

Cross-coupled adaptation of eye and head position commands in the primate gaze control system

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Received 4 April 2005; accepted 18 May 2005

Primates orient visual gaze using different eye–head coordination strategies. To test how these strategies are formed, we trained a macaque monkey to perform ‘head-only’ gaze shifts looking through a 10° head-fixed aperture. When we suddenly relocated this aperture 15° downward, the animal could orient initial eye position toward the new aperture, but during large gaze saccades the eye was mistakenly driven back to the original (now occluded)

aperture. More importantly, this was accompanied by an opposite head movement, such that gaze (although blocked) pointed correctly. We conclude that the gaze control system acquires new strategies through separate but interdependent eye–head controllers, designed primarily to ensure that gaze is placed in the correct direction. *NeuroReport* 16:1189–1192 © 2005 Lippincott Williams & Wilkins.

Key words: Eye–head coordination; Gaze control; Rhesus macaque

INTRODUCTION

Primates analyze detailed retinal images by reorienting them toward the fovea. These reorientations are normally achieved through head-free gaze shifts (i.e. coordinated movements of the eyes and head) [1–3]. Gaze shifts can be decomposed into three main movement components: movements of the eye-in-space or gaze (Es), movements of the head-in-space (Hs) and movements of the eye-in-head (Eh). The relationship among these components is represented by the equation $Es = Eh + Hs$. A central question concerning gaze control is whether the eye and head movements have common or independent control mechanisms.

The ‘common driver’ hypothesis proposes that a single ‘motor error’ signal – equivalent to the current distance between the target and the current gaze position – is used to drive brainstem circuits for both the eye and head [4,5]. In contrast, the ‘independent driver’ hypothesis suggests that movements of the head and the eye are controlled separately by means of independent head and eye ‘motor errors’ [1,6]. These two hypotheses can also have intermediate gradations [7] (i.e. interactions between the commands for eye and head movements).

A theoretical disadvantage of the ‘independent driver’ hypothesis is that a head driver, completely isolated from the eye driver, would not compensate for failures in the oculomotor system, or vice versa, leading to potential errors in gaze orienting. One method of testing this idea is to induce a mistake in the oculomotor system and see how this affects head movement and gaze performance.

We trained macaques to wear pinhole goggles that produce a new eye–head coordination strategy, that is, ‘head-only’ gaze shifts with minimal net change in eye position [8]. Then, we abruptly changed the location of the goggles’ aperture, which has been shown to cause errors in

Eh commands [9]. It is not known how these errors affect Es and Hs movements. The independent error hypothesis predicts that the Eh errors will be independent from changes in Hs movements. The common (correlated) error hypothesis predicts that changes in Eh movements will be accompanied by equivalent but reversed changes in Hs movements.

METHODS

Animal preparation: Two monkeys (*Macaca mulatta*) designated as M1 and M2 underwent aseptic surgery under general anesthesia (isoflurane 1.5% and ketamine 10 mg/kg) during which they were fitted with a head holder, an acrylic skullcap and scleral search coils to measure Es position. Two additional coils were attached to the skullcap in order to measure Hs position. These methods are described in more detail elsewhere [8]. All these procedures were in accordance with the Canadian Council on Animal Care guidelines and were preapproved by the York University Animal Care Committee.

Targets array and training: During the experiments, the animals sat on a primate chair in the interior of a dark room, facing the inside surface of a circular black dome positioned 100 cm away from the animals’ eyes. Animals were allowed to make naturally coordinated eye–head gaze shifts with no encumbrance to their head movement [8,9]. In our standard ‘two target’ task, the animal looked between two light-emitting diodes (LEDs) positioned on the horizontal meridian at 30° to the left and right of the dome’s center.

The trial started when one of the LEDs (randomly chosen) turned on. The animals fixated the LED for 500 ms, after which it turned off and the second LED turned on. The

animals were required to make a saccade toward the second LED within a reaction time window (300 ms). Upon successful fixation of the second LED for 500 ms, the animals were rewarded with a drop of juice. The fixation window for the two LEDs was 10° in diameter.

Pinhole-goggle task: Monkeys were fitted with a pair of opaque plastic goggles. Initially, a single round aperture was positioned at our best estimate of the visual axis of the right eye [8]. This standard aperture provided the eye with a useful visual range of only 10°. Additionally, a second aperture (initially occluded) was placed at 15° below the first [9].

Monkeys were initially trained to visually follow a 'treat' through the initial aperture in order to receive it. A typical training session lasted 1 h and started immediately after the placement of the goggles. This 'rudimentary goggle task' training was maintained for approximately 1 month, until the animals produced a search pattern of rapid 'head-only' gaze shifts in all directions [8,9].

