Relation Between Axon Morphology in C1 Spinal Cord and Spatial Properties of Medial Vestibulospinal Tract Neurons in the Cat

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Perlmutter, S. I., Y. Iwamoto, L. F. Barke, J. F. Baker, and B. W. Peterson. Relation between axon morphology in C1 spinal cord and spatial properties of medial vestibulospinal tract neurons in the cat. J. Neurophysiol. 79: 285–303, 1998. Twenty-one secondary medial vestibulospinal tract neurons were recorded intraaxially in the ventromedial funiculi of the C1 spinal cord in decerebrate, paralyzed cats. Antidromic stimulation in C3 and the oculomotor nucleus identified the projection pattern of each neuron. Responses to sinusoidal, whole-body rotations in many planes in three-dimensional space were characterized before injection of horseradish peroxidase or Neurobiotin. The spatial response properties of 19 neurons were described by a maximum activation direction vector (MAD), which defines the axis and direction of rotation that maximally excites the neuron. The other two neurons had spatio-temporal convergent behavior and no MAD was calculated. Collateral morphologies were reconstructed from serial frontal sections to reveal terminal fields in the C1 gray matter. Axons gave off multiple collaterals that terminated ipsilaterally to the stem axon. Collaterals of individual axons rarely overlapped longitudinally but projected to similar regions in the ventral horn when viewed in transverse sections. The number of primary collaterals in C1 was different for vestibulo-colic, vestibulo-oculo-colic, and C6-projecting neurons: on average one every 1.34, 1.72, and 4.25 mm, respectively. The heaviest arborization and most terminal boutons were seen in the ventral horn, in laminae VIII and IX. Varicosities on terminal branches in lamina IX were observed adjacent to large cell bodies—putative neck motoneurons—in counterstained tissue. Some collaterals had branches that extended dorsally to lamina VII. Neurons with different spatial properties had terminal fields in different regions of the ventral horn. Axons with type I responses and MADs near those of a semicircular canal pair had widely distributed collateral branches and numerous terminations in the dorsomedial, ventromedial, and spinal accessory nuclei and in lamina VIII. Axons with type I responses that suggested convergent canal pair input, with type II responses, and with spatio-temporal convergent behavior had smaller terminal fields. Some neurons with these more complex spatial properties projected to the dorsomedial and spinal accessory but not to the ventromedial nuclei. Others had focused projections to dorsolateral regions of the ventral horn with few branches in the motor nuclei.

INTRODUCTION

Spatial coordination of the vestibulocollic reflex is achieved by an appropriately weighted distribution of semicircular canal and otolith inputs to neck motoneurons. As reported in the previous paper (Perlmutter et al. 1998), the responses of some medial vestibulospinal tract (MVST) neurons suggest that part of the necessary convergence of afferent signals occurs on second-order cells. We hypothesized that components of the input-output transformation of the reflex may be executed by projections of these neurons, which appear to receive convergent horizontal and vertical semicircular canal pair input, to specific groups of motoneurons. However, additional processing of spatial information must occur outside the vestibular nucleus to account for the maximal vertical responses of most neck muscles to rotations about the pitch axis (Iwamoto et al. 1996; Kasper et al. 1988; Wilson et al. 1990). Bolton et al. (1992), who found that the vertical responses of neck muscles were not present on reticulospinal neurons, hypothesized that this convergence of vestibular signals occurs within the spinal cord. Information on the spinal targets of vestibulospinal neurons with identified spatial properties is needed to test both of these hypotheses.

Our previous studies (Iwamoto et al. 1996; Perlmutter et al. 1998) have demonstrated that secondary vestibulospinal neurons with different spatial properties have different gross anatomic projection patterns (e.g., vestibulo-oculo-colic, vestibulo-C6). However, these studies did not provide information on the terminal fields of particular spatial signals within the spinal gray matter. Projections of vestibulospinal neurons to upper cervical interneurons and directly to neck motoneurons both may be involved in executing the spatial transformations of the vestibulocollic reflex.

Electrophysiological studies have shown that stimulation of the vestibular nerve produces postsynaptic potentials with disynaptic, trisynaptic, and longer latencies in neck motoneurons (Shinoda et al. 1994; Sugiuichi et al. 1995; Uchino and Isu 1991; Wilson and Maeda 1974; Wilson and Yoshida 1969; Wilson et al. 1977). Direct recordings of laminae VII and VIII interneurons that probably project to cervical motoneurons also have demonstrated short-latency vestibular inputs (Bolton et al. 1993; Endo et al. 1994; Schor et al. 1986; Sugiuichi et al. 1992; Wilson et al. 1984). However, little information is available on the response properties of vestibulospinal pathways that terminate in specific laminae of the cervical cord.

