Steen J. Vision in the presence of know natural retinal image motion. J Opt Soc Am A 1985;2:226–233.

[10] Steinman RM, Levinson JZ. The role of eye movements in the detection of contrast and detail. In: Kowler E, editor. Eye

Movements and their Role in Visual and Cognitive Processes. Amsterdam: Elsevier Science, 1990:115–212.

Collewijn H, Martins AJ, Steinman RM. Natural retinal image motion: origin and change. Ann New York Acad Sci 1981;374:312–29.

Collewijn H, Martins AJ, Steinman RM. Compensatory eye movements during active and passive head movements: fast adaptation to changes in visual magnification. J Physiol (London) 1983;340:259–86.

[13] Edwards M, Pizlo Z, Erkelens CJ, Collewijn H, Epelboim Kowler E, Stepanov MR, Steinman RM. The Maryland Revo ing-Field Monitor—theory of the instrument and processing data. Technical Report CARTR-711, Center for Automati Research, University of Maryland at College Park, 1994.

[14] Rubens SR. Cube-surface coil for producing a uniform magne field. Rev Sci Instrum 1945;16:243–5.

[15] Epelboim J, Kowler E. Slow control with eccentric targe Evidence against a position-corrective model. Vis R 1993;33:361–80.