

## Research Note

# Compensatory eye and head movements generated by the cat following stimulation-induced perturbations in gaze position

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**Summary.** It is thought that saccades are controlled by signals representing target and instantaneous eye positions coded with respect to the head. To determine the frame of reference relevant to gaze (=eye+head) control, we extended to the cat whose head is unrestrained the original study of Mays and Sparks (Mays and Sparks 1980). We stimulated the superior colliculus (SC) to perturb initial gaze position before the onset of a gaze shift made in the dark to a flashed target. Gaze shifts compensated for this perturbation and reached the target with normal accuracy, despite the absence of visual feedback. This result indicates that gaze shifts were coded in either a body-centered or spatial frame but we could not distinguish between these two alternatives because the cat's body was fixed.

**Key words:** Superior colliculus – Electrical stimulation – Compensation – Head-free cat – Saccade – Gaze control

## Introduction

It is thought that saccadic eye movements are driven by a motor error signal obtained by subtracting current eye position *relative to the head* from target

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position *relative to the head*. We emphasize here the head-centered frame of reference because we examine in this study its appropriateness to gaze control when the head is unrestrained. The head-centered system of reference in the saccadic system was first proposed by Robinson (1975) on the basis of psychophysical data (Hallett and Lightstone 1976). An elegant demonstration of this hypothesis was then provided by Mays and Sparks (Mays and Sparks 1980; Sparks and Mays 1983). They showed in monkeys whose heads were restrained (“head-fixed”) that saccadic responses in the dark to a flashed target compensated for a perturbation in eye position which was unexpectedly induced by electrically stimulating the superior colliculus (SC) during the time interval between target offset and saccade onset. Thus, a saccade brought the eyes on target with almost normal accuracy, indicating that the saccadic system, when programming an eye movement to the target, took account of the new initial eye position.

In conditions in which a subject's head is *unrestrained* (“head-free”), saccadic shifts of gaze (eye relative to space) are the result of an ocular saccade combined with a head rotation. Recent studies conducted with head-free subjects have shown that, for a given target position, gaze was accurate despite important variations in its velocity induced by different contributions of the head (Fuller et al. 1983; Guitton et al. 1984; Laurutis and Robinson 1986; Pélisson and Prablanc 1986; Tomlinson and Bahra 1986; Guitton and Volle 1987; Pélisson et al. 1988). These experiments led to the gaze feedback hypothesis whereby the error signal controlling gaze movements is proportional to the difference between gaze and target positions with respect

to either the body or space. Since the experiments were performed with the body fixed, the data did not permit a distinction between body-centered and inertial (i.e. with respect to space) reference frames. An inertial frame appears preferable in view of the ambiguity of defining target position relative to body (see Discussion).

A key issue regarding the gaze feedback control model is whether the abandonment of the head-centered reference frame, used in the saccadic models, is warranted. To investigate this issue, we extended the Mays and Sparks' paradigm to the head-free condition in the cat. We took advantage of the fact that stimulation of the caudal part of the cat's SC elicits coordinated eye-head movements (Roucoux et al. 1980). Gaze responses following this perturbation of gaze position allowed us to distinguish easily between head-centered and inertial (or body-centered) frames of reference. Indeed in head-centered coordinates, gaze is expected to compensate only for the ocular component of the stimulation-induced gaze deviation, so that gaze should miss the target by an amount equal to the amplitude and direction of the stimulation-induced cephalic component. Only in an inertial or body-centered frame will a gaze response fully compensate for a gaze perturbation, whatever the relative contributions of eye and head in this perturbation may be.

## Methods

Two cats were prepared under aseptic conditions for recording orienting responses and stimulating the SC when each animal's head was unrestrained. In a first surgical intervention (under nembutal anaesthesia), a search coil was sutured on one eye for recording gaze position and, with dental acrylic, a head implant was built to allow, if needed, chronic head restraint and provide a pedestal for another search coil that recorded head position. One hole was drilled in the bone over each colliculus and was filled with bone wax and dental acrylic. In a second intervention (after complete recovery of the animal), the holes were reopened under light ketamine anaesthesia and a bipolar stimulating electrode was lowered into the SC. After identification of an appropriate collicular zone based on the properties of the electrically evoked eye movements (Guitton et al. 1980), a bundle of 11 insulated 25  $\mu\text{m}$ , stainless steel, wires were lowered to the same location and the corresponding pin connectors were embedded into dental acrylic on the head implant (Munoz 1988; Munoz and Guitton 1989).

