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Time Course of Cerebellar Flocculus Visual Complex Spike Responses

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Abstract: It is well known that the flocculus complex spike (CS) is driven by retinal slip. We studied the time course of visual CS responses in the anesthetized and paralyzed cat. Onset of contralaterally-directed constant-velocity visual-pattern rotation evoked an initial increase in the CS rate, which gradually decreased but continued to remain above the spontaneous activity level during rotation periods as long as 50s (onset response). Then, cessation of the rotation caused a decrease in the CS rate, which gradually returned to the spontaneous rate (cessation response). Ipsiversive rotation caused a similar CS time course with an inverse response-polarity. The duration of the cessation response increased with increases in the stimulus duration. Acceleration and deceleration of retinal slip velocity did not affect the time course of the responses. Thus, the flocculus CS is modulated time-dependently during the onset and cessation phases of retinal slip regardless of retinal-slip stimulus parameters such as velocity and acceleration. It is concluded that the flocculus CS encodes time information of the retinal-slip onset and cessation but does not encode precise quantitative information of the retinal-slip velocity and acceleration.

Key words: cat, cerebellum, climbing fiber response

Introduction

There are two distinct afferents in the cerebellar cortex: the mossy fiber afferents which evoke the simple spike (SS) of the Purkinje cells and the climbing fiber afferents which elicit the complex spike (CS) of the cells. Because the CS rate is approximately ten times as low as the SS rate, the CS rate itself does not contribute substantially to the output of the Purkinje cell. The CS activity contributes to transient modulation of the Purkinje cell by affecting SS activity for less than 100 ms after the CS occurrence[1,4,5,7)]. For a better understanding of the transient CS function, we must elucidate the stimulus-parameters and conditions that generate the CS activity in detail.

The flocculus CS is known to be driven by retinal slip. Previous studies[2,3,8)] showed direction and velocity preference, ocular dominance, and receptive field properties of the CS responses, but did not focus on the time course of CS responses. The present study describes the time course of the CS activity during and after retinal slip in the cat.

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Methods

Eleven adult cats were used. Most aspects of experimental procedures were described in a previous paper[2)]. In brief, under ketamine (20–30 mg/kg im) and pentobarbital (<20–30 mg/kg iv) anesthesia, the cats were prepared for unitary recording, from the flocculus Purkinje cells. During recording sessions, anesthesia was supplemented every 2 hr by administration of ketamine hydrochloride (10–20 mg/kg iv), and the cat was immobilized with pancuronium bromide and artificially venti-

