Input Patterns and Pathways From the Six Semicircular Canals to Motoneurons of Neck Muscles. II. The Longissimus and Semispinalis Muscle Groups

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Shinoda, Y., Y. Sugiuchi, T. Futami, N. Ando, and J. Yagi. Input patterns and pathways from the six semicircular canals to motoneurons of neck muscles. II. The longissimus and semispinalis muscle groups. J. Neurophysiol. 77: 1234–1253, 1997. To reveal patterns of input from the six semicircular canals to motoneurons of various neck muscles and their relationship to the mechanical actions of individual neck muscles, patterns of input to neck motoneurons of the longissimus and the semispinalis muscle groups were investigated in the upper cervical spinal cord of anesthetized cats. Intracellular potentials were recorded from motoneurons of the longissimus muscle group (obliquus capitis superior muscle, OCS; splenius muscle, SPL; longissimus muscle, LONG) and the semispinalis muscle group (biventer cervicis muscle, BIV; complexus muscle, COMP), and effects of separate electrical stimulation of the six ampullary nerves on them were analyzed in each preparation. Neck motoneurons usually received convergent inputs from all of the six ampullary nerves, and motoneurons that supplied a particular muscle had a homogeneous pattern of input from the six ampullary nerves. Two different patterns of input were identified for motoneurons of these two muscle groups; one pattern for motoneurons of the longissimus muscle group and the other pattern for motoneurons of the semispinalis muscle group. Motoneurons of the OCS, the SPL, and the LONG muscles received excitation from the three contralateral ampullary nerves and inhibition from the three ipsilateral ampullary nerves. BIV and COMP motoneurons received excitation from the bilateral anterior canal nerves (ACNs) and the contralateral lateral canal nerve (LCN) and inhibition from the bilateral posterior canal nerves (PCNs) and the ipsilateral LCN. Latencies of postsynaptic potentials (PSPs) evoked by stimulation of each of the six ampullary nerves indicated that the earliest component of excitatory PSPs (EPSPs) and inhibitory PSPs (IPSPs) was disynaptic in these motoneurons. However, tri-synaptic IPSPs were evoked by stimulation of the contralateral PCN in a considerable number of BIV and COMP motoneurons. In OCS, SPL, and LONG motoneurons, all of the excitation from the contralateral and all of the inhibition from the ipsilateral ampullary nerves were mediated through the ipsilateral medial longitudinal fascicle (MLF). In BIV and COMP motoneurons, disynaptic excitation from the contralateral ACN and LCN and disynaptic inhibition from the ipsilateral LCN and bilateral PCNs were mediated through the ipsilateral MLF, whereas disynaptic excitation from the ipsilateral ACN was mediated through the ipsilateral lateral vestibulospinal tract. The patterns of semicircular canal input to neck motoneurons of these two muscle groups are related closely to the mechanical actions of individual neck muscles and the optimal stimulus to the semicircular canals such that the connections will tend to stabilize head position in response to head perturbations.

INTRODUCTION

Activation of semicircular canals by head rotation produces compensatory head movement that helps stabilize head position in response to head perturbations. Neural mechanisms underlying this vestibulocollic reflex have been investigated extensively. The pattern of connections from individual ampullary nerves to neck motoneurons was first examined by Wilson and Maeda (1974) in dorsal ramus motoneurons at C3 innervating the biventer cervicis (BIV) and complexus (COMP) muscles. They showed that these motoneurons received excitation from the bilateral anterior canal nerves (ACNs) and the contralateral lateral canal nerve (LCN) and inhibition from the bilateral posterior canal nerves (PCNs) and the ipsilateral LCN. The dorsal ramus at each cervical spinal segment innervates epaxial neck muscles, which consist of the multifidus, the semispinalis, and the longissimus muscle groups (Nishi 1938; Sugiuchi and Shinoda 1992). Therefore a question arose as to whether other patterns of input from the six semicircular canals were seen in motoneurons of other dorsal neck muscles. Our previous paper addressed this issue by examining postsynaptic potentials evoked by separate electrical stimulation of the six ampullary nerves in motoneurons of the multifidus muscle group (Shinoda et al. 1994a). In this previous study, two patterns of input from the six semicircular canals were identified in motoneurons of the multifidus muscle group. In motoneurons of the rectus capitis posterior (RCP) and cervical multifidus muscles, the pattern of input from the six semicircular canals is identical to that reported for BIV and COMP motoneurons by Wilson and Maeda (1974). However, motoneurons of the obliquus capitis inferior (OCI) muscle have a different input pattern; they receive excitation from the ipsilateral ACN and PCN and the contralateral LCN and inhibition from the contralateral ACN and PCN and the ipsilateral LCN. These findings indicate that the pattern of input from the six semicircular canals is not homogeneous but depends on the muscles innervated by the motoneurons and, presumably, their mechanical action. The pattern of input of other neck motoneurons with different mechanical actions is not known.

Neck muscles are organized in a serial array of compartments, and each compartment is defined by the innervation pattern of the segmental spinal nerves (Reighard and Jennings 1963; Richmond and Vidal 1988). It is assumed tacitly
that the characteristics of motoneurons in one segment are representative of motoneurons supplying other compartments, but there is evidence that motoneurons innervating different compartments of a neck muscle receive different innervation patterns from peripheral afferents (Brink et al. 1981). Therefore the possibility remains that different compartments of a neck muscle may have a different pattern of input from the six semicircular canals.

The present study was performed to extend our analysis to motoneurons of dorsal neck muscles other than those in the multifidus muscle group and determine patterns of input from the six semicircular canals to motoneurons of dorsal neck muscles of the longissimus and the semispinalis muscle groups. Stimulating electrodes were implanted on the six ampullary nerves in each preparation, and postsynaptic potentials (PSPs) evoked by separate electrical stimulation of individual ampullary nerves were analyzed with an intracellular recording technique in motoneurons of the longissimus muscle group (the splenius, SPL; the obliquus capitis superior, OCS; the longissimus capitis, LONG muscles) and the semispinalis muscle group (the BIV and COMP muscles) in the upper cervical spinal cord (C1–C2) of anesthetized cats. The results show that there are two different patterns of input from the six ampullary nerves to motoneurons of these dorsal neck muscles; one pattern is observed in motoneurons of the longissimus muscle group and the other is seen in motoneurons of the semispinalis muscle group. A preliminary report of some of these results has been presented previously (Shinoda et al. 1994b; Sugiuchi et al. 1992a).

