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The effect of saccular ablation on vertical optokinetic after-nystagmus in squirrel monkeys

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Summary. The effect of bilateral saccular ablation on the asymmetry of vertical optokinetic after-nystagmus (OKAN) was studied in squirrel monkeys. No significant changes occurred in the initial slow-phase eye velocity (SPEV) or the time constant of the upward or downward OKAN first phase (OKAN-I) under various stimulus conditions. However, with a protracted downward stimulus, the maximum SPEV and the number of beats of the slow-phase-up OKAN second phase (OKAN-II) significantly increased. This increase should be the result from enhancement of the downward optokinetic input. In contrast, there was only minimal change in the slow-phase-down OKAN-II. Thus, the asymmetrical dominance of the vertical OKAN (dominance upward) remained the same after saccular deafferentation.

Key words: Saccule – Vertical optokinetic after-nystagmus – Squirrel monkey

Introduction

Unlike horizontal optokinetic nystagmus (OKN), vertical OKN in an upright position under the Earth's gravity is characterized by a slow-phase-up dominant asymmetry. This asymmetry was found in the squirrel monkey previously [12]. It has recently been reported that this asymmetry is reversed in microgravity, implicating the gravitational influence in vertical OKN [4]. Signals from the retina and vestibular end-organs, which reach the oculomotor output system, play important roles in gaze stabilization. The saccular afferent coordinates vertical eye movement [5], and connects with group y cells which respond in phase with upward head and eye movements [3]. In our previous report, bilateral ablations of the saccular maculae in squirrel monkeys resulted in the reversal of the asymmetric dominance in vertical OKN [9].

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Vertical asymmetry has been found in vertical optokinetic after nystagmus (OKAN). Like horizontal OKAN, vertical OKAN encompasses OKAN-I (OKAN in the same direction as OKN) and OKAN-II (OKAN in the opposite direction of OKN), and so on. This OKAN asymmetry is even more dominant than that of vertical OKN [6, 10, 11], and OKAN-II asymmetry is particularly more dominant than OKAN-I [6]. Thus, it is important to analyze OKAN-I, OKAN-II, and so on, in addition to OKN.

OKAN-II cannot be considered a central response to OKAN-I. The generator of OKAN is considered a second-order system with a leaky integrator [2]. Vertical OKAN-II is a slow-phase-up dominant output in the squirrel monkey [6] and in man [1], similar to OKAN-I [10, 11]. However, the origin of this asymmetry is not well characterized. Vertical OKAN-II has not been studied in microgravity, perhaps due to difficulties in evocation with limited stimulus duration. As previously reported, more vertical OKAN can be seen following a protacted stimulus [6]. Thus, various stimulus conditions were used in this study to clarify the role of the macula sacculi in the asymmetry of vertical OKAN.

Materials and methods

The eye movements of four young adult squirrel monkeys *(Saimiri sciureus)* were recorded with the pericorneal search coil recording method [8]. The animals were restrained (head and neck fixed) in the upright position, with the interaural line aligned at the rotatory axis of a microprocessor-controlled optokinetic drum (60 cm diameter, 16 black stripes, each 1.7 cm wide). This OK stimulator provided a well-illuminated whole visual field rotation around the animal. OK stimulation conditions were 60°/s for 3 min; and 90°/s for 3 min and 60 min. To maintain alertness, amphetamine sulfate (0.25 mg/kg) was injected intramuscularly 15 min prior to testing.

Three preoperative measures were obtained for each animal. Tests were performed at intervals greater than 1 week to prevent any bias from repeated exposure. Methods for the calculation of slow-phase eye velocity (SPEV) and time constant (TC) have been described previously [6]. Bilateral sacculectomy via the transmeatal-oval window approach was performed in one stage [9]. Post-

operative tests were performed weekly for 8 weeks (4 weeks in one animal). Three bilaterally stapedectomized animals served as controls. At the completion of data acquisition, temporal bones were processed by the standard celloidin procedure and studied by light microscopy.