After completing training in the 'two target' task and the 'rudimentary goggle' task separately, animals were trained to perform the 'two target' task with the goggles on. M1 learned to look through the aperture toward the LEDs as expected, but M2 developed a pernicious alternative behavioral strategy. Rather than looking through the goggle aperture, M2 obtained the juice reward by memorizing the spatial locations of the targets using normal eye-head kinematics, rendering it useless for the experiment described below. Extensive retraining could not undo this strategy, so M2 was not tested further. Only data from M1 are presented in the results.

Data analysis: Coil signals from the eye and head were sampled at 1000 Hz and then stored on a PC. These signals were used to compute quaternions representing the three-dimensional orientations of the Es and Hs. The Eh orientation was computed from the Es and Hs signals [10]. The position quaternions were used to compute two-dimensional Es and Hs trajectories [11].

During offline analysis, the beginning and the end of the Es, Hs and Eh movements were visually selected. Eh trajectories were divided into two phases (Fig. 1), the initial 'saccadic phase' (from saccade onset until the Es lands on target) and the 'vestibuloocular reflex (VOR) phase' (from when Es lands on target until the end of the Hs movements). During this last phase, Es remains at the same position but Eh rotates opposite to Hs because of the VOR [12].

RESULTS

When M1 could perform the 'two target' task reliably with the goggles on and using the 'head-only' strategy, we suddenly occluded the original aperture and uncovered the second aperture located 15° down from the original aperture. Figure 1 shows the two-dimensional (horizontal and vertical) trajectories of several Es gaze shifts, before (a) and after (e) the aperture switch. Also shown are the corresponding Eh saccadic phases (b and f), Eh-VOR phases (c and g) and Hs trajectories (d and h).

Panels 'a-d' depict data from one control session before the aperture switch. Es trajectories (a) departed from the right LED (grey circle) and landed at different positions

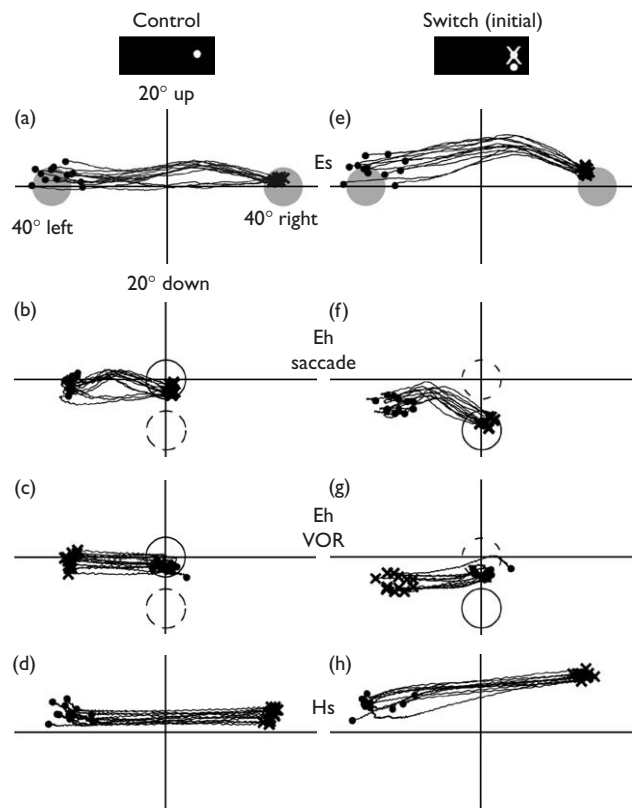


Fig. 1. Two-dimensional trajectories. Traces correspond to one control session (left column) and to one experimental session after immediately switching the aperture (right column). Traces show (a) and (e) eye-in-space or gaze (Es). (b) and (f) saccadic phase of the eye-in-head (Eh). (c) and (g) vestibulo-ocular reflex (VOR) phase of the Eh. (d) and (h) head-in-space (Hs). Small black crosses (×) correspond to the initial positions of the movement and closed circles (●) to the final positions. For the Eh data (b, c, f, g) the circles correspond to the corresponding range of the covered aperture (dashed circles) or the uncovered one (solid circles). As a reference, grey-shaded circles in gaze initial and final positions (top row), show a 10° diameter from the target.

around the left LED. Hs trajectories (d) closely resemble the Es ones (hence the term 'head-only'). However, eye movements were not completely absent. Eh trajectories during the saccadic phase (b) were shorter than the Es and Hs ones but followed the same saccade (from right to left). The end points of these saccades (●) were then aimed such that the subsequent VOR phase, which simply counter-rotates the eye relative to the head, drove the eye back to the original aperture location (c). These observations confirm that the animal had learned to make accurate 60° gaze shifts using the 'head-only' goggles strategy. This was a requirement before proceeding to the 'aperture switch' experiment.