METHODS

Experiments were performed on 16 cats, most of which also were used to obtain material reported previously (Shinoda et al. 1994a). Surgical procedures and animal care conformed to principles approved by the American Physiological Society and to “Guiding Principles for the Care and Use of Animals in the Field of Physiological Sciences, The Physiological Society of Japan, 1988.” The animals were initially anesthetized with ketamine hydrochloride (Ketalar, Parke-Davis; 25 mg/kg im) followed by α-chloralose (50–60 mg/kg iv initial dose, supplemented with additional doses of 10–25 mg/kg). A supplementary dose of pentobarbital sodium (Nembutal, Abbott, Switzerland; 5–10 mg/kg im) was administered when the pulsation of the spinal cord made it difficult to record intracellular potentials. Animal preparation and the main experimental procedures were as described previously (Shinoda et al. 1994a). Briefly, fine bipolar electrodes were implanted on the six ampullary nerves near the ampullae (Suzuki et al. 1969), and the final electrode positions were determined by monitoring characteristic eye movements elicited by stimulation of individual ampullary nerves (Suzuki and Cohen 1964). Glass microelectrodes filled with 3 M KCl were used for intracellular penetration. Intracellular records were collected on the left side from motoneurons of the OCS muscle at C1, the LONG muscle at C1 and C2, the SPL muscle at C1 and C2, the COMP muscle at C1 and C2, and the BIV muscle at C2. The COMP and BIV muscles are innervated by the medial branch of the dorsal rami, whereas the OCS, SPL, and LONG muscles are innervated by the lateral branch of the dorsal rami (Nishi 1938; Reigbad and Jennings 1963; Richmond et al. 1978; Sugiuchi and Shinoda 1992). To check the possibility of current spread to ampullary or macular nerves, intracellular recordings were made from other neck motoneurons; the OCI at C1, the longus capitis at C1, and the RCP at C1. To stimulate individual ampullary nerves, 0.2 ms-negative pulses were passed through a constant current generator. The threshold for evoking PSPs in neck motoneurons was ≤50 µA, usually 20–30 µA, and a stimulus strength of two to five times threshold was usually used for analysis. The maximum current used for data collection was 100 µA. To determine the pathways from individual semicircular canals to neck motoneurons, the medial longitudinal fascicle (MLF) or the lateral vestibulospinal tract (LVST) was sectioned with a fine blade near the obex under visual observation. Lesions in the brain stem were reconstructed for histological examination on celloidin-embedded serial sections of the brain stem stained by the Klüver-Barrera method (Klüver and Barrera 1953). After each experiment, the positions of implanted electrodes in the semicircular canals were carefully examined under an operating microscope, as described previously (Shinoda et al. 1994a).

RESULTS

Motoneurons of different neck muscles of the longissimus and the semispinalis groups were identified by their antidromic responses to stimulation of the respective muscle nerves. The resting membrane potentials ranged from −40 to −75 mV. The general characteristics of excitatory and inhibitory PSPs (EPSPs and IPSPs) evoked by stimulation of individual ampullary nerves in these motoneurons were the same as those previously described for other neck motoneurons (Shinoda et al. 1994a). All lateralities in this paper are described with reference to the recording side of neck motoneurons.

Patterns of synaptic inputs from the six ampullary nerves

OBLIQUUS CAPITIS SUPERIOR MOTONEURONS. The muscle nerve of the OCS muscle divided into three or four branches innervating different portions of this muscle. Some of these ran along the SPL muscle nerve or the LONG muscle nerve, and it was sometimes difficult to separate them. Although different branches were used for stimulation in each experiment, the response pattern obtained was very consistent and, therefore, they were considered together as OCS motoneurons in this paper.

The typical pattern of input from the six ampullary nerves to an OCS motoneuron is shown in Fig. 1. Stimulation of the three ipsilateral ampullary nerves evoked IPSPs (Fig. 1B), whereas stimulation of the three contralateral ampullary nerves evoked EPSPs in an OCS motoneuron (Fig. 1C). This input pattern was found very consistently in 28 of the 29 OCS motoneurons in which the effects of stimulation of all six ampullary nerves were examined. Table 1A summarizes the effects of stimulation of individual ampullary nerves on OCS motoneurons. This table includes the responses of 12 OCS motoneurons from which a complete set of responses to stimulation of all six ampullary nerves was not obtained. There were only a few deviations from this typical input pattern. The most frequent deviation was EPSPs evoked by ipsilateral PCN stimulation (9.8%). As shown in Fig. 1, B and C, the inputs from the six ampullary nerves to OCS motoneurons were the strongest among motoneurons of the neck muscles examined in this series of experiments, although it was not easy to compare the strengths of ampullary inputs in motoneurons of different preparations. This
factor may explain the low percentage of deviations from the typical input pattern in OCS motoneurons. Another cause for this low percentage of deviations was that OCS motoneurons received PSPs of the same polarity from the three ampullary nerves on each side. This result indicated that the evoked responses might not be genuine, but instead, they could be artifacts induced by stimulus current spread to an adjacent ampullary or macular nerve. However, the typical input pattern could be regarded as genuine from several reasons. Thresholds for evoking the typical responses were usually <50 μA and as low as 20 μA in many cases. We always checked positions of six stimulating electrode tips relative to their target ampullary nerves after each experiment and confirmed that the electrode tips were placed properly on their target ampullary nerves. Furthermore, the possibility of current spread was carefully checked in each preparation by recording PSPs in motoneurons of other neck muscles (see Shinoda et al. 1994a for details). The problem of current spread to an adjacent ampullary or macular nerve in atypical responses in the OCS and other motoneurons will be addressed in DISCUSSION. Latency histograms showed that most of the latencies of the PSPs were <1.8 ms (Fig. 2A). Because the shortest latency of the trisynaptic PSPs evoked by ampullary nerve stimulation was 1.8 ms at C1 and C2,
TABLE 1.  Pattern of synaptic inputs to OCS motoneurons before and after sectioning of the ipsilateral MLF

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<td>B. After MLF section</td>
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n, number of motoneurons; OCS, obliquus capitis superior; MLF, medial longitudinal fascicle; EPSP, excitatory postsynaptic potential; IPSP, inhibitory postsynaptic potential; ACN, anterior canal nerve; LCN, lateral canal nerve; PCN, posterior canal nerve.