Results

Postoperatively, the gain and regularity of downward OKN improved. The rapid rise of OKN was found both pre- and postoperatively.

The postoperative OKAN-I did not show any statistically significant differences either in SPEV or TC. Only a noticeable decrease was found in the TC of downward OKAN-I with the prolonged stimulus. Upward OKAN-I was not very much affected with any stimulus conditions (Tables 1, 2).

Table 1. Initial slow phase eye velocity (SPEV) of first-phase optokinetic after-nystagmus (OKAN-I) in pre- and postsacculectomy

Stimulus speed (°/s)		Stimulus duration (min)	Preoperative $\bar{x} \pm$ SEM	Postoperative $\bar{x} \pm$ SEM
60	Up	3	25.74 ± 3.22	28.99 ± 7.16
	Down	3	6.38 ± 2.61	7.57 ± 2.34
90	Up	3	28.30 ± 3.44	44.32 ± 13.02
	Down	3	8.81 ± 2.64	7.88 ± 1.22
90	Up	60	35.15 ± 7.14	24.02 ± 9.15
	Down	60	6.83 ± 0.48	10.94 ± 5.41

Table 2. Time constant of OKAN-I pre- and postsacculectomy

Stimulus speed (°/s)		Stimulus duration (min)	Preoperative $\bar{x} \pm$ SEM	Postoperative $\bar{x} \pm$ SEM
60	Up	3	60.43 ± 21.42	76.33 ± 40.54
	Down	3	41.20 ± 19.18	13.91 ± 2.34
90	Up	3	55.50 ± 12.75	45.17 ± 19.10
	Down	3	23.53 ± 7.38	11.33 ± 4.66
90	Up	60	40.83 ± 10.12	18.00 ± 5.58
	Down	60	18.93 ± 6.80	5.63 ± 2.64

Table 3. Percentage appearance of OKAN-II pre- and postsacculectomy

Stimulus speed (°/s)		Stimulus duration (min)	Preoperative	Postoperative
60	Up	3	0%	0%
	Down	3	75%	75%
90	Up	3	0%	0%
	Down	3	50%	100%
90	Up	60	0%	0%
	Down	60	100%	100%

Up/down, stimulus direction

The asymmetry of vertical OKAN-II remained almost the same after saccular ablation. Only the incidence of slow-phase-up OKAN-II increased with the 90°/s stimulus (Table 3). Slow-phase-down OKAN-II was not found in any of the animals pre- or postoperatively (Table 3).

The maximum SPEV of slow-phase-up OKAN-II increased after saccular ablation ($P < 0.05$) (Fig. 1, left). The difference between the pre- and postoperative values was larger with increased stimulus duration. There was no significant change in the appearance time of maximum SPEV. The number of beats of slow-phase-up OKAN-II also increased (Fig. 1, right). Representative OKAN-II with 60-min downward stimulation is illustrated in Fig. 2.

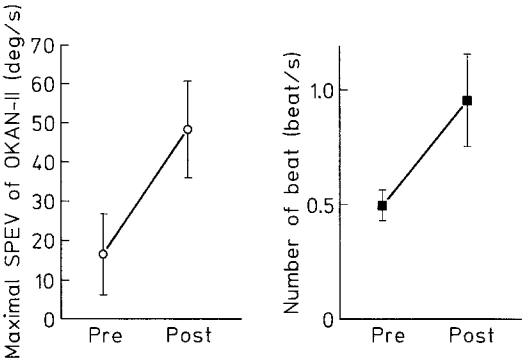

Fig. 1. *Left:* Change of maximal slow-phase eye velocity *(SPEV)* of second-phase optokinetic after-nystagmus (OKAN-II) (upward beating) with downward stimulus before and after total saccular deafferentation. Maximal SPEV significantly ($P < 0.05$) increases after bilateral sacculectomy. *Vertical bar,* SD. OK stimulus condition: 90°/s for 60 min. *Right:* Change in mean number of beats of OKAN with downward stimulus also shows a significant increase ($P < 0.01$) after bilateral sacculectomy

