Acta Medica et Biologica
Vol. 33, No. 3, 143-150, 1985

SPINAL TRIGEMINAL NUCLEAR PROJECTIONS TO THE CEREBELLAR FLOCCULUS IN CATS

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(Received March 30, 1985)

ABSTRACT

Unitary activities were recorded extracellularly by a tungsten microelectrode placed in the caudal part of the dorsal nucleus of the raphe (DNR) in cats. The neurons in the caudal part of DNR activated by electrical stimulation of the contralateral cerebellar flocculus also responded to stimulation of the ipsilateral parvocellular division of the alaminar spinal trigeminal nucleus (5SP)[1]. In addition, a preceeding unitary response to stimilation of 5SP collided with an antidromic unitary response to floccular stimulation. These findings suggest that the afferent projections from 5SP to the contralateral cerebellar flocculus via the caudal part of DNA may exist there.

INTRODUCTION

The cat's cerebellar flocculus can be divided into three zones on the basis of differences in their efferent projection sites.[14,15] Recently, we have shown that electrical stimulation of these floccular zones elicited smooth eye movements: a downward eye movement was produced by stimulation of the caudal zone; a ipsilateral horizontal eye movement, by stimulation of the middle zone; an upward eye movement, by stimulation of the rostral zone[13]. In addition, ablation of the cat's cerebellar flocculus resulted in reduction of the slow phase velocities of optokinetic nystagmus to higher optokinetic stimulus velocities[3,4,7]. Thus, the cerebellar flocculus in cats plays an important role in eye movement control.

Considering the role of the cerebellar flocculus in eye movement control, the afferent projections to the cemebellar flocculus must convey information related to eye movements such as eye velocity or head velocity[8,17]. As for the afferent projections to the cat's cerebellar flocculus, we have also shown that there are four major origins in the

brainstem[16]. Inputs to these prefloccular nuclei may contain information relevant to eye movement control. The caudal part of the dorsal nucleus of the raphe (DNR)[5] is one of these four major nuclei[16]. The present report explains that the parvocellular division of the alaminar spinal trigeminal nucleus (5SP)[1] projects to the cerebellar flocculus via DNR in cats. Preliminary reports have already been published in brief[5,6].

METHODS

The experiments were performed in 23 cats (weighing 2-3 kg) anesthetized with i. p. injection of a mixture of α-chloralose (50 mg/kg) and urethan (0.6 g/kg). The cats were mounted in a stereotaxic apparatus and the posterior vermis of the cerebellum was aspirated, exposing the floor of the fouth ventricle. Next the cats were immobilized with i. v. injection of gallamin triodide (Flaxidil) and artificially respirated with air. Tungsten electrodes (tip diameters of 5-10 μm) were inserted into the brainstem under visual control in order to record extracellularly unitary activities from the caudal part of DNR. For electrical stimulation (pulse width, 0.05 msec) of cerebellar flocculus, bipolar steel electrodes were inserted stereotaxically into the right and the left flocculus, respectively. Concentric electrodes (outside diameters of 0.3 mm) were used for electrical stimulation (pulse width, 0.05 msec) of the medial vestibular nucleus (MV), the superior vestibular nucleus (SV), the magnocellular division of the alaminar spinal trigeminal nucleus (5SM) or 5SP. Discrete stimulation experiments of MV, SV, 5SM or 5SP were carried out on 8, 4, 6 and 5 cats, respectively. The concetric electrodes were inserted stereotaxically into the brainstem. The position of both recording and stimulating electrodes were marked with electrolytic lesion by the passing of a positive DC current (1 mA, 10 sec) at the termination of each experiment and the location of the electrode tip position was histologically determined.

RESULTS

As described previously[6], the neurons in the caudal part of DNR responded to electrical stimulation of MV or SV with a latency of 1-2 msec. In the present experiments, the neurons in the caudal part of DNR also responded to electrical stimulation of the contralateral MV or SV to the recording site with a latency of 0.9-3.0 msec (1.8 ± 0.7 SD, number 53). These unitary responses were superimposed on the field potentials (Fig. 1A). Their latencies fluctuated at each stimulus (Fig. 1A, lower trace). In addition, these unitary responses and field potentials failed to occur at stimulus frequencies above 30 Hz. The lowest threshold current to evoke these responses was 0.05 mA. Some of the neurons in the caudal part of DNR responded to stimulation of the ipsilateral 5SM with a latency of 0.8-2.7 msec (1.4 ± 1.0 SD, number 45, Fig. 1B). These neurons responding to stimulation of MV, SV and 5SM, however, were not activated by stimulation of either side of the cerebellar flocculus.