(Shinoda et al. 1994a; Sugiuchi et al. 1995), they were considered disynaptic from individual ampullary nerves.

To determine the pathways that convey excitatory and inhibitory inputs from individual semicircular canals to neck motoneurons, the MLF ipsilateral or contralateral to the recorded motoneurons was sectioned at the medulla, and the effects of this procedure on evoked PSPs were examined. In each experiment, sufficient cells were sampled before the MLF was sectioned to ensure that stimulation of the six ampullary nerves was effective and evoked the typical response pattern for OCS motoneurons. Figure 1, D–F, illustrates the effects of sectioning the MLF on PSPs evoked by ampullary nerve stimulation in an OCS motoneuron. After the ipsilateral MLF was sectioned in the medulla, no PSPs could be evoked by stimulation of the six ampullary nerves (Fig. 1, E and F). The antidromic spikes in Fig. 1D assured good conditions for intracellular recording. Histological examination showed that the sectioning covered the ipsilateral MLF with some involvement of the adjacent reticular formation (Fig. 1, top middle inset). Similar results for the effect of sectioning the ipsilateral MLF on PSPs were obtained in three experiments (Table 1B). Ipsilateral IPSPs remained in some motoneurons after sectioning, but their amplitudes were very small. Interruption of the contralateral MLF did not affect the responses from the six ampullary nerves in eight of eight OCS motoneurons (not shown).

LONGISSIMUS CAPITIS MOTONEURONS. The muscle nerve to the LONG muscle at C1 was very thin and ran along the muscle nerve to the lateral portion of the OCS muscle. The LONG muscle nerve at C2 ran along the muscle nerve to the SPL muscle and ramified into two or three branches before entering the muscle.

Typical synaptic potentials evoked by stimulation of the bilateral ampullary nerves are shown in Fig. 3. Stimulation of the three ipsilateral ampullary nerves evoked IPSPs (Fig. 3B), whereas stimulation of the three contralateral ampullary nerves evoked EPSPs in a LONG motoneuron (Fig. 3C). This input pattern from the 6 ampullary nerves was observed in 4 of 6 LONG motoneurons at C1 and 9 of 12 LONG motoneurons at C2. Deviations from this pattern were rare (Table 2A). Latency histograms showed that most PSPs had latencies of <1.8 ms and were considered disynaptic from the ampullary nerves (Fig. 2B). The effects of sectioning the MLF on either side were examined by comparing the response patterns of ampullary input before and after sectioning. Interruption of the ipsilateral MLF abolished disynaptic EPSPs from the three contralateral ampullary nerves and disynaptic IPSPs from the three ipsilateral ampullary nerves in a LONG motoneuron (Fig. 3, E and F). Similar results were obtained in most LONG motoneurons (Table 2B), but some ipsilateral IPSPs and contralateral EPSPs remained after sectioning the ipsilateral MLF. However, because the amplitudes of these responses were very small and their latencies were >1.7 ms (Fig. 2B), the ipsilateral disynaptic IPSPs and contralateral disynaptic EPSPs were considered evoked through the ipsilateral MLF in LONG motoneurons.

SPLENIUS MOTONEURONS. We recorded PSPs from 63 SPL motoneurons, of which 16 were located at C1 and 47 were at C2. Figure 4 shows a typical pattern of input from the six ampullary nerves to a SPL motoneuron at C2. Stimulation of the three ipsilateral ampullary nerves evoked IPSPs (Fig. 4B), whereas stimulation of the three contralateral ampullary nerves evoked EPSPs in this SPL motoneuron (Fig. 4C). This input pattern was found most consistently in 19 of the 45 SPL motoneurons (42.2%) in which the effects of stimulation of the six ampullary nerves were examined (Table 3A). However, the response pattern of SPL motoneurons was not easy to determine in some SPL motoneurons, and deviations from the typical input pattern were found most frequently in SPL motoneurons among motoneurons of all of the neck muscles examined in this series of experiments (Shinoda et al. 1994a; Sugiuchi et al. 1995). In SPL motoneurons, the most reliable responses were excitation from the contralateral ACN (55/61, 90.2%) and LCN (50/56, 89.3%) and inhibition from the ipsilateral LCN (47/59, 79.7%). In the responses from the three other ampullary nerves, both excitation and inhibition were found among the responses for each ampullary nerve. Furthermore, the number of negative responses was greatest among SPL motoneurons. When the responses were not clear, hyperpolarizing or depolarizing currents were injected into cells through a glass microelectrode filled with 3 M KCl to unveil the presence of either EPSPs or IPSPs. But this maneuver did not reveal
**Fig. 2.** Latency histograms of PSPs evoked by stimulation of 6 ampullary nerves in OCS (A), longissimus (LONG; B), and splenius (SPL; C) motoneurons. a-f: ipsilateral ACN (a), LCN (b), and PCN (c) stimulation and contralateral ACN (d), LCN (e), and PCN (f) stimulation. In A and B, top and bottom histograms indicate latency distribution of PSPs with typical response patterns before and after sectioning of ipsilateral MLF, respectively. In C, top 2 and bottom 2 histograms indicate latency distribution of PSPs before and after sectioning ipsilateral MLF, respectively.
FIG. 3. Typical postsynaptic potentials in LONG motoneurons at C2 evoked by stimulation of 6 ampullary nerves (A–C) and effects of sectioning MLF on PSPs (D–F). A–C: before sectioning. A: antidromic identification. B and C: PSPs evoked by stimulation of ipsilateral (B) and contralateral ampullary nerves (C). Stimulus intensity: 100 µA for all ampullary nerves. D–F: after sectioning ipsilateral MLF in another motoneuron. D: antidromic identification. E and F: PSPs evoked by stimulation of ipsilateral (E) and contralateral (F) ampullary nerves. Stimulus strength: 100 µA for all ampullary nerves. Lesion of MLF ipsilateral to the motoneuron was reconstructed on serial sections (shaded area in top middle figure). Calibration in A applies to D and that in Cb applies to all other traces.

