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Reflex Action of the Semicircular Canals on Cervical Extensor and Flexor Muscles in Cats*

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=ABSTRACT=

In urethane-anesthetized cats, each vestibular semicircular canal nerve was electrically stimulated, and reflex responses of the cervical extensor and flexor (the splenius capitis and sternomastoid muscles) were recorded by means of electromyography. Stimulation of a unilateral (anterior, horizontal or posterior) canal nerve elicited excitation of the contralateral cervical muscles and inhibition of the ipsilateral ones; during the canal nerve stimulation, the two muscles in one side of the neck revealed synergistic responses. Based on these experimental results, we formulated a diagram showing the functional connections between the vestibular semicircular canals and the cervical muscles in the vestibulocollic reflex.

Key Words: Vestibular semicircular canal; Cervical muscle; Vestibulocollic reflex; Axial muscle.

INTRODUCTION

Angular acceleration of the head elicits various postural regulations such as vestibulo-ocular, vestibulo-collic, and vestibulo-spinal reflexes (Cohen, 1974; Goldberg & Fernandez, 1975; Wilson & Jones, 1979). Neuroanatomical and physiological studies have revealed that the elementary pathways for these reflexes are composed of three neurons; primary vestibular afferents, vestibular nuclear neurons and final motoneurons (Szentagothai, 1950; Brodal et al, 1962; McMaster et al, 1966; Carpenter, 1971; Fuchs, 1981). Nevertheless, patterns of the interconnections between vestibular semicircular canals and final motoneurons are controversial (Wilson, 1975; Goldberg & Fernandez, 1984; Ito, 1985; Büttner & Büttner-Ennever, 1988).

In order to explore the neural connections for the vestibulo-collic reflex system, Wilson and Maeda (1974) recorded the synaptic potential changes of the cervical extensor motoneurons in response to stimulation of each semicircular canal nerve in the cat, and they presented a schematic diagram showing the interconnections between the semicircular canals and the cervical extensor muscles. Fukushima et al (1979) also carried out similar experiments on the canal-flexor muscle relation in the same species and formulated a new diagram. The two diagrams revealed some contradictory patterns instead of coordinating one such as synergism or reciprocalism, and such discrepancies still remain unexplained in spite of extensive citation of the papers by many other publications (Wilson, 1975; Wilson & Peterson, 1978, 1981; Wilson & Jones, 1979; Goldberg & Fernandez, 1984; Ito, 1985).

Recently, Kim and his associates (1990) observed cervical extensor responses to stimulation of each semicircular canal nerve in the rabbit, and they found that the response patterns of the extensor muscles are similar to that of

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flexors reported by Fukushima et al (1979) in the cat. Scrutinization of these experimental results obtained by the different groups (Tokumasu et al, 1971; Graf & Simpson, 1981; Simpson & Graf, 1981; Kim et al, 1987, 1988) in the cat and rabbit led us to conclude that such discrepancies may have not been derived from species differences but from inherent difficulties of selective stimualtion of each canal nerve. Poor reproducibility in recording the synaptic potential changes of the motoneurones during the canal nerve stimulation may also be a factor of critical importance (Maeda et al, 1975; Uchino et al, 1978, 1980).

The present experiment was designed to observe responses of the cervical extensor and flexor muscles during excitation of the vestibular semicircular canal. In cats, we stimulated each canal nerve selectively and recorded the reflex responses of the cervical muscles by means of electromyography, which gives excellent reproducibility and is entirely free from those technical difficulties inherent in the synaptic potential recording. Based on the experimental results, we were able to formulate a diagram showing the functional relationship between the semicircular canals and the cervical muscles in the vestibulo-collic reflex system.

METHODS

Twenty-five adult cats of either sex, weighing 2.2∼3.2 kg were used. Animals were anesthetized with 1 g/kg urethane i.p. and small doses were additionally given when needed. Airway was secured by inserting a T-tube into the trachea. Animals were fixed to a stereotaxic apparatus without earbar so that the osseous semicircular canals could be surgically exposed.

