Research Note

Floucullar lesions abolish adaptive control of post-saccadic ocular drift in primates

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Summary. After several days of exposure to optically-imposed post-saccadic retinal slip, the saccades of normal monkeys acquire an exponential ocular drift. This drift is in the direction of the imposed image motion, and persists in the dark. It has been argued that these changes result from the operation of a visually mediated adaptive mechanism that normally functions to minimize post-saccadic ocular drift. Adaptation to persistent post-saccadic retinal slip was assessed in two rhesus monkeys before and after bilateral ablations of the flocculi and portions of the paraflocculi (“flocculectomy”). After flocculectomy, both monkeys showed some post-saccadic ocular drift. Flocculectomized animals also failed to adapt to optically-imposed post-saccadic slip. We infer from this that the flocculi and/or paraflocculi are necessary for the successful suppression of post-saccadic ocular drift.

Key words: Eye movements - Saccades - Flocculus - Rhesus monkey - Ocular drift - Adaptive control

Introduction

Saccadic eye movements are used to transfer fixation from one object of interest to another, and are characterized by their high velocities and abrupt endings. Saccadic innervation consists of pulse, slide, and step components. The amplitude and duration of the pulse determine the velocity and duration of a saccade; the amplitude of a saccade is essentially the area under the pulse. The step determines the final eye position. The slide is the transition between the pulse and step and determines how abruptly the saccade ends (Robinson 1964; Fuchs and Lunchei 1970; Goldstein 1983).

Optican and Robinson (1980) showed that complete removal of the cerebellum resulted in saccades that were too large and were followed by post-saccadic ocular drift. Ablations of the vermis, paravermis and fastigial nuclei alone resulted in saccades that were too large, but without post-saccadic ocular drift. The vermiectomy also abolished the adaptive control of saccadic amplitude, but spared the ability to suppress post-saccadic ocular drift. From these earlier studies we infer that adaptive control of the pulse of innervation (which controls saccade amplitude) is dependent upon the midline structures of the cerebellum. The control of the slide-step, however, must be dependent upon a different part of the cerebellum.

The vestibulocerebellum (flocculus, modulus, portions of the uvula, and paraflocculus) is involved in maintaining gaze stability through control of the gain of the vestibular ocular reflex (Ito et al. 1974; Robinson 1976; Liaberger et al. 1984). Zee and colleagues (1985) showed that bilateral ablations of the cerebellar flocculi and portions of the paraflocculi interfered with gaze stability and led to post-saccadic ocular drift. The velocity and accuracy of saccades in this study were normal, but had exponential post-saccadic ocular drifts lasting 40-150 MS. This post-saccadic ocular drift was usually outward, and could have amplitudes up to 15% of, the amplitude of the antecedent saccade. The direction and amplitude of the drift varied from animal to animal. Zee et al. (1981) suggested that the effect of flocculectomy on saccades is the loss of adaptive control over the slide-step of innervation. Hence it seemed reasonable to investigate the role of the vestibulocerebellum in maintaining gaze stability through suppression of post-saccadic ocular drift.
To determine the effect of a flacculecotomy on the adaptive control mechanism for suppression of post-saccadic drift we measured the ability of optically-imposed retinal image motion to induce post-saccadic ocular drift. Optican and Miles (1985) used exponential post-saccadic image motion to induce a compensatory post-saccadic ocular drift. The ocular drift was exponential and occurred with spontaneous saccades in darkness. The post-saccadic ocular drift elicited by Optican and Miles could be accounted for quantitatively by assuming that two of the components of saccadic innervation (the slide and step) were adapted to minimize post-saccadic retinal slip (1985).

After flacculecotomy, such post-saccadic ocular drift was markedly reduced. A preliminary account of these results was reported elsewhere (Optican et al. 1980).

**Methods**

Two juvenile theta monkeys (Macaca mulatta) were used in this study. Monkeys LN and RS are monkeys 3 and 6 of an earlier study, and details of general procedure have been given in the report of that work (Zee et al. 1981).

After preoperative testing, bilateral ablations of the floucculi and portions of the paraflocculus were made under Nembutal anesthesia. Monkey LN had a less complete lesion than monkey RS. The lesions included most of the flocculi on both sides, as well as the ventral paraflocculus and lobules 7-10 of the dorsal paraflocculus. Portions of lobules 9 and 10 of the flocculus were spared on the right in both animals. (Fig. 1 of Zee et al. (1981) shows a photomicrograph of the lesion in monkey LN).