TABLE 2. Pattern of synaptic inputs to LONG motoneurons before and after sectioning of the ipsilateral MLF

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n, number of motoneurons; LONG, longissimus. For other abbreviations, see Table 1.
FIG. 4. Typical postsynaptic potentials in SPL motoneurons at C2 evoked by stimulation of 6 ampullary nerves (A–C) and effects of sectioning ipsilateral MLF on PSPs (D–F). A–C: before sectioning. A: antidromic spikes. B: stimulation of ipsilateral ampullary nerves. C: stimulation of contralateral ampullary nerves. Stimulus strength: 100 μA for all ampullary nerves. D–F: after sectioning MLF ipsilateral to a motoneuron (shaded area in top middle figure). D: antidromic identification. E and F: stimulation of ipsilateral (E) and contralateral (F) ampullary nerves. Stimulus strength: 100 μA for all ampullary nerves. Threshold for excitatory PSPs (EPSPs; Ea) was 85 μA. Calibrations in A and Cb apply to D and all other traces, respectively.

any PSPs, suggesting that the inputs from these ampullary nerves, if any, were weak. The responses from the ipsilateral PCN were expected to be inhibition, because almost all of the responses from the contralateral ACN were excitation (Shinoda et al. 1994a; Wilson and Maeda 1974). However, excitation was observed only in 28.8% of the motoneurons examined (17/59), whereas inhibition was observed in 40.7% of them (24/59). Therefore it was most likely that this excitation was due to current spread to an adjacent ampullary or macular nerve. In fact, a decrease in stimulus TABLE 3. Pattern of synaptic inputs to SPL motoneurons before and after sectioning of the ipsilateral MLF

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n, number of motoneurons; SPL, splenius muscle. For other abbreviations, see Table 1.
intensity in such cases often induced only IPSPs, even though stronger stimuli induced EPSPs that masked the presence of the IPSPs. The most serious problems were the responses from the ipsilateral ACN and the contralateral PCN. In 22 SPL motoneurons in which stimulation of the ipsilateral ACN evoked inhibition, stimulation of the contralateral PCN evoked excitation in 19 motoneurons (86.4%) and no response in 3 motoneurons. In 17 SPL motoneurons in which stimulation of the ipsilateral ACN evoked excitation, stimulation of the contralateral PCN evoked inhibition only in 8 motoneurons, excitation in 6 motoneurons, and no response in 3 motoneurons. As a result, 7 of the 45 IPL motoneurons (15.6%) in which a complete set of responses were examined received excitation from the bilateral ACNs and contralateral LCN and inhibition from the bilateral PCNs and ipsilateral LCN. In preparations in which IPSPs were evoked by stimulation of the three ipsilateral ampullary nerves in OCS motoneurons, stimulation of the ipsilateral ACN and LCN usually evoked EPSPs and IPSPs, respectively, in COMP and RCP motoneurons. This finding indicates that the possibility of current spread from an electrode for the ACN to the LCN or vice versa was unlikely in such preparations (Shinoda et al. 1994a; Wilson and Maeda 1974). However, in some of these preparations, stimulation of the ipsilateral ACN sometimes evoked a mixture of IPSPs and EPSPs in SPL motoneurons. In such cases, a decrease in stimulus intensity often left only IPSPs, suggesting that these IPSPs most likely were due to current spread to the utricular nerve (Bolton et al. 1992).

Latencies of the earliest component of EPSPs evoked by stimulation of a contralateral ampullary nerve ranged from 0.8 to 3.2 ms and those of the IPSPs evoked by stimulation of an ipsilateral ampullary nerve ranged from 0.8 to 3.1 ms (Fig. 2C). PSPs with latencies of ≈1.8 ms were slightly more frequent in SPL motoneurons, probably because of the weaker inputs from the ampullary nerves, but most of the PSPs were considered disynaptic from the ampullary nerves.

The effect of sectioning the MLF on the pattern of the responses to stimulation of the six ampullary nerves was examined in 31 SPL motoneurons. A typical example is shown in Fig. 4, D–F. Stimulation of the three contralateral ampullary nerves evoked no response (Fig. 4F). Stimulation of the three ipsilateral ampullary nerves evoked no IPSPs (Fig. 4E). However, stimulation of the ipsilateral ACN sometimes evoked small EPSPs as shown in Fig. 4Ea. Thresholds for these EPSPs were usually rather high (80–150 μA), as compared with thresholds for IPSPs (20–40 μA) evoked by stimulation of the same ipsilateral ACN. Therefore, judging from their small amplitude and higher thresholds, some of these EPSPs may be due to current spread to nerves innervating the utricle (Bolton et al. 1992).

Table 3B summarizes the results after sectioning the MLF. Most EPSPs evoked by contralateral ampullary stimulation disappeared, and most IPSPs evoked by ipsilateral ampullary stimulation disappeared. However, small EPSPs were often evoked by stimulation of the ipsilateral ACN as in Fig. 4Ea, and the percentage of the EPSPs evoked by stimulation of the ipsilateral ACN (14/31, 45.2%) was much higher after MLF sectioning than in control (17/63, 27.0%). This is probably because small EPSPs might be unveiled by removing larger IPSPs, which masked them before MLF sectioning. Interruption of the contralateral MLF did not influence the response pattern in five of the five motoneurons examined.