To produce excitatory effect of semicircular canal, the ampullary nerve was electrically stimulated. A small hole was made on the osseous canal wall with a dental drill, and an insulated wire (0.18 mm in diameter) with cut naked end was inserted into the ampulla through the hole (Kim, 1968; Kim, 1976). Square wave pulses with fixed duration (0.1 msec) and high frequency (240 Hz) were applied as described previously (Kim & Partridge, 1969). The stimulation intensity was adjusted to an optimum level by observing the magnitude of the characteristic eye movements, as described by others (Cohen et al, 1964; Tokumasu et al, 1965; Suzuki et al, 1964; Kim, 1974, 1976).

In order to observe reflex responses of the cervical extensor and flexor muscles, the activities of the splenius capitis and sternomastoid muscles were recorded by means of both plain and integrated electromyographies. Two recording electrodes were inserted into the muscles and fixed (Basmajian & Stecko, 1962; Basmajian, 1972; Basmajian & De Luca, 1985). For some instances, changes in isometric tension of the muscles were also recorded according to Barmack et al (1971).

RESULTS

The bilateral horizontal canals vs. the unilateral neck muscles

Recording the electromyographic responses from the sternomastoid and splenius capitis muscles in a unilateral side of the neck, the bilateral(right and left) horizontal canal nerves were stimulated in the separate procedures. Stimulation of a horizontal canal nerve evoked an increased muscle activity in the contralateral cervical muscles, but a decrease in the ipsilateral ones; the sternomastoid and splenius capitis muscles in the contralateral side were excited and those in the ipsilateral were inhibited. Since such response patterns of the two cervical muscles were demonstrable with good reproducibility, we could predict the muscle responses depending upon the laterality of the horizontal canal nerve stimulated. Conventionally the sternomastoid and splenius capitis muscles have been described as extensor and flexor of the neck respectively, however, these two muscles in the ipsilateral side of the neck revealed synergism instead of antagonism during the canal nerve stimulation (Fig. 1).

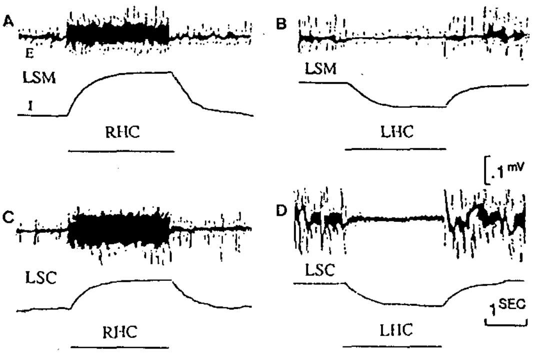

Fig. 1. Responses of the cervical muscles to stimulation of a unilateral horizontal canal nerve. A, response of the left sternomastoid muscle (LSM) to the contralateral (right) horizontal canal nerve (RHC) stimulation; B, response of the same muscle to the ipsilateral (left) horizontal canal (LHC) stimulation; C, response of the left splenius capitis muscle (LSC) to the contralateral (right) horizontal canal stimulation; D, response of the same muscle to the ipsilateral (left) horizontal canal stimulation; E, electromyographic activities; I, integrated EMG; the horizontal line indicate the period of stimulation. Square wave pulses with fixed duration (0.1 msec) and frequency (240 Hz) were applied and the intensity was adjusted to an optimum level by observing the magnitude of the responses.

A unilateral anterior canal vs. the bilateral neck muscles

Monitoring the EMG responses of the bilateral homonymous (right and left sternomastoid or splenius capitis) muscles in the neck, a unilateral anterior canal nerve was stimulated. In the experiments on the sternomastoid muscle, stimulation of an anterior canal nerve caused inhibition of the ipsilateral muscle and excitation of the contralateral one; in the experiments on the splenius capitis muscle, similar responses were also demonstrated. Thus stimulation of a unilateral anterior canal nerve always produced antagonistic responses between the bilateral homonymous muscles (Fig. 2).

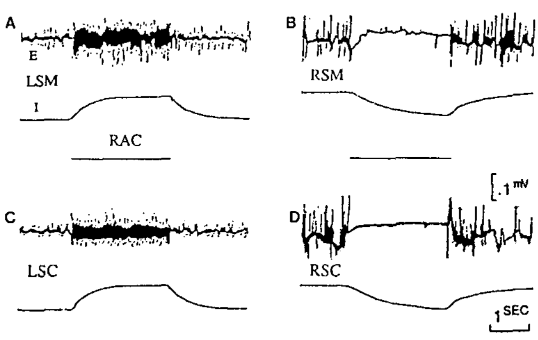

Fig. 2. Responses of the cervical muscles to stimulation of a unilateral anterior canal nerve. A, response of the left sternomastoid muscle (LSM) to stimulation of the right anterior canal nerve (RAC); B, response of the right sternomastoid muscle (RSM) to the same canal stimualtion; C, response of the left splenius capitis muscle (LSC); D, resposne of the right splenius capitis muscle (RSC); the other notations are as in the previous figure.