Anatomic studies have described heavy vestibular nucleus projections to laminae IX, VIII, and VII the central cervical nucleus (Carleton and Carpenter 1983; Donevan et al. 1990; Holstege 1988; Isu and Yokota 1983; Nyberg-Hansen 1964; Petras 1967; Shinoda et al. 1986a). Terminations in laminae II–VI and X also have been reported (Donevan et al. 1990, 1992b). The morphological characteristics of single secondary MVST axons in the upper cervical cord were described in detail by Shinoda et al. (1988, 1992). They found that single neurons had terminations in multiple motor nuclei and in laminae VII and VIII. However, the spatial properties of these cells were unknown because their responses to natural vestibular stimuli were not examined.
In the present study, we further examine the relationship between axonal morphology and response properties of secondary MVST neurons. To extend the anatomic work of Shinoda et al. (1988, 1992), the spatial properties of intraaxonally recorded neurons are characterized by their responses to three-dimensional rotations. Tracers then are injected into the same neurons to visualize their axonal morphologies. Results will show extensive divergence of canal pair signals at C1, and a more restricted projection of neurons carrying more highly processed spatial signals.

A preliminary report of the results was presented in Perlmutter et al. (1991).

METHODS

Axons of 21 secondary vestibulospinal neurons recorded in eight decerebrated, paralyzed cats were labeled and reconstructed. Vestibular responses of these neurons were included in the data set of the preceding paper (Perlmutter et al. 1998), which describes the methods for animal preparation (Fig. 1B of that paper), unit recording, and physiological data analysis.

Neuronal recording

Neurons were recorded intraaxonally in the ventromedial funiculi in C1 (Fig. 3A) within the anatomically defined borders of the bilateral medial vestibulospinal tracts (Holstege 1988; Nyberg-Hansen 1964). Recordings were made with glass micropipettes of 8–40 MΩ impedance, filled with 0.5–1.0 M KCl and either 10% horseradish peroxidase (HRP) or 4% Neurobiotin (Vector Laboratories) dissolved in 0.05 M Tris (hydroxymethyl) aminomethane buffer (pH 7.6). Secondary neurons were identified (Fig. 1Aa) by consistent activation within 1.5 ms of single-pulse stimulation of either labyrinth (Wilson and Melvill Jones 1978; see Perlmutter et al. 1998 for details). Antidromic responses to C5 and oculomotor nucleus stimulation (Fig. 1Ab) identified axons as vestibulo-oculocollic, vestibulo-colic, vestibulo-C5, or vestibulo-oculo-C5 neurons. For most axons, a collision test between stimulus-evoked and spontaneously occurring action potentials was performed to confirm that the former were antidromically conducted spikes and not synaptic responses (Fig. 1Aa). Each axon was identified as ipsilaterally or contralaterally projecting by the relation between the recording side and the labyrinth from which the neuron was monosynaptically activated (Fig. 1Ab).

The responses of axons to 0.5-Hz, 5° peak-to-peak, whole-body rotation in several vertical and the horizontal planes were recorded. During rotation, intraaxonal DC potential and action potential amplitude and waveform were monitored continuously to confirm stable recording of a single axon. Data collection was discontinued if a sudden change in one of these parameters occurred. The spatial properties of 19 of the 21 labeled neurons were summarized as three-dimensional maximum activation direction vectors (MAD), depicted as if the axon’s cell body was located in the left vestibular nucleus (Perlmutter et al. 1998). Neuronal MADs were compared with those of the semicircular canal pairs. Canal pairs were referenced by listing the canal with excitatory inputs first; for example, type I responses are produced by inputs from: left horizontal-right horizontal canal pair (lhc/rhc); left anterior-right posterior canal pair (lac/rpc); left posterior-right anterior canal pair (lpc/rac; see Fig. 3 of Perlmutter et al. 1998). The other two cells exhibited strong spatio-temporal convergence with a minimum response ratio >0.2 (see Perlmutter et al. 1998).

Morphological characterization

Well-penetrated axons were injected iontophoretically with HRP or Neurobiotin after recording their responses to three-dimensional orientations. Axons were injected if the measured resting potential was at least −20 mV (DC) or action potential amplitude was ≥10 mV. Positive pulses of 10–20 nA and 100-ms duration (50% duty cycle) were passed through the pipette for 5–20 min. Intraaxonal DC potential and responses to weak labyrinth shock were monitored continuously during the injection, which was terminated if spike amplitude or resting potential deteriorated severely. Threshold and latency of responses to labyrinth, oculomotor nucleus, and C5 stimulation were reexamined after several minutes of injection. One to six injections were made in each animal. Two to 18 h after the first of these injections, the animal was anesthetized deeply with pentobarbital sodium (50 mg/kg iv), heparinized, and perfused transcardially. Animals in which Neurobiotin had been injected were perfused with 0.9% saline followed by 4% paraformaldehyde in 0.1 M phosphate buffer. Fixative was infused for 30–60 min and frequently followed by infusion of a solution of 30% sucrose.
Staining in 49 of the 138 collaterals was classified as completely or mostly stained and served as our database for examining branching patterns and terminal field distribution. Collaterals shown in Figs. 4–9 are projected onto a single frontal section of the spinal cord, representing 400- to 1,840-μm-thick blocks of tissue.