Figure 1e-h shows data recorded immediately after the 'aperture switch'. Before the onset of the gaze shift (e), the animal was able to place its eye downward at the new aperture to look at the rightward LED through a series of eye movements (not shown). As a result, the initial Eh positions (×) were located within the circumference of the new aperture (f). However, this time, the subsequent saccades had additional vertical components, so that the final Eh positions (●) were directed up and to the left of the

new aperture. As a result, during the VOR phase (g), the eye did not return to the new aperture (solid circle). Rather, it counter-rotated in a direction toward the occluded original aperture (dashed circle). Note that from this position the eye cannot visualize the target because the original aperture is occluded. These observations (to this point) were reported before [8].

Our new observations arose from the behavior of Es and Hs during this test. The starting positions of the Hs movements (h) were elevated, allowing the animal to visualize the target through the downward-deviated new aperture. The Hs trajectories were directed, as expected, to the left. However, unlike the purely horizontal Hs trajectories before the aperture switch (d), they also have a downward component that compensates for the deviation of the Es position (f, g). This result contradicts the predictions of the 'independent driver' hypothesis that Hs trajectories will remain unaffected by changes in Es saccades.

As a result of the complementary behaviors of the Eh (net upward rotation) and Hs (leftward and downward rotation), the final Es position (e) remained reasonably accurate despite the fact that eye position had been considerably deviated to a blind location. Es trajectories (e) were thus similar to their control counterparts (a), except that they were transiently deviated upward and had slightly more scatter in their end points.

Figure 2 quantifies these new observations by plotting the Hs (ordinate) versus the Eh vertical displacements, before the aperture switch (a, b) and during the first 12 min after the switch (c-f). The best linear fits to these data are also shown. Because the aperture was shifted down vertically, with these plots, we are correlating the adjustment of the eye and head after the switch.

The data of two control sessions (a, b) show a small distribution in the Hs and Eh vertical displacements accompanied by a low negative correlation. Control session 1: mean Hs displacement (-0.278 ± 2.459), Eh displacement (0.31 ± 1.375), $r = -0.576$. Control session 2: mean Hs displacement (0.7135 ± 1.544), Eh displacement (0.475 ± 1.500), $r = -0.698$. As a result, it is difficult to establish a clear association between these variables in the control condition. On the other hand, immediately after the aperture switch, an instant increase in the variability of both variables (c) was observed, and a high negative correlation was found between Eh and Hs vertical displacements ($r = -0.812$, mean Hs displacement $= -7.138 \pm 3.771$, Eh displacement $= 5.680 \pm 3.258$). Similar results were obtained after 4, 8 and 12 min of the aperture switch (d-f). After 12 min, the animal began to develop a compensatory strategy (i.e. making slow corrective head rotations toward the end of the gaze shift, such that the VOR placed the eye at the new aperture location). These corrections appear in Fig. 2f as a gradual shift of the data distribution average toward zero.

Clearly, following the aperture switch (Fig. 2c-f), the Eh and Hs displacements showed a strong negative correlation (see legend box). The dashed-dotted line represents the predicted regression line for the independent driver hypothesis (i.e. the Hs will move independently from the Eh). The dashed line represents the predicted regression line for the common driver hypothesis (i.e. the Eh and Hs move by similar amounts and in opposite directions). Finally, the solid line represents the regression line fitted to the