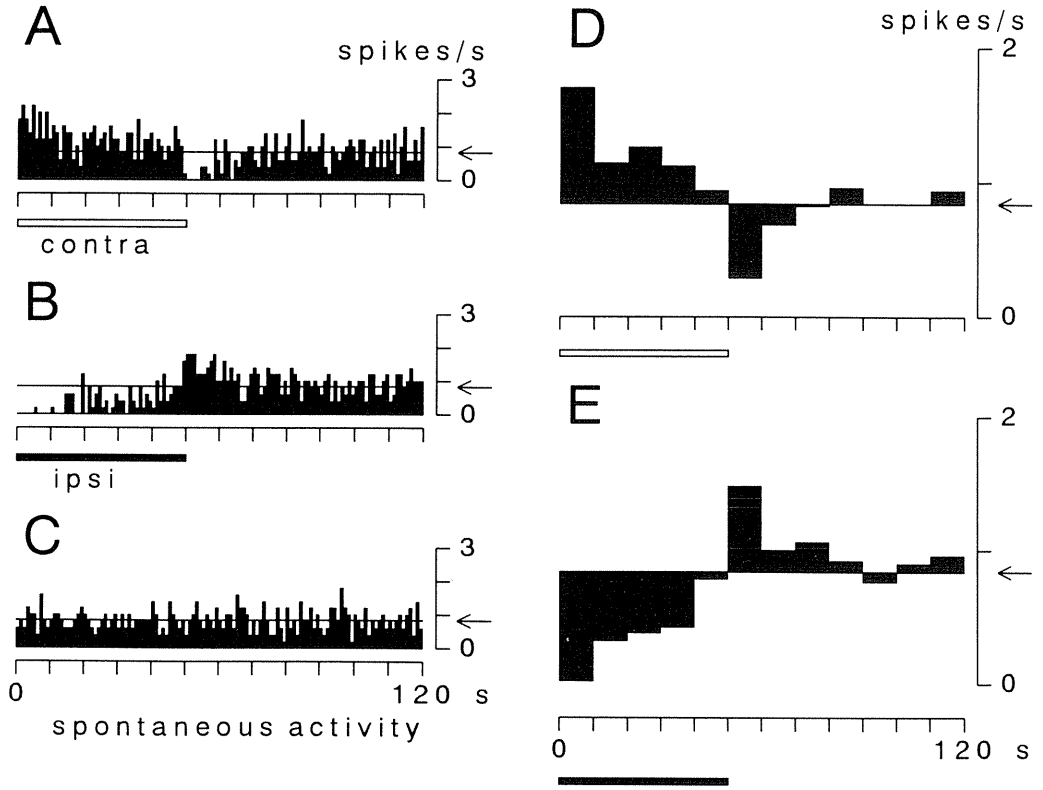

Fig. 1. Time course of complex spike (CS) activity in response to constant-velocity (2°/s) visual pattern rotation. In CS density histograms (A-C, 5 repetitions, binwidth 1s) and CS modulation histograms (D-E, 5 repetition, binwidth 10s) the horizontal line with an arrow indicates spontaneous level. Open and black bars show the duration of contralaterally and ipsilaterally directed stimuli. Absence of a bar under the histogram shows the stationary phase of the visual-pattern.

lated. The CS was isolated from the simple spike (SS). For visual stimulation, a random dot pattern was projected on to a half-cylinder screen (152°X50°). At the end of each experiment, the animal was deeply anesthetized with pentobarbital and perfused with 10% formalin. The experiment was performed in accordance with Guidelines for Animal experiments, Toyama Medical and Pharmaceutical University.

Results

We recorded the CS activity of 29 Purkinje cells that responded to horizontal rotation of the visual pattern at a constant velocity of 2°/s (velocity step by 100°/s^2 acceleration and deceleration). In accordance with Fushiki *et al.*[2], the cells responded direction-selectively to the rotation: CS firing increased during contralaterally directed rotation and decreased during ipsilaterally directed rotation. The CS time course is shown in Fig. 1. Onset of contralaterally directed rotation evoked an initial transient increase in the CS rate, which gradually decreased but continued to remain above the spontaneous activity level during rotation periods as long as 50s (contra-onset response) (Fig. 1A). Then, cessation of the contralaterally directed rotation caused a pause in CS activity, which gradually returned to the spontaneous level (contra-cessation response) (Fig. 1A). However, onset of ipsi-