The animals' ability to suppress post-saccadic ocular drift was evaluated with the adaptive paradigm of Optican and Miles (1985) both before and after surgery. Testing involved recording saccades made spontaneously in the dark before and after an adaptation period. During the two-day adaptation period, the animal faced a translucent screen onto the back of which was projected a densely textured target (3040 × 1000). Eye movements were measured with a magnetic field/search coil technique, yielding a resolution of 0.25° and a bandwidth (-3 dB) of 240 Hz (Robinson 1963). At the end of every saccade a computer caused the visual scene to drift exponentially with a time constant of 50 ms and an amplitude half that of the antecedent saccade's amplitude. In one experiment, the direction of the drift was outward, and in another it was backward, relative to the antecedent saccade.

Post-saccadic ocular drift in the dark was quantified by measuring the size of the rapid, pulse-driven, portion of the saccade (P), and the change in the final, step-determined, position (S) (see Fig. 1). The pulse-step ratio (P/S), calculated as P/S, would be 1.0 for an ideal saccade. Ratios larger than 1.0 indicate a post-saccadic ocular drift backward, and ratios less than 1.0 indicate a post-saccadic ocular drift forward. The amplitude of the post-saccadic ocular drift is essentially a fraction of the amplitude of the antecedent saccade. Hence, a single number can be used to quantify the drift over all saccade amplitudes (Optican and Miles 1985). Thus, even if the range or distribution of saccade sizes changes after flacculecotomy, the P/S can still be used to compare pre- and post-operative data.

The change in the saccadic innervation does not compensate completely for the 50% amplitude of the image slip (Optican and Miles 1985). The effectiveness of the adaptive mechanism was quantified by calculating the range of the P/S values. The range was calculated as the percentage change from the P/S after outward adaptation to that after backward adaptation: (backward - outward) / outward) × 100%. The post-operative change in this range quantifies the effects of ablation.

**Results**

After flacculecotomy saccades were still accurate, with only a small amount of post-saccadic drift (Zee et al. 1981). As shown in Fig. 1, however, there was a marked reduction in the ability of optically-induced post-saccadic retinal image slip to elicit a compensatory ocular motor adaptation. Table 1 shows the pulse-step ratios for both monkeys. Preoperatively, both monkeys had pulse-step ratios close to the ideal value of 1.0 (0.98 and 0.97), and developed appreci-
able post-saccadic ocular drift during the adaptation paradigm. In monkey RS, adaptation caused a change in the psl to 0.78 in response to onward, and to 1.11 in response to backward slip, an adaptive range of 42%. In monkey LN, the psl was lowered to 0.73, and raised to 1.17, a range of 60%.

After flocculotomy the psl was 0.96 in monkey RS, and 1.01 in monkey LN. When we attempted to elicit an adaptive response by moving the visual scene, however, there was very little change in the post-saccadic ocular drift. In response to onward retinal slip, both animals showed a slight reduction in the psl (to 0.90 in monkey RS, and 0.97 in monkey LN). These reductions were significant (p < 0.005). In response to backward retinal slip, however, neither animal showed significant changes in the psl. The adaptive range was thus reduced by a factor of six for monkey RS (from 42% to 7%) and by a factor of 15 for monkey LN (from 60% to 4%).

Discussion

Normal animals use an adaptive mechanism to suppress post-saccadic ocular drift and thereby maintain good ocular stability immediately after a saccade. This suppression requires the balancing of different components of saccadic innervation, so that the pulse-slide-step exactly compensates for the dynamics of the ocular motor plant. Previous work established that suppression of ocular drift is dependent on both the amplitude of the saccade and the ocular movements. One component is the pre-saccadic inhibition of the antagonist muscles. These changes in the pre-saccadic inhibition require the suppression of saccades when the eyes are restrained. This has been observed in patients with lesions of the superior colliculus and the basal ganglia. The results of the present study support the hypothesis that the adaptive mechanism involves the cerebellum and the brainstem. Therefore, the adaptive mechanism is part of a network that includes the cerebellum and the brainstem. The adaptive mechanism is responsible for the suppression of post-saccadic ocular drift. The residual ability to change the pulse-slide-step ratio was asymmetric in both monkeys, allowing for some reduction of the psl, but not for much of an increase. This asymmetry is consistent with the observation that flocculotomized and cerebellar-lesioned monkeys develop small amounts of post-saccadic ocular drift (usually in the onward direction, i.e., psl less than 1.0) (Optican and Robinson 1980; Zee et al. 1981). These ocular drifts are never corrected.

We conclude that the adaptive mechanism for suppression of post-saccadic ocular drift is dependent upon the flocculus and/or paraflocculus. This is consistent with the concept that the vestibulocerebellum has a general role in stabilizing gaze (Zee et al. 1981). Suppression of ocular drift could be achieved by adjusting the gains and time constants of the slide-step of innervation (Optican and Miles 1985). A slide-step adaptive controller would have two components: one to determine an error signal (to indicate whether the signal should be raised or lowered), and one to adjust the gains. The vestibulocerebellum could be acting as either or both parts of the controller.

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References


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