RESULTS

Twenty-one neurons recorded intraaxonally in C1 were injected with HRP or Neurobiotin and labeled sufficiently to reconstruct their axonal morphology (Fig. 1B). These neurons were activated monosynthetically by single-pulse stimulation of one labyrinth, and had activity modulated during 0.5-Hz whole-body rotation. Staining was seen in 138 collaterals from five contraterally projecting vestibulo-oculo-collic (c-VOC) neurons (39 collaterals), eight ipsilaterally and two contraterally projecting vestibulo-collic (i-VC, c-VC) neurons (82 collaterals), one contraterally projecting vestibulo-oculo-C6 (c-VO-C6) neuron (2 collaterals), and five ipsilaterally projecting vestibulo-C6 (i-VO-C6) neurons (15 collaterals).

Stem axons and primary collaterals

Seven stem axons were injected with HRP and stained for distances of 6.3–12.1 mm (mean ± SD, 8.9 ± 2.3 mm). Fourteen stem axons were injected with Neurobiotin and stained for 9.5–30.7 mm (15.7 ± 6.4 mm). Terminal branches were labeled primarily in C1, and Neurobiotin-injected axons often could be traced into C2 and the caudal medulla (Fig. 2). Stem axons traveled in the dorsal two-thirds of the medial ventral funiculus, usually dorsal to the tip of the ventral horn (Fig. 3A). Their position relative to the gray matter border usually was fixed as the axon descended below rostral C1 (e.g., Fig. 4A). Contraterally projecting axons tended to lie closer to the midline than those descending ipsilaterally (Fig. 3A), but there was no clear correlation between an axon’s location within the ventral funiculus and its spatial properties or projection type (i.e., VOC, VC, V-VO-C6).

Stem axons gave off primary collaterals over their entire stained length. Intercollateral distances for 122 spinal collaterals within C1 ranged from 200 to 4,800 μm (1,230 ± 920 μm). All labeled C1 collaterals except one remained ipsilateral to the stem axon and coursed laterally or dorsolaterally across the funiculus to the medial border of the lower half of the ventral horn. Primary collaterals usually bifurcated at least once before, or on entering, the gray matter (e.g., Figs. 4 and 5), sometimes close to the stem axon. One neuron (8005 in Fig. 2) had one C1 collateral that crossed the midline through the anterior commissure, in addition to several collaterals that remained ipsilateral to the stem axon (Fig. 7). The crossing collateral was stained too weakly to visualize its arborization in the contralateral gray matter.

Sixteen collaterals, from four neurons, were stained in the caudal brain stem and most traveled to ipsilateral regions continuous with the C1 ventral horn. The entire medulla was processed in one animal with two well-stained c-VOC axons (8102 and 8103 in Fig. 2). Both neurons had one collateral that came off the stem axon in the caudal medulla and crossed the midline. These collaterals were traced to the vestibular nucleus contrateral to the stem axon (i.e., ipsilateral to the cell body). The stem axons could not be traced rostrally to their cell bodies.

The number of primary collaterals given off by an axon in C1, measured as the number of collaterals per unit length, was dependent on the neuron’s projection pattern (Fig. 2; F ratio significant at P < 0.001). VOC (n = 5) and VC (n = 10) neurons had many collaterals, on average one every 1.72 ± 0.41 mm and 1.34 ± 0.37 mm, respectively. Cc projecting neurons (n = 6) had fewer, more widely separated collaterals in C1—one every 4.25 ± 2.19 mm. Intercollateral distance did not vary systematically along the rostrocaudal length of individual axons, but collaterals were not always evenly spaced (Fig. 2). Axons that could be traced through the spino-medullary junction gave off one or two collaterals in the caudal brain stem, except cell 8412, which had many collaterals near the obex (Fig. 2).

Branching patterns within C1 gray matter

Staining in 49 of the 138 collaterals was classified as complete or mostly complete (see METHODS) and their branching patterns were analyzed. The general observations of collateral morphology reported in this section are in good agreement with the more complete anatomic work of Shi- noda et al. (1988, 1992) and Donevan et al. (1992a).

Most collaterals branched three or more times before synaptic boutons were observed. Boutons terminaux and en pas-
FIG. 2. Schematic of collateral distribution and rostrocaudal extent of terminal branches for all stained neurons (format from Shinoda et al. 1986a, 1992). Each stem axon is represented as a vertical line scaled to show the length over which it was stained. Horizontal lines depict the relative position of all primary collaterals. Short vertical lines correspond to the distance over which branches were stained for each collateral; for many collaterals, the full rostrocaudal extent of branching was probably larger because branches were not completely stained. Large dots show injection sites for each axon. Neuron and collateral labels are referred to in the legends of Figs. 4–9. Axons are grouped by projection pattern (see text for description).