COMPlexus motoneurons. We recorded PSPs from 49 COMP motoneurons at C1 and 23 at C2. A typical response pattern of a COMP motoneuron to stimulation of the six ampullary nerves is shown in Fig. 5. Stimulation of the ipsilateral ACN produced EPSPs and that of the ipsilateral LCN and PCN produced IPSPs (Fig. 5B), whereas stimulation of the contralateral ACN and LCN produced EPSPs and that of the contralateral PCN produced IPSPs (Fig. 5C). Table 4A summarizes the effects of stimulation of individual ampullary nerves on COMP motoneurons. This table includes responses in 67 COMP motoneurons from which a complete set of responses from the six ampullary nerves could be examined and responses in 5 other COMP motoneurons. This typical response pattern of input from the six ampullary nerves was observed in 41 of 47 COMP motoneurons at C1 and in 16 of 20 COMP motoneurons at C2. In the other motoneurons, input from one or two ampullary nerves was lacking, or there were some departures from this typical pattern (Table 4A). A frequent deviation was the appearance of EPSPs evoked by stimulation of the ipsilateral PCN (5.6%) and the contralateral PCN (7.5%) and IPSPs evoked by stimulation of the ipsilateral ACN (4.2%). When an EPSP-IPSP complex was evoked by stimulation of the ipsilateral or contralateral PCN, or by stimulation of the ipsilateral ACN, a decrease in stimulus intensity left only IPSPs in the former case, whereas it left EPSPs in the latter case. Therefore deviations from the typical response pattern might be due to current spread to an adjacent ampullary or macular nerve. The latency histograms of the PSPs evoked in COMP motoneurons are shown in Fig. 6A. Because most of the PSPs had latencies of <1.8 ms, they were considered disynaptically induced by stimulation of the ampullary nerves. However, the latencies of the IPSPs evoked by stimulation of the contralateral PCN contained a higher percentage of IPSPs with latencies of ≈1.8 ms (21/57, 36.8%).

The effects of sectioning the MLF on PSPs evoked by stimulation of the ampullary nerves were examined in 15 COMP motoneurons in four experiments, of which the effects of stimulation of all six ampullary nerves were examined in 12 motoneurons. An example of the responses in one of these motoneurons is shown in Fig. 5. After the MLF ipsilateral to the recorded motoneuron was sectioned near the obex, stimulation of the ipsilateral LCN and PCN did not evoke any PSPs, whereas stimulation of the ipsilateral ACN evoked disynaptic EPSPs (Fig. 5E). Stimulation of the contralateral ACN, LCN, and PCN did not evoke PSPs with latencies <1.8 ms (Fig. 5F). However, stimulation of the contralateral PCN evoked IPSPs at a latency of 2.0 ms (Fig. 5Fc). The lesion completely covered the ipsilateral MLF and extended further laterally without involving the LVST (Fig. 5, top middle inset). As in this example, after ipsilateral sectioning of the MLF, disynaptic LCN- and PCN-evoked IPSPs from the ipsilateral side usually disappeared, whereas ACN-evoked EPSPs were almost always observed (14/15; Table 4B and Fig. 6A). The disynaptic ACN-
LCN-evoked EPSPs and PCN-evoked IPSPs from the contralateral side were absent after ipsilateral sectioning of the MLF (Table 4B and Fig. 6A), but PCN-evoked IPSPs with latencies of <1.8 ms were observed in 5/12 of the 14 motoneurons examined (Fig. 6AF).

The effects of sectioning the LVST on inputs from the six ampullary nerves were examined in 14 COMP motoneurons at C1 and C2 in two experiments. After the ipsilateral LVST was sectioned in the medulla, EPSPs were not evoked by stimulation of the ipsilateral ACN in 12 of the 14 motoneurons examined, but small EPSPs and small IPSPs were evoked in one motoneuron each. In contrast, sectioning of the LVST had no effect on the occurrence of EPSPs evoked by stimulation of the contralateral ACN and LCN, and the occurrence of IPSPs evoked by stimulation of the contralateral PCN and ipsilateral LCN and PCN (Table 4C and Fig. 6A).

**BIVENTER CERVICIS MOTONEURONS.** Intracellular potentials were recorded from 35 BIV motoneurons at C2. The pattern of PSPs evoked by stimulation of the six ampullary nerves in Fig. 7 is typical of a BIV motoneuron. Stimulation of the bilateral ACNs and contralateral LCN evoked EPSPs, whereas stimulation of the bilateral PCNs and ipsilateral LCN evoked disynaptic IPSPs in this BIV motoneuron (Fig. 7B and C). This response pattern was consistently found in 23 of 30 BIV motoneurons in which the effects of stimulating all six ampullary nerves were examined. Deviations from this typical input pattern were rare (Table 5A). The latency histograms indicate that most PSPs had latencies of <1.8 ms (Fig. 6B).

The effects of sectioning the MLF on ampullary inputs to a BIV motoneuron are shown in Fig. 7D-F. After sectioning of the ipsilateral MLF, EPSPs evoked by stimulation of the ipsilateral ACN remained, but IPSPs evoked by stimulation of the ipsilateral LCN and PCN disappeared (Fig. 7E). In contrast, EPSPs were not evoked by stimulation of the contralateral ACN and LCN, but IPSPs were evoked at a latency of 3.2 ms by stimulation of the contralateral PCN (Fig. 7F). The results obtained in all of the section experiments are summarized in Table 5B. Sectioning of the MLF had almost no effect on the occurrence of EPSPs evoked by stimulation of
Table 4. Pattern of synaptic inputs to COMP motoneurons before and after sectioning of the ipsilateral MLF and after sectioning of the ipsilateral LVST