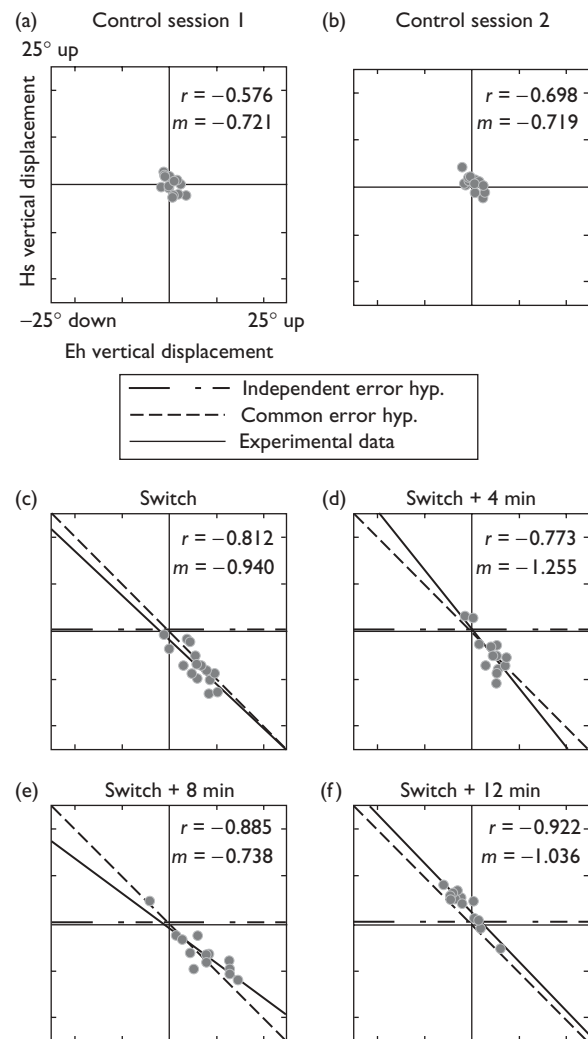


Fig. 2. Correlation analysis. Shows scatter plots of the head-in-space (Hs) vertical displacement (ordinate) against the eye-in-head (Eh) vertical displacement. (a) and (b) correspond to control sessions. (c) Data immediately after the switch. (d) Data 4 min after the switch. (e) Data 8 min after the switch. (f) Data 12 min after the switch. Correlation coefficient values (r), slope values (m), and lines of the best fit are shown (see legend box and text for details).

experimental data. Remarkably, it closely matches the regression line predicted by the common error hypothesis.

DISCUSSION

The main contribution of the present study is to demonstrate that adaptation of Eh and Hs position error signals is not independent. When perturbation of an adapted eye-head coordinate strategy produces perseverant errors in Eh position commands, these commands are accompanied by compensatory Hs commands, ensuring that the final Es position lands on the desired target.

It takes considerable time to train monkeys at the goggle task (approximately one month just for the rudimentary task), but this ensures a true sensorimotor learning. This is probably necessary for the perseverant errors that we observed in the aperture switch experiment, which were a necessary condition for the current study. In contrast,

humans cope with this task through rapidly formed 'cognitive strategies' [13] that preclude testing in this paradigm.

In a previous study [9], macaques were trained to wear goggles. Authors reported a similar effect of the 'aperture switch' on Eh control. As in [8], we found that a perseverant eye position command was implemented through a coordinated combination of saccades and VOR slow phases, such that together they drove Eh upward toward the location of the old occluded aperture. However, the previous investigation did not test gaze accuracy or whether the Hs movements compensated for the induced Eh perturbation.

By testing these additional factors, we have found that during the aperture switch paradigm, the head mirrors the upward eye 'mistake', by moving both horizontally (toward the target) and *downward* (Fig. 1h) in opposition to the eye movement. These oppositely directed Eh and Hs components (Fig. 1f–h) are inconsistent with simple, early versions of the 'common driver' model [4,5]. However, they are consistent with studies showing independent behavior in the eye and head [6,14,15]. Clearly, the eye and head required different drive signals in order to produce movements in the opposite direction.

Second, when examining the overall pattern of eye-head coordination during the aperture switch experiment, and the relative accuracy of final gaze direction, one is forced to reject the 'completely independent driver' hypothesis. The dependency between the Eh and Hs movements after the aperture switch is reflected in the increased absolute value of the correlation coefficients shown in Fig. 2c and d relative to the ones shown in Fig. 2a and b. Whenever the system made its perseverant 'eye mistake', it was accompanied by coordinated, oppositely directed Hs movements, with the net result that the gaze landed on target.

These results suggest that the errors observed in the aperture switch experiment arise from perseverant adaptations to a set of interdependent computations for coordinated eye and head position commands. In other words, whereas the oculomotor system was adapted to place the Eh at the original aperture location by accounting for oncoming head rotation [9], the cephalomotor system was adapted to place Es on target by taking Eh position into account.

Thus, our results contradict both the extreme common drive hypothesis and the extreme independent drive hypothesis. Instead, our data are consistent with an intermediate approach, in which independent drivers are interlinked by intermediary feedback loops [7]. Adaptation between these interdependent circuits allows the system to

develop different eye-head coordination strategies, while preserving the most important variable for normal vision – gaze accuracy.

CONCLUSION

The gaze control system acquires new strategies through adaptation of separate but interdependent eye-head controllers, designed to ensure that the gaze is placed in the correct direction.

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Acknowledgements: This work was supported by the Canadian Institutes of Health Research. J.A.M. is supported by the Consejo Nacional de Ciencia y Tecnología. J.D.C. is supported by a Canada Research Chair. We thank D. Tweed, M. Vesia for editorial comments and A. Clarke, S. Sun, X. Yan, T. Lew, L. Troc and N. Down for technical support.