FIG. 3. A: location of stained stem axons in the ventral funiculus at the mid-C1 level, shown in a sketch of a frontal section. ●, ipsilaterally projecting axons, ×, contralaterally projecting axons. Outline of ventral horn and bottom of spinal cord are drawn; central canal is small circle at upper right; vertical line denotes midline. ---, approximate borders between laminae VII and VIII and between laminae VII and VI. B: distribution of large thionin-stained neurons, probably motoneurons, in the rostral C1 segment of one animal; 5 transverse sections (500 μm) superimposed. Shaded cells appeared to be contacted by small varicosities, presumably synaptic boutons, on fine axonal branches of cell 5605 (Fig. 6B); C and D: general location of neck motor nuclei within the rostral (C) and mid (D) C1 gray matter. Nuclei were defined by columns of large cell bodies, like those in B, in superimposed frontal sections counterstained with thionin or cresyl violet. Spinal accessory nucleus migrates from a central and dorsal position in lamina VIII at rostral C1 (C) to a lateral position in caudal C1 (D) (Brichta et al. 1987; Rapoport 1978; Uchino et al. 1990). VM, ventromedial nucleus; DM, dorsomedial nucleus; SA, spinal accessory nucleus; CCN, central cervical nucleus; VII, VIII, Rexed’s laminae.
sant were seen on completely stained, higher-order branches (Fig. 1, B and C). Many secondary or tertiary branches traveled long distances through the ventral horn, giving off thin terminal branches along the way. Others ramified several times within localized regions to create dense tangles of fine diameter branches. Some thin branches had many en passant boutons close together, interleaved with short terminal branches ending in a bouton terminus. This gave the appearance of multiple synaptic contacts within a small area, perhaps with a single target neuron. Other branches had en passant boutons widely spaced over distances of a few hundred microns.

As a population, the stained neurons had a much higher density of fine diameter branches and terminal boutons in the ventral horn than in other regions of the gray matter. All collaterals arborized in lamina VIII and many projected to lamina IX. Some collaterals extended to lamina VII, but branches rarely were detected above the dorsoventral level of the central canal.

Adjacent collaterals of individual axons projected to similar regions in the frontal plane of the cord (except for two neurons with MADs nearly aligned with the horizontal canal pair vector). However, the terminal fields of adjacent collaterals rarely overlapped rostrocaudally, except for three VC neurons (8408, 8412, and 8605; Fig. 2). Branches for the 49 well-stained collaterals (≈1 from each neuron) extended rostrocaudally between 400 and 1,840 μm (802 ± 304 μm). However, it is possible that the rostrocaudal extent of collaterals classified as mostly stained was slightly underestimated because of incomplete staining of some branches. The rostrocaudal extent of collateral branching was not correlated to projection pattern (Fig. 2).

Fine diameter branches in the ventral horn often had boutons that were located close to large counterstained cell bodies (Fig. 1C) and, in some cases, appeared to make synaptic contact with them (Fig. 1C, right). Figure 3B shows the distribution of these somata in rostral C1 in one animal. The shaded cells appeared to receive presynaptic terminals from collateral c of the axon shown in Fig. 6A. These large cells were probably motoneurons and were found in rostrocaudal columns that corresponded to the ventromedial, dorsomedial, and spinal accessory nuclei. These nuclei are identified in Fig. 3, C and D, and shown in all subsequent figures. At the most rostral levels of C1, the dorsomedial and spinal accessory nuclei were not distinguishable.

**Terminal fields and spatial properties**

The responses of 19 neurons were well described by the "cosine-tuned gain" model (see Perlmutter et al. 1998) and MADs were calculated. Fifteen of these exhibited only type I yaw and/or roll responses (i.e., activated by rotation in directions that excite ipsilateral canal afferents), and 4 neurons exhibited type II responses (activated by rotation in directions that excite contralateral canal afferents). Two i-V-Cx neurons exhibited spatio-temporal convergent behavior with no clear null response plane (Baker et al. 1984; Iwamoto et al. 1996) and MADs were not calculated. The terminal fields of the 49 best-stained collaterals from these axons (≈1 for each neuron) were examined for correlations with the neurons’ spatial properties.