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<th>Contralateral</th>
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<tr>
<td></td>
<td>EPSP</td>
<td>IPSP</td>
<td>No effect</td>
<td>n</td>
</tr>
<tr>
<td>A. Control</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ACN</td>
<td>63</td>
<td>3</td>
<td>6</td>
<td>72</td>
</tr>
<tr>
<td>LCN</td>
<td>0</td>
<td>63</td>
<td>7</td>
<td>70</td>
</tr>
<tr>
<td>PCN</td>
<td>4</td>
<td>64</td>
<td>4</td>
<td>72</td>
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<tr>
<td>B. After MLF section</td>
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<tr>
<td>ACN</td>
<td>14</td>
<td>0</td>
<td>1</td>
<td>15</td>
</tr>
<tr>
<td>LCN</td>
<td>0</td>
<td>2</td>
<td>10</td>
<td>12</td>
</tr>
<tr>
<td>PCN</td>
<td>1</td>
<td>2</td>
<td>9</td>
<td>12</td>
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<tr>
<td>C. After LVST section</td>
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<tr>
<td>ACN</td>
<td>1</td>
<td>1</td>
<td>12</td>
<td>14</td>
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<tr>
<td>LCN</td>
<td>0</td>
<td>13</td>
<td>1</td>
<td>14</td>
</tr>
<tr>
<td>PCN</td>
<td>0</td>
<td>13</td>
<td>1</td>
<td>14</td>
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n, number of motoneurons; COMP, complexus muscle; LVST, lateral vestibulospinal. For other abbreviations, see Table 1.

the ipsilateral ACN (Table 5B and Fig. 6Ba). Stimulation of all of the ampullary nerves except the ipsilateral ACN did not evoke any PSPs at latencies of <1.8 ms after ipsilateral sectioning of the MLF (Fig. 6B, b–f). However, late IPSPs were evoked by stimulation of the contralateral PCN in four of eight BIV motoneurons, as shown in Fig. 7F (Fig. 6Bf). In three section experiments, sectioning of the ipsilateral MLF was extended to the contralateral MLF, but this procedure did not further influence the input pattern. In one experiment, the contralateral MLF was interrupted first without any change in the input pattern. Then, while recording PSPs from the same BIV motoneuron, slight extension of the sectioning across the midline to the ipsilateral MLF abolished contralateral disynaptic PSPs, and further lateral sectioning within the ipsilateral MLF eliminated ipsilateral IPSPs but not EPSPs evoked by stimulation of the ACN (not shown).

Discussion

The present study has demonstrated two patterns of input from the six ampullary nerves to motoneurons of the longissimus and the semispinalis muscles at the upper cervical cord of the cat. Motoneurons that supplied a particular neck muscle of the longissimus and the semispinalis groups had a homogeneous pattern of input from the six semicircular canals, as observed previously in other neck muscles (Shinoda et al. 1994a; Wilson and Maeda 1974). Motoneurons of the longissimus muscle group (OCS, SPL, and LONG motoneurons) had a common pattern of input: excitation from the three contralateral ampullary nerves and inhibition from the three ipsilateral ampullary nerves through the ipsilateral MLF. This input pattern was previously found in motoneurons of the neck flexor muscle (the sternocleidomastoid muscle) (Fukushima et al. 1979) but has been seen in motoneurons of the neck extensor muscles in the present study. Motoneurons of the semispinalis muscle group (COMP and BIV motoneurons) at C1 and C2 had a common pattern of input from the six ampullary nerves: excitation from the bilateral ACNs and the contralateral LCNs and inhibition from the bilateral PCNs and the ipsilateral LCN. This pattern was found in dorsal ramus motoneurons at C3 (Wilson and Maeda 1974).

In this series of the experiments, connections from all six ampullary nerves were examined for most of the motoneurons studied. This strategy helped to reduce the risks associated with combining data from different motoneurons obtained in different experiments where different degrees of current spread from the electrodes on the semicircular canal afferents may obscure the pattern of input. Since the technique for electrically stimulating individual ampullary nerves (Suzuki and Cohen 1964) was introduced to analyze the central pathways for different canal inputs, implanted electrode positions in the semicircular canals have not been verified visually. However, we always confirmed visually under a dissecting microscope the proper positions of implanted electrode tips relative to their target ampullary nerves after each experiment. This supports the reliability of our technique of selective stimulation of individual ampullary nerves. Although the stimulating electrodes seemed to be placed properly on the ampullary nerves, anatomic locations of adjacent ampullary and/or macular nerves near the stimulating electrodes caused some problems in current spread. The main problems of current spread for separate electrical stimulation of individual ampullary nerves have been discussed in detail previously (Shinoda et al. 1994a). Therefore, only some of the specific problems related to the present study will be discussed here. Motoneurons of the longissimus muscle group received disynaptic PSPs of the same polarity from the three unilateral ampullary nerves. Therefore, based solely on this response pattern (Fukushima et al. 1979), it is impossible to determine whether this input pattern is genuine or contains an artifact due to current spread to an adjacent ampullary or macular nerve. As discussed
FIG. 6. Latency histograms of PSPs evoked in COMP (A) and biventer cervicis (BIV; B) motoneurons by stimulation of 6 ampullary nerves. Figure is arranged same as Fig. 2. In each panel, histograms in 1st and 2nd rows indicate latency distribution before and after sectioning ipsilateral MLF, respectively. In A, bottom histogram indicates latency histogram after sectioning ipsilateral lateral vestibulospinal tract.

previously (Shinoda et al. 1994a), the most likely stimulus spread would be from an LCN electrode to the ACN or from an ACN electrode to the LCN, but it is safe to conclude that the ACN and the LCN are activated separately, when typical PSPs evoked by stimulation of the unilateral ACN and LCN show opposite polarities. The typical inputs from the ipsilateral ACN and LCN are excitation and inhibition, respectively, in OCI and RCP motoneurons and those from the contralateral ACN and LCN are inhibition and excitation, respectively, in OCI motoneurons (Shinoda et al. 1994a).