In the series of the experiments mentioned above, furthermore, some other neurons

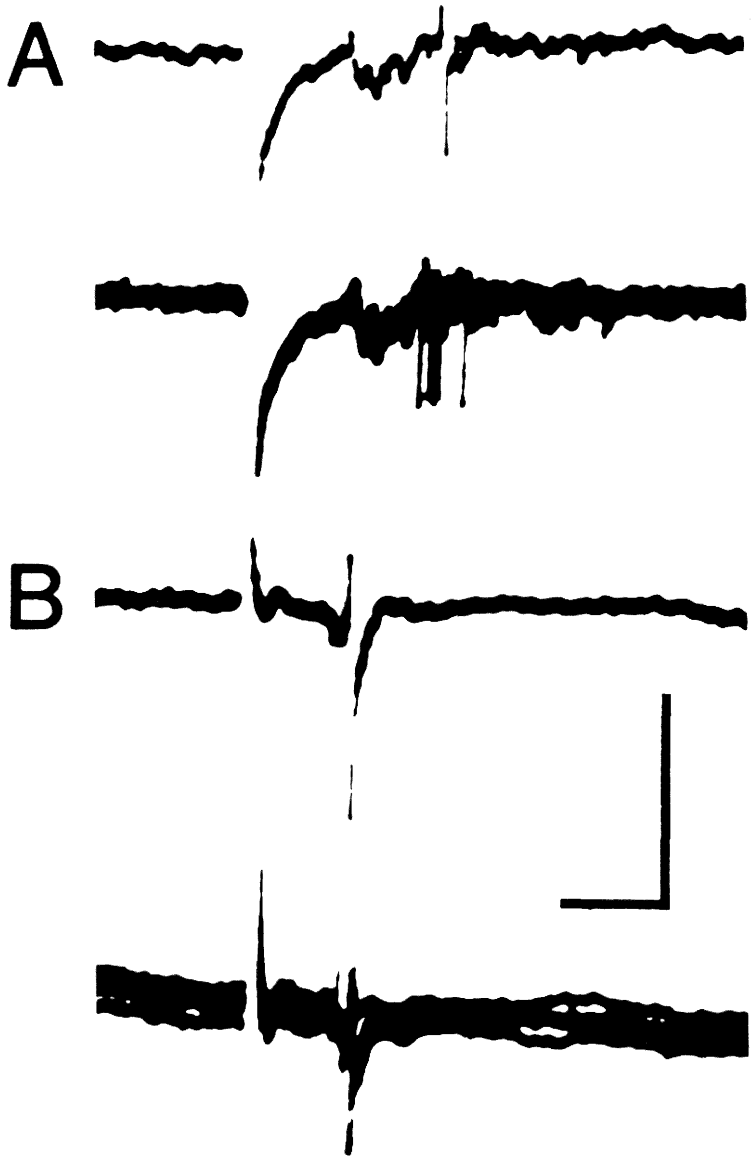

Fig. 1. A: unitary responses recorded in the caudal part of the dorsal nucleus of the raphe (DNR) to stimulation of the contraralateral superior vestibular sucleus, being superimposed on the field potentials. The lower trace is 5 successive superimposed sweeps at the same stimulus intensity (0.15 mA, three times of threshold) showing fluctutation in the latency of unitary responses. B: unitary responses recorded in the caudal part of DNR to stimulation of the ipsilateral parvocellular division of the alminar spinal trigeminal nucleus. Calibration bars in B are voltage and time scales, 1 mV and 1 msec for A and B.