### TABLE 1. Morphophysiological properties of 21 stained MVST axons

<table>
<thead>
<tr>
<th>Neuron</th>
<th>Inputs*</th>
<th>Projection Pattern</th>
<th>Terminal Distribution</th>
<th>Figure</th>
</tr>
</thead>
<tbody>
<tr>
<td>8412</td>
<td>lhc/rhc</td>
<td>i-VC</td>
<td>DM, VM, SA, IVIII, dVIII</td>
<td>4A</td>
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<td>i-VC</td>
<td>DM, VM, SA, IVIII, dVIII</td>
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<td>c-VC</td>
<td>DM, VM, SA, dVIII</td>
<td></td>
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<tr>
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<td>c-VC</td>
<td>DM, VM, SA, IVIII</td>
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<tr>
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<td>c-VOC</td>
<td>DM, VM, VIII, dVIII</td>
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<tr>
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<td>lac/rpc</td>
<td>c-VOC</td>
<td>DM, VM, SA, IVIII</td>
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<td>6B</td>
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<td>SA, IVIII</td>
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<td>8001</td>
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<td>DM, SA, IVIII</td>
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<td>STC</td>
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<td>SA, IIVIII</td>
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DM, dorsomedial nucleus; VM, ventromedial nucleus; SA, spinal accessory nucleus; IVIII, lamina VIII lateral to motor nuclei; dVIII, lamina VIII dorsal to DM and SA; VII, lamina VII; MVST, medial vestibulospinal tract; i- and c-VC, ipsi- and contra-laterally projecting vestibulo-collic; c-VOC, contralaterally projecting vestibulo-oculo-collic; i-V-Cx, ipsilaterally projecting vestibulo-Cx; lhc/rhc, left horizontal-right horizontal canal pair; lac/rpc, left anterior-right posterior canal pair; lpc/rac, left posterior-right anterior canal pair; rhc/lhc, right horizontal-left horizontal canal pair. * Semicircular canal pair inputs consistent with the neuron’s maximum activation direction vector (MAD); each cell represented as if its cell body were on the left side of the brain stem (i.e., lhc/rhc, lac/rpc, and lpc/rac input produce type I responses; rhc/lhc, rac/lpc, and rpb/lac input produce type II responses. † Spatio-temporal convergent responses—see text.
FIG. 4. Reconstructions of C1 collaterals and responses to 0.5 Hz, whole-body rotations for 2 secondary MVST neurons with maximum activation direction vectors (MADs) aligned with the left horizontal-right horizontal canal pair (lhc/rhc) vector. Average responses to rotations in the horizontal and one vertical plane are shown in bottom inset as cumulative spike histograms for many cycles of rotation. Upward deflection of table (i.e., head) position trace corresponds to rotation to the side ipsilateral to the neuron’s cell body for yaw and to ipsilateral ear down rotation for roll (Figs. 4A, 6B, and 8A) or nose up rotation in other vertical planes (other figures). Top inset: MAD normalized to a length of 1. Front view: components of the MAD for yaw and pitch rotations, as shown. Top view: pitch and roll components. Reconstructions show morphology of each collateral projected onto 1 frontal section of the C1 spinal cord. Most rostral collateral is shown top, most caudal at bottom. Border of ventral horn drawn for all collaterals; midline structures drawn for most rostral collateral. Stem axon is short, thick line in the ventral funiculus. A: axon 8412, an ipsilaterally projecting vestibulocollic (i-VC) neuron activated by horizontal rotations to the ipsilateral side (yaw gain = 2.8 spikes s⁻¹ deg⁻¹); MAD nearly aligned with that of lhc/rhc vector (see Fig. 3, Perlmutter et al. 1998 for canal MADs). Collaterals j, k, and l (Fig. 2) are shown. Central canal is flattened circle at top right, anterior median fissure is at bottom right. B: axon 8702, a contralaterally projecting vestibulocollic (c-VC) neuron, with similar spatial properties (yaw gain = 2.7 spikes s⁻¹ deg⁻¹). Collaterals d, e, and f are shown.
The terminal fields of MVST neurons with type I responses and MADs suggesting input from a single canal pair tended to be different from those of neurons with more complex spatial properties (Table 1). In the following description, collateral branching is described with reference to the laminae borders shown in Fig. 3, C and D. Projections to lamina VIII are divided into those extending lateral to the motor nuclei and those extending dorsal to the dorsomedial and/or spinal accessory nuclei. Rostral to caudal collaterals are shown from top to bottom in Figs. 4–9. Cell numbers and collateral labels in the figure legends refer to Fig. 2.

Neurons with type I responses consistent with single canal pair Input. Neurons with type I responses and MADs suggesting input from a single canal pair tended to project to a wide area in the C1 ventral horn (Table 1).
The motor nuclei were the primary targets, and most axons terminated in the dorsomedial, ventromedial, and spinal accessory nuclei. Collaterals also branched extensively in lamina VIII, often including regions lateral and dorsal to the motor nuclei. Figures 4–6 show data from neurons with maximal responses in planes near those of the ipsilateral horizontal, anterior, and posterior canals, respectively.

Two i-VC neurons (8004 and 8412 in Fig. 2) with MADs aligned with the lhc/rhc vector had collateral morphologies like those shown in Fig. 4A. This axon (8412), injected with Neurobiotin, fired 1.0 ms after stimulation of the labyrinth ipsilateral to the recording site and was not activated by stimulation of the oculomotor nucleus or C₃ segment; it was classified as a secondary i-VC neuron. Firing rate increased during horizontal rotations to the ipsilateral side and was only weakly modulated by rotations in vertical planes (Fig. 4A, inset). The 3 most caudal of 12 stained primary collaterals are shown. Each collateral arborized in similar regions of the ventral horn and had terminal boutons in the ventromedial, dorsomedial, and spinal accessory nuclei. To some extent different regions of each motor nucleus were targeted by different collaterals, but the projections of all three collaterals combined appeared to extend throughout each nucleus. Long secondary or tertiary branches of each collateral traveled laterally or dorsolaterally across the ventral horn and gave off terminal branches in areas of lamina VIII lateral to the motor nuclei. Medial branches of the middle and caudal collaterals coursed to dorsomedial lamina VIII and ventromedial lamina VII where numerous boutons were observed. The middle collateral bifurcated into ventrally and dorsally projecting secondary branches that terminated in distinct regions of the ventral horn.