### TABLE 5. Pattern of synaptic inputs to BIV motoneurons before and after sectioning of the ipsilateral MLF

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<td>EPSP</td>
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<tr>
<td><strong>A. Control</strong></td>
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<tr>
<td>ACN</td>
<td>31</td>
<td>3</td>
</tr>
<tr>
<td>LCN</td>
<td>2</td>
<td>24</td>
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<tr>
<td>PCN</td>
<td>3</td>
<td>29</td>
</tr>
<tr>
<td><strong>B. After MLF section</strong></td>
<td></td>
<td></td>
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<tr>
<td>ACN</td>
<td>7</td>
<td>0</td>
</tr>
<tr>
<td>LCN</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>PCN</td>
<td>1</td>
<td>1</td>
</tr>
</tbody>
</table>

n, number of motoneurons; BIV, biventer cervicus muscle. For other abbreviations, see Table 1.
Examination of these ACN- and LCN-evoked PSPs in these motoneurons is useful for detecting stimulus current spread from an LCN electrode to the ACN or vice versa in each preparation. Therefore we always recorded PSPs from OCI and RCP motoneurons in every experiment and confirmed, by sampling a sufficient number of such motoneurons, that unilateral stimulation of the ACN and the LCN evoked PSPs of the opposite polarity in OCI and RCP motoneurons. Because the present study was performed using such preparations, current spread from an LCN electrode to the ACN or vice versa is probably negligible in the present study. Current spread to the utricular nerve is another problem. Stimulation of the utricular nerve evokes EPSPs in neck motoneurons on the ipsilateral side and IPSPs on the contralateral side (Bolton et al. 1992). Therefore the typical responses in OCS, SPL, and LONG motoneurons were probably not contaminated by an artifact due to current spread to the utricular nerve. However, some rare atypical PSPs with a polarity opposite the typical responses in Tables 1–3 might be ascribed to stimulus spread to the utricular nerve. Stimulus spread from a PCN electrode to the ACN or LCN is rare due to the anatomic distance (Kasahara and Uchino 1971; Wilson and Maeda 1974), but stimulus spread from a PCN electrode to the saccular nerve is another possible problem. Stimulation of the saccular nerve produces bilateral excitation in extensor motoneurons and bilateral inhibition in flexor motoneurons (Uchino et al. 1994). Therefore some atypical IPSPs evoked from the contralateral PCN and EPSPs evoked from the ipsilateral PCN in motoneurons of the longissimus muscle group (Tables 1–3) most likely reflect current spread to the saccular nerve. Based on these considerations, we have concluded that the typical responses observed in this study were due to proper stimulation of individual ampullary nerves.

The input pattern from individual ampullary nerves to neck motoneurons was first reported by Wilson and Maeda (1974) for dorsal ramus motoneurons at C3; these motoneurons contain both BIV and COMP motoneurons. The present study gave additional evidence that these connections between the six ampullary nerves and motoneurons also apply to BIV motoneurons at C2 and COMP motoneurons at C1 and C2. Taken together, these results indicate that COMP and BIV motoneurons, which are located at different cervical segments and innervate different muscle bundles of each of these muscles, show a homogeneous pattern of inputs from the six ampullary nerves. In the present study, only trisynaptic IPSPs were evoked by stimulation of the contralateral PCN in some BIV and COMP motoneurons and at a higher frequency (41.7%) after the lesion of the MLF (Fig. 6A). Before sectioning the MLF, the presence of disynaptic PCN-evoked IPSPs made it difficult to determine whether second peaks of IPSPs were caused disynaptically or trisynaptically because double spikes are often evoked in secondary vestibulospinal neurons by single shock stimuli of the primary vestibular afferents (Sugiuchi et al. 1995). These trisynaptic IPSPs might be caused by stimulus spread to the saccular nerve (Wilson et al. 1977). However, the origin of this trisynaptic input is most likely the PCN, because its threshold was as low as that for disynaptic IPSPs from the same PCN. This interpretation is supported by the recent finding that stimulation of the saccular nerve evoked EPSPs rather than IPSPs in contralateral extensor motoneurons (Uchino et al. 1994). The present study also has shown that all dorsal ramus motoneurons do not have the same pattern of ampullary inputs as BIV and COMP motoneurons. OCS, SPL, and LONG motoneurons have another pattern of ampullary inputs, although their axons travel in the dorsal rami. The pattern of input to OCS and LONG motoneurons is inhibition from the three ipsilateral ampullary nerves and excitation from the three contralateral ones. This pattern was found consistently from one experiment to another. This input pattern also was found in 42.2% of the SPL motoneurons in which the effects of stimulation of the six ampullary nerves were examined. However, a fraction of SPL motoneurons received little or no input from the ipsilateral ACN and PCN and the contralateral PCN, and there were a considerable number of exceptions to this general input pattern for SPL motoneurons that were probably due to current spread (Table 3A). Therefore the input pattern to SPL motoneurons is basically similar to that observed in other motoneurons belonging to the longissimus muscle group, but seems to be slightly different from it in terms of input strengths from individual ampullary nerves and macular nerves. The input pattern from the six ampullary nerves to SPL motoneurons was reported previously by Wilson and Maeda (1974). The present result is somewhat different from their result. They found that stimulation of the bilateral ACNs usually evoked excitation and stimulation of the PCN gave variable results, although IPSPs were observed in about half of the contralateral SPL motoneurons examined. They concluded that “the pattern is somewhat different in splenius motoneurons. They are influenced most consistently from the horizontal canal, which produces ipsilateral inhibition and contralateral excitation. Stimulation of the anterior ampullary nerves usually evokes excitation, but stimulation of the posterior nerves is often ineffective.” The pattern that they reported is rather similar to the pattern obtained in BIV and COMP motoneurons, but the pattern that we found is similar to that in OCS and LONG motoneurons. An input pattern similar to the typical input pattern from the six ampullary nerves to RCP, BIV, and COMP motoneurons was found only in 7 of the 45 SPL motoneurons (15.6%) in this study. The difference between the two results involves the inputs from the ipsilateral ACN and the contralateral PCN. Our data agree with those reported by Wilson and Maeda (1974) in that the effects of stimulation of an ampullary nerve were not so clear-cut in SPL motoneurons as in other neck motoneurons. Compared with the responses in OCS and LONG motoneurons, deviations from the typical pattern were observed more often in SPL motoneurons (Table 3). This finding is probably due to weak inputs from the ampullary nerves to SPL motoneurons, especially from the PCNs as reported by Wilson and Maeda (1974). Furthermore, current spread to the macular nerves also might produce these deviations. Stimulation of the contralateral PCN evoked IPSPs in 11 of 57 SPL motoneurons. In such preparations, the same stimulation sometimes evoked EPSPs or an EPSP-IPSP complex rather than IPSPs in RCP and COMP motoneurons, suggesting current spread to the saccular nerve (Uchino et al. 1994). When stimulation of the ipsilateral ACN evoked...
tion from the vestibular nerves is transmitted to neck moto-
This research was supported in part by a research grant from ... and spinal interneurons through the LVST, whereas Ministry of Education, Science and Culture for Scienti®c Research.