The cats were then trained to orient toward a light emitting diode (LED), using methods described elsewhere (Guitton et al. 1984). Briefly, an opaque barrier was placed 40 cm in front of the hungry animal. A small spoon filled with a food purée was moved behind the barrier from one side to the other, protruding sequentially on each side. The cat was rewarded whenever it oriented to the food. In a subsequent step, the spoon, initially visible on one side, was hidden behind the barrier and a LED flashed on-off at a location where the spoon would ultimately reappear on the opposite side. By using the 2 visual

cues (spoon disappearance on one side and target flash on the other), cats quickly learned to make reliable gaze shifts toward the LED target.

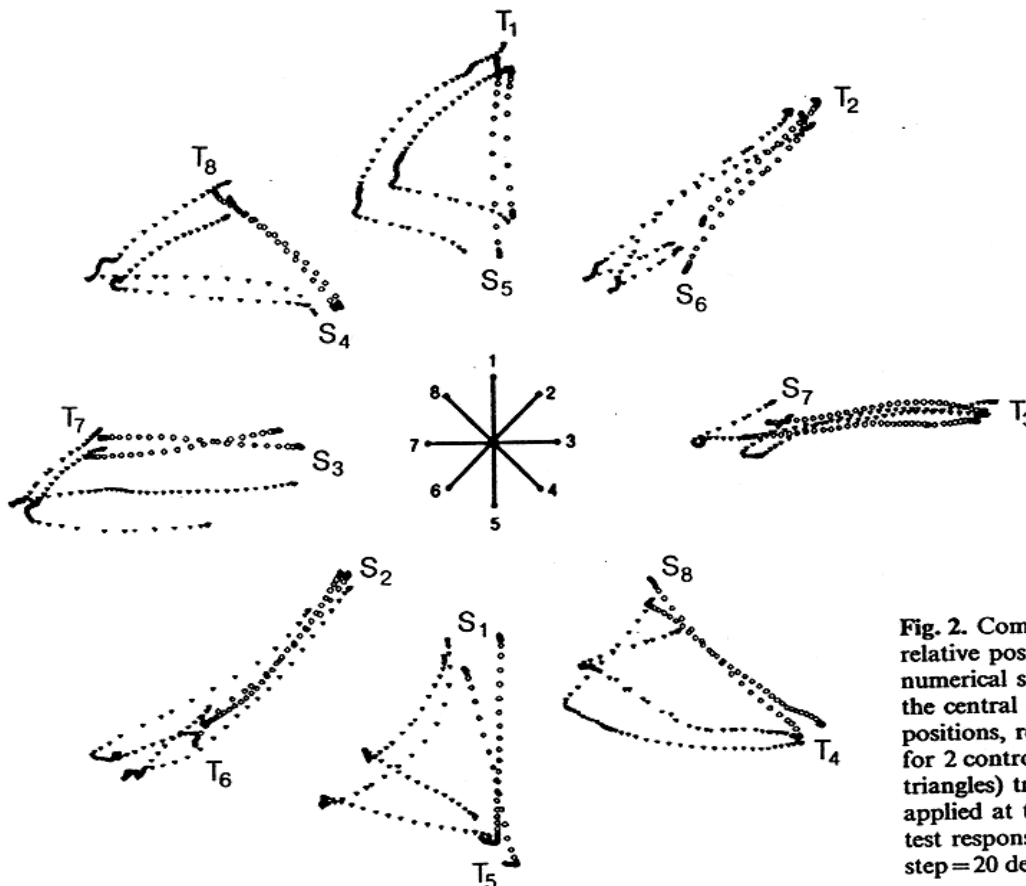
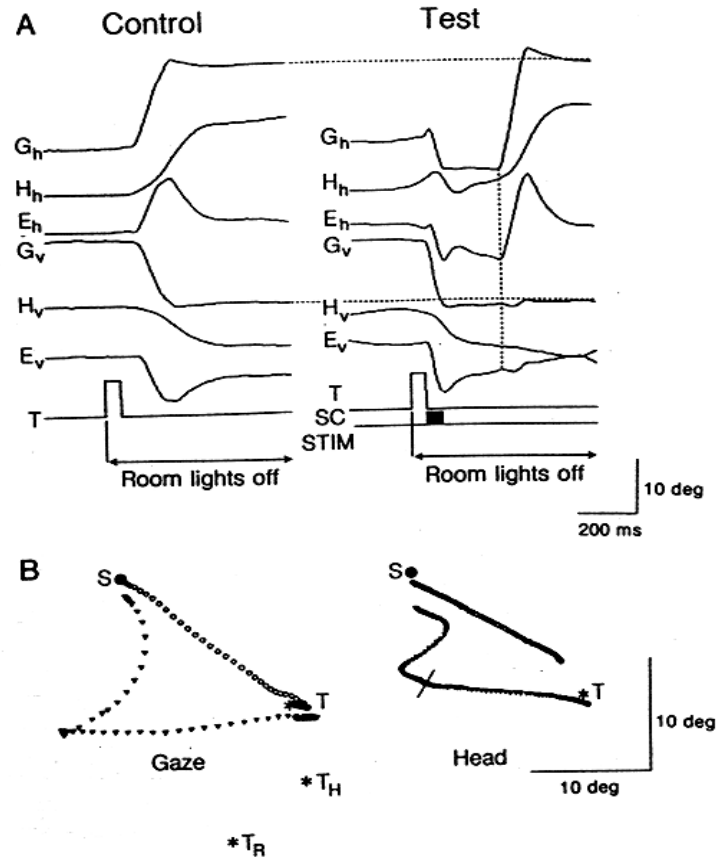
An experiment was run as follows: A stroboscope flashing at 60 Hz and providing the ambient light was turned off for 1 s at the time of target onset and the target was turned off 50 ms later, leaving the cat in the dark during the whole orienting gaze shift. A stroboscope was used to assure that, when ambient light was extinguished, it would decrement with a time constant much less than the cat's 200 ms reaction time to orient to the LED. Note also that the 1 s period of darkness was far less than that required for complete dark adaptation. The ultimate test of whether or not an animal could see during the period of darkness was to present food at a location about the barrier other than where the LED was located and determine whether this produced a corrective gaze shift. To do this, in some preliminary trials, we extended the dark period to 5 s and presented the food at a variety of different positions around the barrier. Never did the cat orient to these new target positions. In the test trials, interleaved randomly with control trials, the SC was stimulated during the period of darkness, at the time the target went off (train duration = 50 ms, train rate = 300 Hz, pulse width = 0.5 ms, current = 1.5 \* threshold).