Two other secondary c-VC neurons with MADs aligned with the lhc/rhc vector (8408 and 8702) also had projections to all three motor nuclei but individual collaterals arborized in more restricted regions of the ventral horn. Figure 4B shows the middle three of nine collaterals from one of these neurons (8702), stained with Neurobiotin. The terminal fields of these collaterals overlapped much less than those of the axon in Fig. 4A. The ventromedial nucleus received projections primarily from the rostral collateral, and only the caudal collateral gave off terminal branches in the spinal accessory nucleus. Many terminals of the middle and caudal collaterals, but not the rostral collateral, were seen in the dorsomedial nucleus. Branches of these collaterals also extended into lamina VIII dorsal to the dorsomedial nucleus and sparsely into lamina VII.

Six of seven axons with spatial properties similar to those of ipsilateral vertical canal afferents also arborized extensively in the C₁ motor nuclei. Two neurons (5807 and 5809) with MADs near the lpc/rpc vector had terminal fields similar to those of the yaw-sensitive neuron in Fig. 4A. Figure 5 shows three (of 5) HRP-stained collaterals from one of these neurons (5809). It was driven monosynaptically by contralateral labyrinth stimulation (latency = 1.1 ms) and antidromically from the oculomotor nucleus but not from C₃ (secondary c-VOC neuron). The axon was maximally activated by nose down rotations near the plane of the ipsilateral anterior–contralateral posterior canal pair (i.e., MAD near the lpc/rpc vector). Collaterals split in the white matter into ventrally and dorsally projecting branches. Each ventral branch arborized in the ventromedial nucleus and extended laterally to lamina VIII. Dorsal branches arborized in the dorsomedial and spinal accessory nuclei and continued dorsally to the border between laminae VIII and VII.

A third neuron (8102) with a MAD near the lpc/rpc vector also projected heavily to the ventromedial and dorsomedial nuclei and sent long collateral branches to lateral and dorsomedial lamina VIII. Fewer branches were seen in the spinal accessory nucleus, although it could not be clearly distinguished from the dorsomedial nucleus at the level of the most rostral collateral.

Two ipsilaterally projecting neurons (5605 and 8601) with MADs near the lpc/rac vector had similar widespread projections, exemplified by Fig. 6A (5605). This neuron discharged 1.3 ms after stimulation of the ipsilateral labyrinth. C₃ stimulation evoked antidromic firing but oculomotor stimulation was ineffective. Neuron 5605 was classified as an i-V-C₆ neuron and was activated by nose up rotations in the plane of the ipsilateral posterior–contralateral anterior canal pair. One brain stem and five spinal collaterals were stained with HRP. The rostral two collaterals shown in Fig. 6A arborized densely in the dorsomedial and spinal accessory nuclei and had branches extending to the ventromedial nucleus and laterally into lamina VIII. Other branches extended into lamina VIII dorsal to the dorsomedial nucleus. The third collateral shown in Fig. 6A bifurcated into ventrally and dorsally projecting secondary branches on entering the gray matter.

Figure 6B (8706) shows data from a c-VOC neuron with spatial properties similar to those of the neuron in Fig. 6A but that had more localized terminations in C₁. Two adjacent (500-μm apart) Neurobiotin-stained collaterals terminated in the dorsomedial and spinal accessory nuclei but did not project to the ventromedial nucleus. Some branches extended dorsal to the dorsomedial nucleus with numerous terminations in lamina VIII.

One neuron with a MAD near the lpc/rac axis had a different pattern of termination. Axon 6209, an i-VC neuron, had some terminals in the spinal accessory nucleus but projected primarily to the dorsolateral ventral horn in a region of lamina VIII lateral and dorsolateral to the motor nuclei.

In summary, 9 of 11 neurons with type I responses and MADs near one single canal pair vector had projections to all three C₁ motor nuclei and branches in lateral and dorsal lamina VIII. One neuron also projected primarily to the motor nuclei but had more restricted terminations in and around the dorsomedial and spinal accessory nuclei. Only one neuron with responses that resemble those of ipsilateral canal afferents had sparse arborization in the motor nuclei. It apparently targeted interneuronal fields in lamina VIII.

**Neurons with More Complex Spatial Properties**. Neurons with either type I responses that suggested convergent input from more than one canal pair, type II responses or spatio-temporal convergent (STC) behavior tended to have more focused terminal fields in the C₁ gray matter and appeared to project less densely to the motor nuclei. Localized projections to dorsal and/or lateral portions of the ventral horn, rare in the population of type I neurons
with single canal pair input, were observed for some axons
(Table 1).