The bilateral posterior canal vs. the unilateral muscles

Recording the electromyographic changes of muscle activity and tension from a unilateral neck muscle, the bilateral posterior canal nerves were stimulated in the separate procedures. Stimulation of the ipsilateral posterior canal nerve produced inhibitory responses, decreased activity and tension, and that of contralateral posterior canal excitatory ones, increased activity and tension. Thus changes in the EMG activity and tension of the muscle recorded were always in unison and reproducible (Fig. 3).

DISCUSSION

The vestibular semicircular canals are receptor organs for vestibular reflexes during rota-

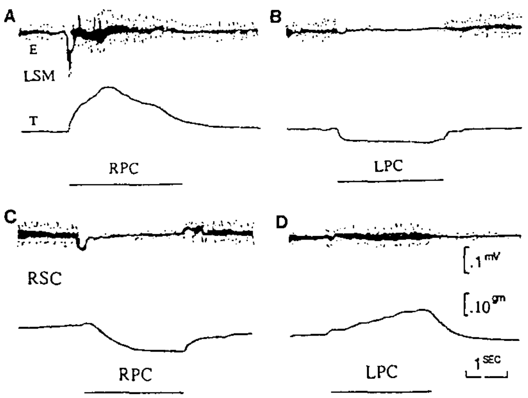

Fig. 3. Responses of the cervical muscles to stimulation of a unilateral posterior canal nerve. A, response of the left sternomastoid muscle to stimulation of the contralateral (right) posterior canal nerve (RPC); B, response of the same muscle to stimulation of the ipsilateral (left) posterior canal nerve (LPC); C, response of the right splenius capitis muscle to the ipsilateral (right) posterior canal nerve stimulation; D, response of the same muscle to the contralateral (left) posterior canal stimulation; T, isometric tension.

tional movement of the head and are composed of three functional pairs, the left horizontal vs. right horizontal canal, the left anterior vs. right posterior canal, and the left posterior vs. right anterior canal. The paired canals share the equiaxial plane in the space and hold reciprocal orientation. Therefore, rotation of the head will elicit reciprocal reactions between the two ampullary organs of the paired canals. Depending upon the direction of rotation, an excitation of one canal and an inhibition of the other will be elicited (Goldberg & Fernandez, 1984; Kelly, 1986; Fuchs, 1989).

Cervical muscles, effector organs of the vestibulo-collic reflex, are known as typical axial muscles, and are different from the muscles of other regions such as girdles and limbs. Phylogenetically, the horizontal and vertical myosepta demarcate the cervical muscles into different subdivisions. The horizontal septum divides the muscles into two groups, the dorsally located expaxial (extensor) and the ventrally located hypaxial (flexor): and the vertical septum divides the muscles into another two groups, the left and right lateral muscles (Sisson & Grossman, 1961; Romer, 1971; Kent, 1983).

In the present experiment we intended to explore the functional connections between the semicircular canals and the cervical muscles in vestibulo-collic reflex action. Stimulation of a unilateral (anterior, horizontal or posterior) canal nerve produced inhibitory responses in the ipsilateral cervical muscles and excitation in the contralateral; the extensor (splenius capitis) and flexor (sternomastoid) muscles in one side of the neck, either the left or right, revealed the same responses depending upon the laterality of the canal nerve stimulated.

The results of the present study are shown schematically in the Fig. 4. Vestibular semicircular canals are drawn as three functional pairs, one horizontal (A) and two vertical ones (B, C). The diagrams support the following axioms: 1) Semicircular canals in a unilateral vestibular system, either horizontal or vertical, exert similar influence upon a given cervical muscle; 2) Two canals in a pair produce opposite responses of the muscle to each other; 3) Both extensor and flexor muscles in one side of the neck reveal synergistic responses (Fig. 4).