Wilson and Yoshida 1969 ) and unidenti®ed spinal neurons quantitative analysis of various neck muscle activities is re-

The present study gives additional evidence that trisynaptic side are activated and those on the other side are depressed,

In motoneurons of the longissimus muscle group, disynap-
trisynaptic inhibition from the three ipsilateral ampullary nerves and disynaptic excitation from the three contralateral ampullary nerves are induced through the ipsilateral MLF. The path-
ways revealed in the present study for BIV and COMP moto-
eurons at C 3 by Wilson and Maeda (1974). In these motoneurons, disynaptic EPSPs from the ipsilateral ACN are transmitted through the ipsilateral LVST and disyn-
aptic EPSPs and IPSPs from the other ampullary nerves are transmitted through the ipsilateral MLF. These disynaptic connections are consistent with previous morphological re-
sults that secondary vestibulospinal axons directly terminate on neck motoneurons (Shinoda et al. 1986, 1988, 1992). The present study gives additional evidence that trisynaptic IPSPs from the contralateral PCN are conveyed to these motoneurons through an extra- MLF pathway. The pathway for trisynaptic inhibition from the contralateral ACN or PCN to some neck motoneurons recently has been identified (Su-
giuchi et al. 1992b, 1995). This inhibition is conveyed via the LVST and inhibitory spinal commissural neurons in lam-
ina VIII. This pathway also is associated with BIV and COMP motoneurons (Sugiuchi et al. 1995). The pathways revealed for motoneurons of the longissimus and the semi-
spinasis muscles groups in the present study are consistent with the previous conclusion regarding the pathways from the vestibular nerves to other neck motoneurons (Shinoda et al. 1994a; Uchino and Isu 1992; Wilson and Maeda 1974; Wilson and Yoshida 1969) and unidentified spinal neurons (Akaike et al. 1973). Namely, ipsilateral disynaptic excita-
tion from the vestibular nerves is transmitted to neck moto-
eurons and spinal interneurons through the LVST, whereas bilateral disynaptic inhibition and contralateral disynaptic excitation are conveyed through the MVST. Excitation may be mediated mainly by vestibuloculocoric neurons from the three contralateral ampullary nerves (Isu and Yokota 1983; Isu et al. 1988; Uchino and Hirai 1984) and also by vestibul-
locoric nerves but not from the contralateral ACN (Isu and Yokota 1983; Isu et al. 1988; Uchino et al. 1988). Inhibition may be mediated mainly by vestibuloculocoric neu-
rons from the three ipsilateral ampullary nerves and the con-
tralateral PCN (Isu et al. 1990; Uchino et al. 1990) and also by vestibuloculocoric neurons from the ipsilateral LCN (Isu et al. 1991; Ohgaki et al. 1988).

The patterns of ampullary inputs to neck motoneurons of the longissimus and semispinalis muscle groups are consis-
tent with head movements produced by electrical stimulation of the ampullae (Suzuki and Cohen 1964). Virtually all of the motoneurons examined showed excitation from the con-
tralateral LCN and inhibition from the ipsilateral LCN. Therefore, all of the neck muscles of the semispinalis and longissimus groups on one side may contract more or less in response to contralateral head rotation in the horizontal plane and relax in response to ipsilateral head rotation. This suggestion is consistent with the result obtained in quantita-
tive analysis of the vestibulocollic reflex by Baker et al. (1985). Bilateral electrical stimulation of the ACNs causes upward head movement (Suzuki and Cohen 1964). The same movement is produced by downward rotation of the head, in which bilateral anterior semicircular canals are acti-
vated and bilateral posterior semicircular canals are depressed. Therefore, excitation from the bilateral ACNs and disinhibition from the bilateral PCNs in BIV and COMP motoneurons produce contraction of BIV and COMP mus-
cles, so that the head may be rotated upward to be kept in a normal position in response to downward head movement disturbance. In this condition, OCS, SPL, and LONG moto-
eurons receive inhibition from the ipsilateral ACN and exci-
tation from the contralateral ACN. These inputs from the bilateral ACNs more or less cancel each other at a motoneu-
ron level, so that contraction of the OCS, SPL, and LONG muscles is considered to be minor. However, when the head is rotated on a naso-occipital axis or tilted in a frontal plane, the anterior and posterior semicircular canals on the tilted side are activated and those on the other side are depressed, which may result in relaxation of the OCS, SPL, and LONG muscles on the tilted side and their contraction on the other side. In fact, the response patterns of the SPL and BIV muscles evoked by roll tilt are consistent with these sugges-
tions. In response to lateral roll tilt, SPL muscle was most active during contralateral side down tilt and the electromyo-
graphic responses in left and right SPL muscles were recipro-
cal whereas left and right BIV muscles had the same, rather than the opposite, responses (Schor and Miller 1981). This result indicates that neck muscles of the longissimus and semispinalis groups may function differently in the vestibu-
locoric reflex. To understand the involvement of individual neck muscles in different vestibuloculocoric reflexes, further quantitative analysis of various neck muscle activities is re-
quired using natural rotation of the head.
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