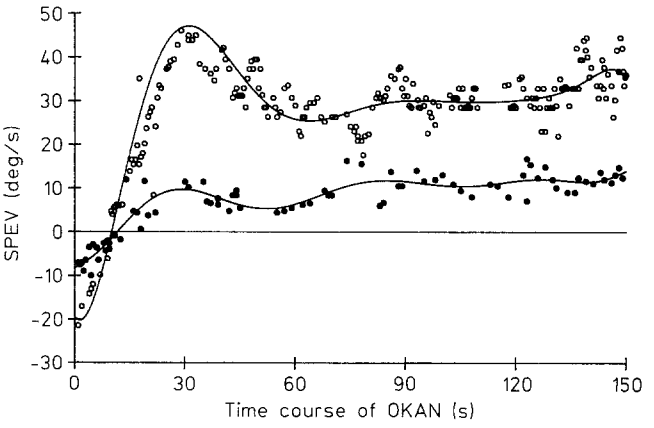

Fig. 2. Representative time course of OKAN pre- and postbilateral sacculectomy using the protracted downward stimulus (90°/s, for 60 min). This case shows increased initial SPEV of OKAN-I. The increased maximal SPEV and number of beats are seen postoperatively in OKAN-II (upward beating). *Vertical axis,* Positive values signify upward SPEV and negative values signify downward SPEV. *Closed circles,* Preoperative OKAN; *open circles:* postoperative OKAN. Superimposed *solid lines* represent the regression curves of points

Control animals did not show any significant change after bilateral stapedectomy.

Histological studies revealed that the macula sacculi were completely destroyed, with the macular area occupied by connective tissue partly abutting the oval window. All neighboring end-organs, including the crista of the horizontal semicircular canal and macula utriculi, were morphologically intact in all cases.

Discussion

It has been reported previously, in general agreement with the results of human experiments during space flight [4], that total ablation of the saccular maculae in squirrel monkeys will enhance down eye movements by reduction of the static input [9]. In an earlier study, an enhancement of down eye movement was found in vertical OKN after utriculo-sacculectomy [7]. The reduction in otolithic input was considered responsible for the altered asymmetry found in vertical oculomotor functions.

The vertical OKAN system, like the vertical OKN system, has been characterized as upward dominant. This has been clearly observed in OKAN-II. Although downward OK stimuli evoked dominant slow-phase-up outputs, upward OK stimuli evoked only little slow-phase-down outputs [6].

The previous finding that enhancement of the downward OK stimulus results in increased slow-phase-up OKAN-II is consistent with the results of our present study. Bilateral saccular ablations resulted in the enhancement of downward eye movements, thus resulting in a significant increase in slow-phase-up OKAN-II. No significant change was found in slow-phase-down OKAN-II, the upward OK input of which was similar pre- and post-sacculectomy. Thus, we conclude that the saccule has little influence on the asymmetrical dominance of vertical OKAN-II.

Combined bilateral utriculo-sacculectomy also failed to change vertical OKAN asymmetry (unpublished data). It is possible that, in contrast to vertical OKN, the second-order system is somewhat independent of gravitational receptor input. This is similar to the horizontal oculomotor system in which it has been found that even bilateral labyrinthectomies do not reduce OKAN-II with a prolonged OK stimulus [8].

Which neural structures are responsible for the asymmetrical behavior of the vertical OKAN system? We recently completed a study (unpublished) in which slow-phase-down OKAN was increased by removal of the cerebellar uvula and nodulus. Thus, the asymmetry of vertical OKAN does not appear to be related to the vestibular periphery, but rather is influenced by the vestibulocerebellum.

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