Comparing these experimental results to those of the previous authors, the muscle responses to the horizontal canal nerve stimulation were all identical, whereas those to the vertical canal stimulation were in discordance. Neural connections from vertical canals to the neck extensor muscle according to Wilson and Maeda are shown in Fig. 5-A and those of our observation are in 5-B. The connections from the ipsilateral anterior and the contralateral posterior canals are different and such discordance give a clear contrast in the overall pattern of neural connections between A and B. In the previous study in rabbits, the authors and associates have observed the vertical canal-cervical muscle relations, which were identical to the findings in B (Park et al, 1991). Recent publications suggest that the neural linkages for

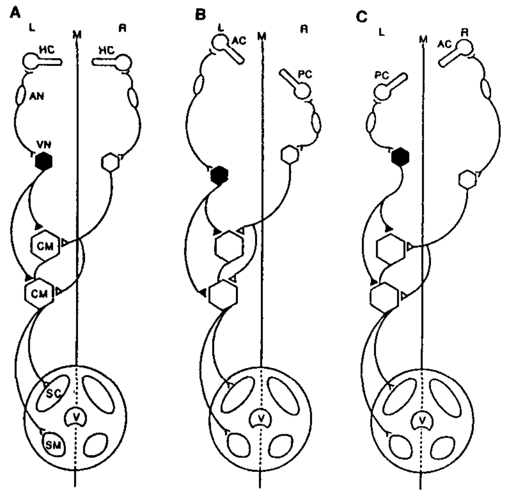

Fig. 4. *Functional interrelation between the paired semicircular canals and the cervical muscles according to the present study. A, the bilateral (left and right) horizontal canal pair; B, left anterior vs. right posterior canal; C, left posterior vs. right anterior canal; L & R, left and right; M, midline; HC, horizontal canal; AC, anterior canal; PC, posterior canal; AN, ampullary neuron; VN, vestibular nuclear neuron; CM, cervical motoneuron; SC, splenius capitis muscle; SM, sternomastoid muscle; V, vertebra; vestibular inhibitory neurons and their terminals are shown in black and excitatory ones in white.*

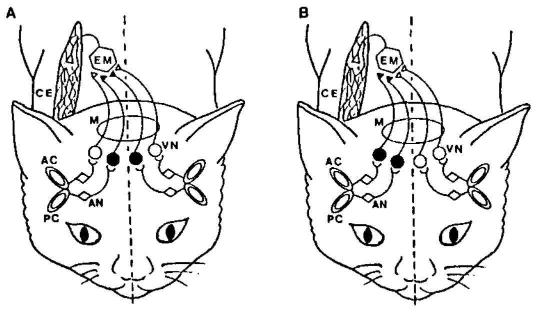

Fig. 5. *The elementary neural connections from the vertical semicircular canals to neck extensor muscles in the cat. A, connections described by Fuchs, A.F. (1989) based on the experimental evidences of Wilson and Maeda (1974); B, connections formulated by the present authors; AC, anterior semicircular canal; PC, posterior canal; AN, ampullary neuron; VN, vestibular nuclear neuron; EM, cervical extensor motoneuron; CE, cervical extensor muscle; M, medial longitudinal fasciculus. Vestibular excitatory neurons are shown in white and inhibitory ones in black.*

vestibulo-collic and vestibulo-ocular reflexes may be similar between the lateral eyed rabbit and the frontal eyed cat (Graf & Simpson, 1981; Simpson & Graf, 1981; Kim et al, 1987, 1988).

A similar pattern of neural linkage was observed in the canal-extraocular muscle relation for vestibulo-ocular reflex. During excitation of a unilateral canal, the superomedial muscles (the superior oblique, superior rectus, and medial rectus) contract and the inferolateral muscles (the inferior oblique, inferior rectus, and lateral rectus) relax in the ipsilateral eye, whereas the superomedial muscles relax and inferolateral muscles contract in the contralateral eye (Kim et al, 1988).

Vestibular semicircular canal system is divided into the bilateral (right and left) canals making the three different pairs as shown in Fig. 4. Likewise, the cervical muscles are functionally demarcated into the bilateral muscle groups in the neck. Thus, both receptor and effector organs located in the bilateral side of the head and neck reveal reciprocal actions in the vestibulo-collic reflex. Neural linkages from the semicircular canals to the cervical muscles may be composed of the two bilaterally opposing pathways, the ipsilateral inhibitory path and the contralateral excitatory one, as shown explicitly in Fig. 5-B.

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