## Results

The sequence of events in an experiment is illustrated in Fig. 1A by 2 typical responses toward a target located right and down (target 4, of Fig. 2). Both responses were completed in darkness toward the remembered location of the flashed LED. The control response (left portion of Fig. 1A) consisted of a coordinated eye-head single-step gaze shift in the oblique direction. In the test trial (right), the right SC was stimulated for 50 ms at the time the LED went off producing a leftward and downward gaze shift involving both eye and head. In this example, the electrically evoked gaze movement interrupted just at its onset an anticipatory gaze shift to the target. About 200 ms after the perturbation, an accurate compensatory response, almost confined to the horizontal plane, brought gaze quickly onto the same location (T) reached by the control response (horizontal dashed-lines). The trajectories of gaze and head, as projected onto a frontal plane parallel to the barrier, are shown in Fig. 1B. The point marked  $T_R$  indicates where gaze would have landed had there been no compensation for the electrically evoked gaze movement. The point labelled  $T_H$  indicates where gaze would have landed had the system compensated for only eye deviation in the head but not head deviation relative to the body. Clearly, the fact that gaze compensation was accurate implies that the nervous system had to take into account the vector sum of the displacements of both the eye and head. This indicates that either an inertial or a body frame of reference was used to drive gaze relative to the remembered location

of the target. It is also interesting, as shown in Fig. 1B, that a head movement compensated for the perturbation in head position such that final head position was close to that in the control response. Thus head displacements themselves may have been controlled in the same reference frame as gaze shifts.

**Fig. 1A, B.** Eye, head, and gaze trajectories of responses toward the remembered location of a target. **A** Control response (left) and test response (right) in which the eyes and head were deviated by electrical stimulation of the right SC. Also shown are target flash (T) and SC stimulation (SC STIM); room lights were turned off for 1 s at the onset of target flash. Horizontal dashed-lines represent final gaze position in the control situation and vertical dashed-line indicates onset of compensatory gaze shift in the test situation. Note that both eye and head participate both in the electrically evoked gaze perturbation and in the subsequent compensatory gaze shift.  $G_h$ ,  $G_v$ ,  $H_h$ ,  $H_v$ ,  $E_h$ ,  $E_v$ : horizontal and vertical gaze, head, and eye positions, respectively. **B** Superimposed gaze (left) and head (right) planar trajectories of the control (open circles) and test responses (filled triangles) shown in **A**. S = start position; T = target position (final gaze position in control trial);  $T_R$  = final gaze position if the animal had compensated for the electrically evoked gaze shift had occurred;  $T_H$  = final gaze position if the animal had compensated for only eye deviation in the head but not head deviation relative to the body. Tick mark on head trajectory indicates where gaze compensatory response started



**Fig. 2.** Compensatory responses for 8 different relative positions of the start and target. The numerical subscripts on S and T indicate, using the central diagram, the start and target positions, respectively. Planar plots are shown for 2 control (open circles) and 2 test (filled triangles) trials. Electrical stimulation was applied at the same site in the right SC as for test response in Fig. 1. Amplitude of target step = 20 deg