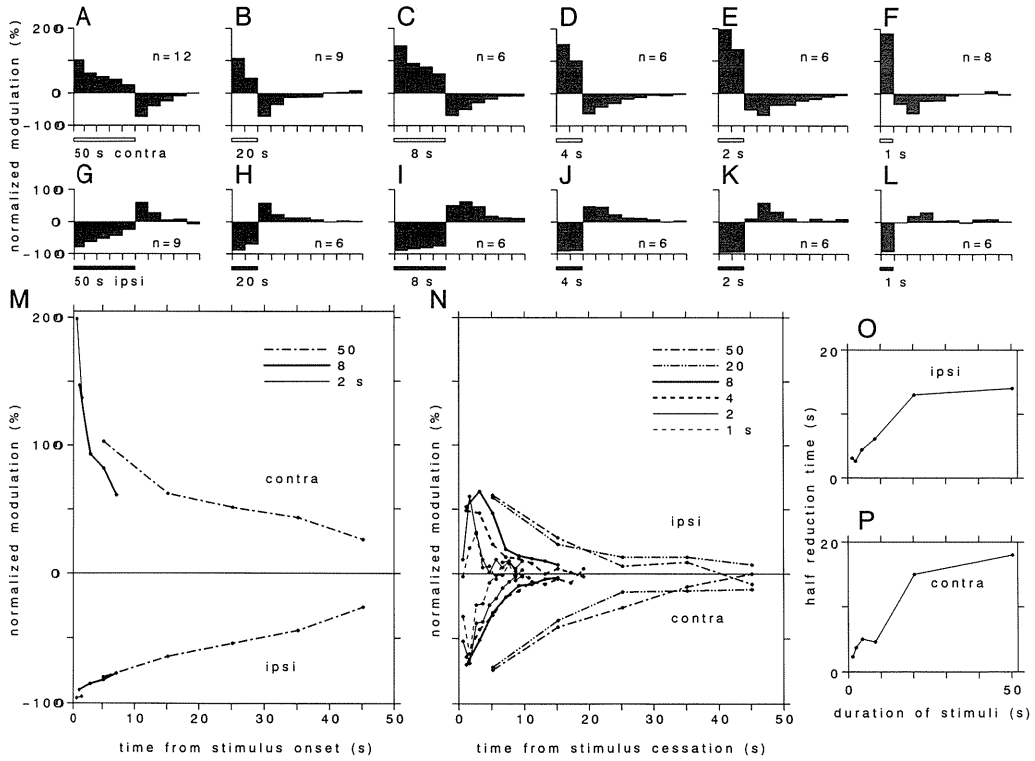

Fig. 2. Population data showing time course of CS modulation in response to constant velocity (2°/s) visual-pattern rotation. A-L: normalized CS-modulation histograms (5 repetitions, binwidth 10s for A, B, G, H; 25 repetitions, binwidth 2s for C, D, I, J; 50 repetitions, binwidth 1s for E, F, K, L) in response to contralaterally (open bar) and ipsilaterally (black bar) directed rotation for the indicated stimulus duration. 0%, no CS modulation; 200%, 200% increase above the spontaneous level; −100%, 100% decrease (firing pause) below the spontaneous level. M: normalized time course of CS modulation during contralaterally and ipsilaterally directed stimuli. N: normalized time course of CS modulation after cessation of contralaterally and ipsilaterally directed stimuli (cessation response). O-P: half reduction time of the cessation responses plotted against the stimulus duration.

laterally directed rotation caused a pause in the CS rate, which gradually increased but continued to remain below the spontaneous level during the rotation period (ipsi-onset response) (Fig. 1B) Then, cessation of the ipsiversive rotation evoked an increase in CS activity, which gradually returned to the spontaneous level (ipsi-cessation response) (Fig. 1B). This modulation in CS activity above and below the spontaneous level (mean CS rate in Fig. 1C) is illustrated in Figs. 1D and 1E, which were constructed from Figs. 1A and 1B, respectively.

Figures 2A-L show average modulation in CS activity above and below the spontaneous level at various stimulus durations (50, 20, 8, 4, 2, and 1s). From data in Figs. 2A (stimulus duration, 50s), 2C(8s), and 2E(2s), average time courses of the contra-onset response were evaluated and are shown in Fig. 2M. Excitatory modulation was large (199% increase above the spontaneous activity level) only at 0–1s after stimulus-start, and decreased rapidly to approximately 100% at 5s, and then decreased gradually to 26% at 45s. From data in Figs. 2G (stimulus duration 50s), 2I(8s), and 2K(2s),