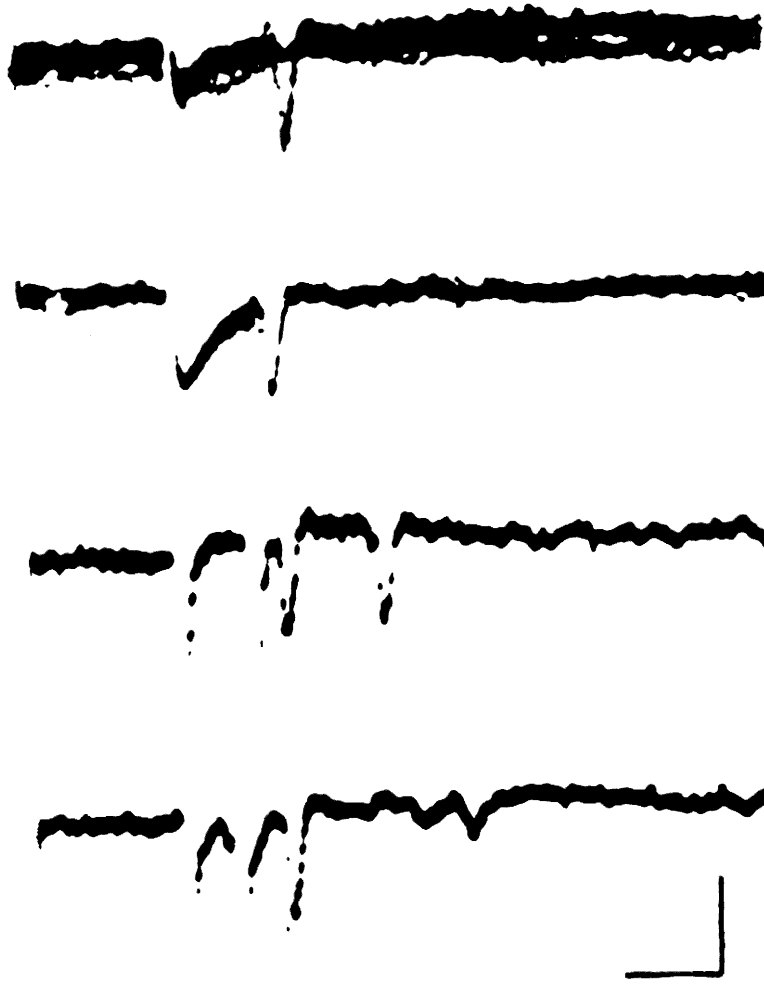

Fig. 2. Unitary responses evoked antidromically in the caudal part of DNR by stimulation of the contralateral cerebellar flocculus. The first trace: 5 successive superimposed sweeps at the same stimulus intensity (0.05 mA pulse, threshold). A unitary response is evoked on three occasions. The second trace: 5 successive superimposed sweeps at the same intensity (three times of threshold) showing a stable latency of the unitary responses. The third and fourth trace: unitary responses to double stimuli (two times of threshold) showing a refractory period of a neuron; its responses are represented in the first and the second trace. Calibration bars below the fouth trace are voltage and time scales, 0.5 mV and 1 msec.