Neuron 8005, a secondary i-VC cell, had type I responses suggesting input from lhc/rhc and lpc/rac. Reconstructions of three of five Neurobiotin-stained primary collaterals are shown in Fig. 7. The morphologies of these collaterals were similar to those of three other neurons with type I responses and convergent canal pair input

(5903: lhc/rhc and lpc/rac input; 8001: maximal responses to ipsilateral ear down roll rotations; 8103: lhc/rhc and lac/rpc input). Each collateral coursed dorsolaterally through the gray matter giving off fine branches in the dorsomedial and spinal accessory nuclei but sending few or no projections to ventral regions of the ventral horn. Branches also arborized in lamina VIII lateral to the motor nuclei. The extent of the terminal fields of these three
neurons was significantly smaller than those of the axons shown in Figs. 4, 5, and 6A.

Two of four axons with type II yaw responses had morphologies that were clearly different from those described to this point (Fig. 8). These axons had the fewest C1 collaterals and the smallest terminal fields of all stained neurons (Table 1). Collaterals arborized sparsely within the ventral horn and had few terminal branches in the motor nuclei. Instead, collaterals projected primarily to dorsal areas of lamina VIII or lamina VII.
Figure 8A shows data from a secondary i-V-C neuron (8003) that had increased activity for horizontal rotations to the contralateral side and was not modulated by vertical rotations. The neuron's MAD nearly was aligned with that of the rhc/lhc. Three Neurobiotin-stained primary collaterals (2 shown in Fig. 8A) arborized along a narrow zone as they ran dorsolaterally through the ventral horn. The most rostral of these extended to the lateral edge of the gray matter in lamina VII. The other collateral had a branch that traveled medially through dorsal lamina VIII into lamina VII. Branching and terminal boutons of these collaterals were seen in the dorsal spinal accessory nucleus, but not in the dorsomedial or ventromedial motor nuclei.

Figure 8B shows data from an axon (8006) driven from the labyrinth contralateral to the recording site with a latency of 1.3 ms and antidromically activated from both oculomotor and C₆ electrodes. This secondary c-VO-C₆ neuron had responses consistent with input from rhc/lhc and lac/rpc. The collateral shown in Fig. 8B, one of two primary collaterals stained with Neurobiotin, sent off branches that coursed dorsally to ventromedial lamina VII and a few that projected ventrally along the medial border of the gray matter.

Two other stained neurons (8605 and 5811) also were activated by horizontal rotation to the contralateral side and appeared to receive convergent input from lpc/rac. The terminal fields of these neurons were similar to each other and among the most widespread of all labeled axons. Figure 9 shows data from one of these (8605), a secondary i-VC neuron injected with Neurobiotin. Two (of 10) collaterals in mid-C₁ are shown. The rostral collateral projected to the ventromedial, dorsomedial, and spinal accessory nuclei and to regions of lamina VIII lateral to the motor nuclei. A long branch also traveled dorsal to the dorsomedial nucleus into lamina VII. The caudal collateral branched throughout the ventral half of the ventral horn with dense projections to the ventromedial nucleus, the ventral part of the spinal accessory nucleus, and a wide area of lamina VIII lateral to those cell columns.

Two neurons (6601 and 8404) exhibited STC behavior, with constant response gain for all earth-vertical rotations, and response phase that shifted from velocity phase to position phase for rotations in different vertical planes. These axons gave off few collaterals in C₁ (Fig. 2). The stem axon of neuron 8404 was stained for ~13.5 mm, but only one collateral was observed. In addition, the collaterals had sparse terminations in the ventral horn. Of the motor nuclei, only the spinal accessory nucleus was targeted by these axons. Each collateral traveled through the middle of the ventral horn to dorsolateral lamina VIII and lamina VII, similar to the branching pattern seen in Fig. 8A.

In summary, 8 of 10 neurons with convergent canal pair inputs, type II or STC responses had projections in C₁ that were more focused than those of neurons with type I responses and single canal pair input. None of these eight axons terminated extensively, if at all, in all three motor nuclei. Projections to the ventromedial nucleus were particularly sparse. Some of these neurons did have extensive terminations in laminae VIII and IX (e.g., Fig. 7), whereas others projected to narrow regions of the ventral horn (e.g., Figs. 8).

**DISCUSSION**

We have studied 21 secondary MVST neurons with three different approaches to elucidate the functional organization of the medial vestibulospinal projection. Each of the methods provides independent information on the morphophysiological properties of the cells. First, the projection pattern of each
neuron was identified electrophysiologically. Second, their spatial response properties were characterized by applying rotations in many planes in three-dimensional space. Finally, the neurons were labeled with intraaxonal injection of HRP or Neurobiotin to reveal the morphology of C1 collaterals. These experiments suggest a correlation between the spatial properties and anatomic projections of secondary MVST neurons. In the following text, we discuss the validity and limitations of the anatomic method used, compare our morphological observations with those in previous studies, and consider how electrophysiological, functional, and morphological attributes of vestibulospinal neurons are correlated. Finally, we consider possible mechanisms for the spatial transformations of the vestibulocollic reflex based on the morphophysiological characteristics of secondary MVST neurons.