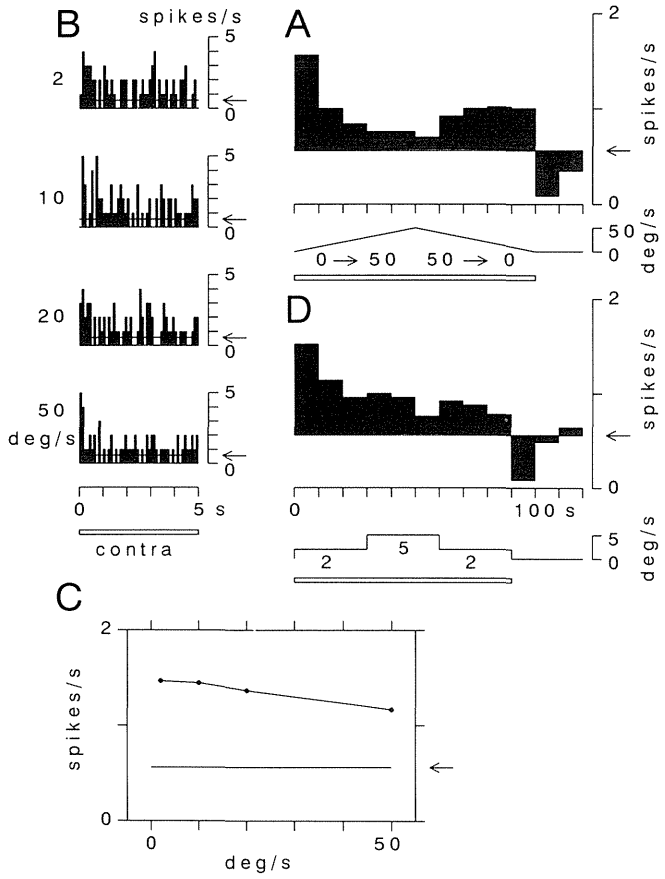

Fig. 3. Time course of CS modulation in response to velocity changes of visual pattern movement. The horizontal line with arrow shows the spontaneous level. A: CS-modulation histogram (5 repetition, binwidth 10s) in response to $1°/s^2$ acceleration and deceleration of the visual pattern. B: CS density histograms (10 repetition, binwidth. 1s) during contralaterally (open bar) directed stimuli for indicated stimulus velocities. C: velocity-tuning curves of the CS activity. D: CS-modulation histograms (5 repetition, binwidth 10s) in response to velocity-step of 5°/s during 2°/s during 2°/s constant velocity stimuli.

average time course of the ipsi-onset response were evaluated in Fig. 2M. Inhibitory modulation was large (−96%) at 0–1 s after stimulus onset, then decreased gradually to −26% at 45s.

The cessation response was present at all stimulus durations tested (Figs. 2A-L), suggesting that the response was not due to a prolonged stimulation-period of 50s. From data in Figs. 2A-F and 2G-L, average time courses of the contra- and ipsi-cessation responses at each stimulus duration were evaluated, respectively, and were shown in Fig. 2N. The duration of the cessation responses tended to increase with increase in the stimulus duration. Half reduction time of the ipsi- and contra-cessation responses was calculated from Fig. 2N, and was presented as the function of

the stimulus duration in Fig. 2O and 2P, respectively. The half reduction time tended to increase with the increase in stimulus duration.

The time course of the CS modulation in response to triangle velocity stimuli (1°/s^2 acceleration and deceleration) was studied (Fig. 3 A). A large transient increase in CS rate at stimulus onset was followed by a rapid adaptation of the response during the acceleration phase. The CS rate tended to increase during the deceleration phase. During both stimulation-phases, the CS rate remained above the spontaneous level. Finally, stimulus cessation caused the CS rate to decrease below the spontaneous level. The velocity sensitivity in this unit was checked by applying various constant-velocity stimuli (2, 10, 20, 50°/s) in the contralateral direction (Fig. 3B). By averaging CS rates during each stimultation, a velocity-turning curve was drawn in Fig. 3C. The CS activity during the triangle velocity stimuli (Fig. 3A) was below the velocity-tuning curve level (Fig. 3C) except for that during the initial 10s. These results suggest that 1) transient responses at the onset and cessation of velocity-step stimuli are not due to large (100°/s^2) acceleration and deceleration components of the stimuli, and 2) the quick adaptation in CS responses during stimulation period is not due to the constant velocity component of the stimuli. The stimulus velocity suddenly (100°/s^2 acceleration and deceleration) changed from 2°/s to 5°/s, and then to 2°/s (Fig. 3D), but this did not evoke prominent changes in the time course of CS modulation (Fig. 3D), suggesting that the CS responses are not affected by sudden velocity changes during retinal image movement. Similar results were obtained in 3 other cells tested.

Discussion

The present study demonstrated that 1) the flocculus CS response is well characterized by its time dependency during retinal slip stimuli, that is, the CS is strongly modulated only during the onset and cessation phases of retinal slip and 2) retinal-slip parameters such as velocity and acceleration do not affect the time dependency. In conclusion, the flocculus CS encodes time information of the rtinal-slip onset and cessation but does not encode precise quantitative information of the retinal slip velocity and acceleration.

It has been reported that the flocculus is responsible for reducing retinal slip[2] by its eye movement control mechanisms[5]. The time information of the CS may contribute to floccular eye movement control mechanisms[5] at onset and cessation of the retinal slip.

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