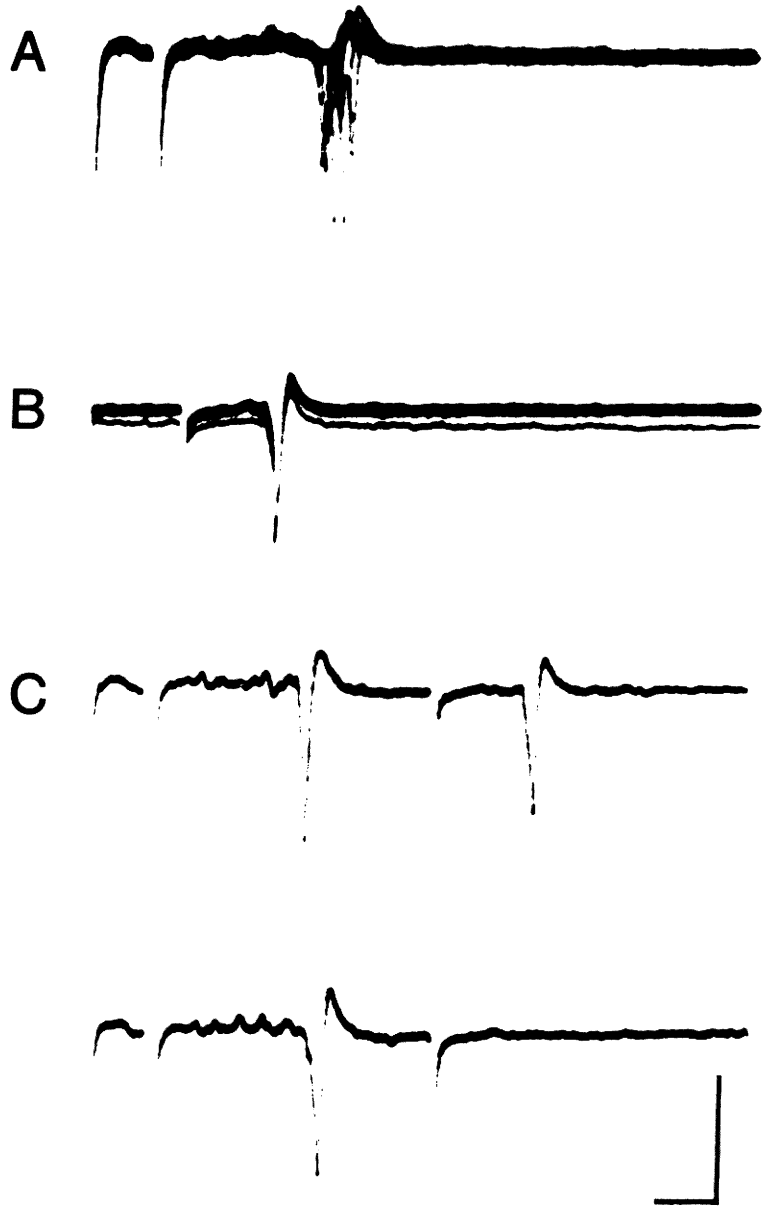

Fig. 3. Unitary responses recorded from a neuron in the caudal part of DNR which was activated antidromically by stimulation of the contralateral cerebellar flocculus and also orthodromically by stimulation of the ipsilateral parvocellular division of the alaminar spinal trigeminal nucleus (5SP). A: 5 successive superimposed sweeps at the same stimulus intensity (two times of threshold) showing fluctuation in the latency of unitary responses evoked by stimulation of the ipsilateral 5SP. B: 5 successive superimposed sweeps at the same stimulus intensity (two times of threshold) showing a stable latency of unitary responses evoked by stimulation of the contralateral cerebellar flocculus. The refractory period in this case was 0.6 msec. C: single sweep showing unitary responses to stimulation of both 5SP (left) and the contralateral cerebellar flocculus (right). Stimulus is first given to 5SP, and then to the flocculus. In the upper trace, each stimulus is effective in evoking a response. In the lower trace, however, stimulus to the flocculus does not evoke a response though the stimulus intensity is the same as that in the upper trace. Calibration bars below C are voltage and time scales, 0.5 mV and 1 msec.

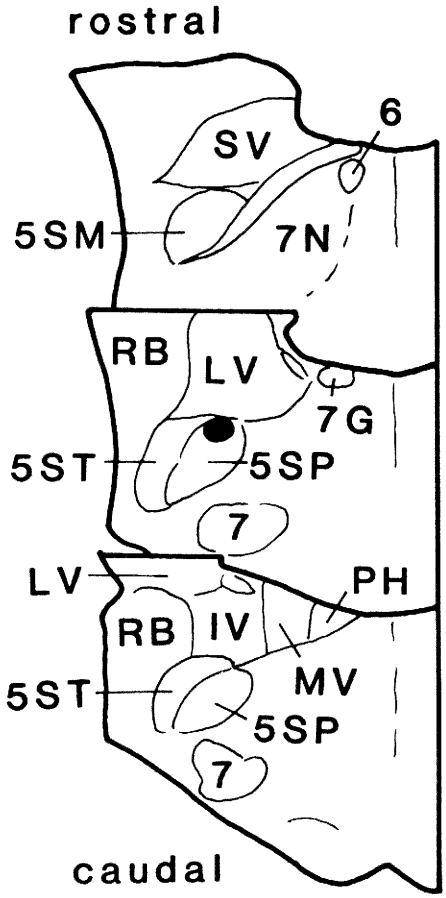

Fig. 4. Line drawings of selected transverse sections of the brainstem showing a stimulating site in the case from which the unitary responses obtained are shown in Fig. 3. The distance of each section is 1 mm. Blackened area represents the electrolytic lesion site. Abbreviations: IV, inferior vestibular nucleus; LV, lateral vestibular nucleus; MV, medial vestibular nucleus; PH, prepositus hypoglossi nucleus; RB, restiform body; SV, superior vestivular nucleus; 5SM, magnocellular division of the alaminar spinal trigeminal nucleus; 5SP, parvocellular division of the alaminar spinal trigeminal nucleus; 5ST, spinal trigeminal tract; 6, abducens nucleus; 7, facial nucleus; 7G, genu of the facial nerve; 7N, facial nerve.