One cat was extensively tested for 8 target positions and compensatory responses could be observed for all of them (Fig. 2). In these plots, 2 control responses and 2 test ones are superimposed for each target position. In control trials, a single step gaze shift ended on the target. In test trials, the collicular stimulation evoked a leftward gaze movement but, as previously reported for head-fixed animals (Schiller and Sandell 1983; Noda and Murakami 1986; Sparks et al. 1987, 1983), both the amplitude and the direction of the electrically evoked gaze movement depended on the relative positions of the start (S) and target (T). The reason why this interactive effect was strong in our conditions might be that SC stimulation was applied at or close to the onset time of the putative control response (Sparks et al. 1987). Some 200–400 ms after the electrically evoked gaze shift, the cat made a saccadic gaze shift which compensated for this perturbation, i.e., it ended at the spatial location reached by control responses. As stated above with regards to Fig. 1, a complete compensation was observed even when early gaze shifts, initiated in anticipation of the target flash, were electrically deviated in mid-flight away from the target (e.g. target positions no 5, no 6 and no 7). Accurate compensatory responses were obtained in both cats. Inaccuracies in compensation, when they occurred, were usually observed near the end of experimental sessions, when the cat was no longer hungry. This observation points toward the motivational state of the animal as a crucial factor in its behavior in test trials.

## Discussion

The existence of responses compensating for an unexpected simultaneous perturbation of eye and head positions indicates that the programming of a saccadic gaze shift can be achieved in a body frame of reference. This reference frame is inherently ambiguous since the body is not a rigid structure and one would have to define a specific body region as being *the* reference point: e.g. the thoracic midline. Alternatively, it is possible that the ultimate frame of reference is an absolute spatial one. Indeed, the semi-circular canals report on head velocity relative to space and it would be a matter of integrating (mathematically) the signal to yield head position in an inertial frame. Unfortunately, our experiment could not address this problem since each animal's body was restrained. The present experimental results nevertheless validate the hypothesis postulated in recent models suggesting that coordinated, orienting, eye-head movements

are controlled on the basis of a comparison between a reference signal of target position and a signal of actual gaze position, both coded at least with respect to the body (Fuller et al. 1983; Guitton et al. 1984; Lauritis and Robinson 1986; Pélisson and Prablanc 1986; Tomlinson and Bahra 1986; Guitton and Volle 1987; Pélisson et al. 1988). In the case of a visual target, these two signals result from a combination of information about target-re-eye position, eye-re-head position and head-re-body position. While the first one (retinal error) is topographically represented in various visual maps within the CNS and the second is a copy of the saccadic ocular command (Guthrie et al. 1983), the origin of the head position signal is still unclear. As stated above it has been proposed in humans that the vestibular system contributes largely in monitoring head position (Lauritis and Robinson 1986). However, considering the improvement of gaze shift accuracy (variable error in particular) when subjects actively oriented their head as compared to a situation of passive head rotation (Pélisson et al. 1988) and considering also the velocity saturation of the vestibular system (Pulaski et al. 1981), other information such as efference copy and nuchal proprioception might be involved as well. The paradigm of the present experiment could be used in neck deafferented or labyrinthectomized cats to further clarify this issue.

The finding of a body-centered (or inertial) frame of reference for gaze shift control might provide new guidelines for studies of the neurophysiological substrate of the gaze feedback loop. Recent electrophysiological data are very relevant with respect to this problem. By recording from tectoreticulo-spinal neurons in alert head-free cats, Munoz and Guitton (1985, 1989) and Munoz (1988) showed that these collicular output cells encode gaze motor error. The discharge characteristics of these neurons suggested that the superior colliculus lies within the gaze feedback loop. Furthermore, a preliminary study of omnipause neurons in head-free cats has shown that the pause duration is strongly correlated to gaze shift duration, but not to either ocular saccade duration or head movement duration (Paré and Guitton, unpublished observations), thereby suggesting that the oculomotor circuitry is under the control of a gaze error signal.

*Acknowledgements.* This work was supported by the Medical Research Council of Canada (MRC) and the Fonds de la Recherche en Santé du Québec. D. Pélisson was supported by Fondation Simone et Cino del Duca (Paris), MRC, and l'Office Franco-Québécois pour la Jeunesse. D. Munoz was supported by a MRC studentship. The assistance of J. Thibaudeau (secre-

tarial), J. Roy (electronics), and the Neurophotography Unit are gratefully acknowledged.

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Received February 3, 1989 / Accepted June 22, 1989