were activated antidromically by stimulation of the cerebellar flocculus, but did not respond to stimulation of MV, SV, or 5SM. As can be seen in Fig. 2, the neurons responded to stimulation of the cerebellar flocculus in an all-or-none fashion (Fig. 2, the first trace), with a stable latency at each stimulus (Fig. 2, the second trace) and with a short refractory period of less than 0.8 msec (Fig. 2, the third and fourth trace). These findings indicate that the neurons were activated antidromically by stimulation of the cerebellar flocculus. The latency of these antidromic unitary responses to stimulation of the contralateral cerebellar flocculus was 0.8-2.1 msec (1.3 ± 0.3 SD, number 42) and that to stimulation of the ipsilateral cerebellar flocculus was 0.7-2.0 msec (1.2 ± 0.3 SD, number 46).

On the other hand, fourteen out of twenty eight neurons in the caudal part of DNR responded to electrical stimulation of both the ipsilateral 5SP (Fig. 3A) and the contralateral cerebellar flocculus (Fi. 2B) to the recording site. As can be seen in Fig. 3, the former response was characterized by a latency of 3-4 msec (3.1 ± 0.6 SD, number 14) which fluctuated at each stimulus (Fig. 3A), while the latter was characterized by a latency of 0.9-1.8 msec which was stable at each stimulus (Fig. 3B) and by a short refractory period of less than 0.8 msec. Furthermore, a unitary response to floccular stimulation was inhibited by a preceeding unitary response to stimulation of 5SP. This inhibition occurred during a period which corresponded with the sum of both the refractory period and two times that of the latency of the unitary response to stimulation of the cerebellar flocculus (Fig. 3C). As long as the stimulating electrodes were in 5SP (Fig. 4) or the cere-

bellar flocculus, the threshold current to evoke these responsess was lower than 0.1 mA. The lowest threshold current was 0.05 mA. These findings indicate that there exist some neurons in the caudal part of DNR activated orthodromically by stimulation of the ipsilateral 5SP and also invaded antidromically by stimulation of the contralateral cerebellar flocculus.

DISCUSSION

In the present experiments, some neurons in the caudal part of DNR responded to both stimulation of the ipsilateral 5SP and that of the contralateral cerebellar flocculus with low stimulus current. In addition, a collision occurred between these two responses (Fig. 3C). The projections from the caudal part of DNR to the cerebellar flocculus have been already demonstrated by anatomical studies with the method of retrograde axonal transport of horseradish peroxidase (HRP)[5,16]. This anatomical fact corresponds well with the findings in the present experiments in that the neurons in the caudal part of DNR were activated antidromically by stimulation of the cerebellr flocculus (Fig. 2 and 3B). These findings may support the view that the projections from 5SP to the contralateral cerebellar flocculus via the caudal part of DNR exist there.

As mentioned above, there is a high possibility that the neurons in 5SP project to the ipsilateral caudal part of DNR. They may, however, project not monosynaptically but polysynapiticall to the caudal part of DNR, because the latencies of the unitary reponses in the caudal part of DNR to stimulation of 5SP were longer than those to stimulation of MV, SV, or 5SM. This view may be supported by the fact that injection of HRP in the caudal part of DNR labeled the neurons in MV, SV, and 5SM, while it did not labeled those in 5SP[6]. Since degeneration fibers from 5SP enter into the medullar reticular formation after lesion of 5SP[2], the unitary responses in the caudal part of DNR to stimulation of 5SP may be relayed through the medullar reticular formation.

Recently, the primary afferent projections from the extraocular muscle to the brainstem via the ophthalmic subdivisitn of the ipsilateral semilunar ganglion have been reported as results when using the method of retrograde axonal transport of HRP[12]. These primary projection fibers terminate in 5SP[10,11]. The second order neuros in the spinal trigemenal nucleus could provide the basis for the extraocular musclar afferent projections to the cerebellar flocculus[9]. There follows a possibility that the projectitns from 5SP to the cerebellar flocculus via the caudal part of DNA may be a part of the extraocular afferent projections to the cerebellar flocculus and may be involed in eye movement control.

Finally, the projections from MV, SV and 5SM were confirmed by the present electrophysiological experiments. The functions of these projections is obscure at present. Further study is neccessary to clarify these functions.

ACKNOWLEDGEMENTS

We are grateful to Mr. K. Ikarashi for his photographic assistance and histological preparations. This investigation was partially supported by Grant No. 59570054 of The Ministary of Education of Japan

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