Interpretation of morphological data

Our intraaxonal recordings were maintained while the animal was rotated in many three-dimensional planes before injection of tracer. This undoubtedly caused deterioration of some electrode penetrations before injection, and consequently some staining was not optimal. For example, terminal boutons were not always seen on fine diameter branches of collaterals near the injection site. However, we believe for the following reasons that many collaterals were sufficiently labeled to estimate the extent of the terminal fields of 21 MVST neurons. First, when observed under the light microscope at high magnification, it was clear which collaterals had dense staining that remained deep through repeated levels of ramification, down to fine diameter branches. Collater-
als that were stained poorly, like those far from injection sites, had a much different appearance under the microscope. The density of staining was weaker and became fainter as the distance from the stem increased. On this basis, we classified the 49 best-stained collaterals as completely stained (terminal boutons observed) or mostly stained (some branches without terminals). Our conclusions on terminal field distribution were based only on these collaterals. Second, the rostrocaudal extent of branching of the 49 collaterals and those of MVST neurons completely stained with HRP by Shinoda et al. (1988, 1992) and Donevan et al. (1992a) was similar (see further). Third, the general pattern of collateral morphology and terminal distribution for secondary MVST axons reported by Shinoda et al. (1992), where terminal boutons were stained for almost all branches, are similar to those described here. Nonetheless, it is possible that the extent of collateral branching and terminal field distribution for neurons that we classified as mostly stained were underestimated slightly because of incomplete staining.

We have interpreted the presence of terminal branches and boutons to indicate synaptic contact with cell bodies or proximal dendrites. It is possible that terminations were, instead, on distal dendrites of neurons the cell bodies of which were at some distance away. Neck motoneurons have far-ranging dendrites that extend over large portions of the ventral horn (Keirstead and Rose 1983; Vanner and Rose 1984). However, many boutons appeared to be contacting large, counterstained cell bodies when viewed at high magnification (Figs. 1 and 3). Shinoda et al. (1992) also have reported axonal terminals of MVST neurons contacting cell bodies and proximal dendrites of presumed neck motoneurons in the upper cervical cord. The time course of excitatory postsynaptic potentials (EPSPs) produced by secondary vestibulospinal neurons in neck motoneurons also suggests that synapses are made on cell bodies and/or proximal dendrites (Isu et al. 1988; Uchino et al. 1988, 1990).

Finally, our sample of 21 stained axons is not sufficient to characterize the entire population of secondary MVST neurons. Because of the small sample size, we have grouped MVST neurons into two broad categories based on their spatial properties—neurons with responses that resemble ipsilateral semicircular canal afferents and those with more complex responses. There is considerable variability of axonal morphology for neurons within these groups probably because each category includes neurons with different roles in the vestibulocollic reflex and perhaps with other vestibular functions. In addition, several cell types described in the previous paper (e.g., Cc-projecting neuron with MAD near the roll axis) were not stained. Our conclusions, therefore, are not intended to be comprehensive but rather to indicate a trend relating the physiological and morphological properties of neurons studied to date. Further elaboration of the relationship between spatial properties and terminal field distribution must await morphophysiological characterization of a larger sample of MVST neurons.

**Morphology of MVST axons**

The collateral morphology and overall distribution of terminal branches and boutons of the 21 stained axons were in agreement with data on MVST neurons from previous autoradiographic and HRP labeling studies (Donevan et al. 1990, 1992a; Holstege 1988; Isu and Yokota 1983; Nyberg-Hansen 1964; Petras 1967; Shinoda et al. 1988, 1992). There were no clear differences between the morphology of ipsilaterally and contralaterally projecting axons, consistent with Shinoda et al. (1992).

Inter collateral distances were similar to those reported for lateral vestibulospinal neurons in lower cervical segments (Shinoda et al. 1986a) and for MVST neurons in the upper cervical cord (Donevan et al. 1992a; Shinoda et al. 1992). The rostrocaudal extent of branching of individual collaterals (mean = 802 μm for the 49 best-stained collaterals) was also similar to those of secondary MVST axons stained with HRP by Shinoda et al. (1992; 819 μm) and Donevan et al. (1992a; 760 μm). Corticospinal and rubrospinal (Shinoda et al. 1982, 1986b) neurons, in contrast, have more widely spaced collaterals with more longitudinally expansive arborization. The branches of all but one stained MVST collateral remained ipsilateral to the ventral funiculus in which the stem axon was recorded. Shinoda et al. (1992) and Donevan et al. (1992a) also found very few MVST collaterals crossing in the spinal cord. Collaterals that cross the midline in the spinal anterior commissure are more common for lateral vestibulospinal neurons projecting to lower cervical segments (Shinoda et al. 1986a). In most cases, sibling collaterals from the same stem axon projected to similar regions in the frontal plane of C, as described by Shinoda et al. (1992) and Donevan et al. (1992a).

Laminae VIII and IX were the primary targets of 17 of the 21 labeled MVST neurons, suggesting that they participated in execution of the vestibulocollic reflex. Dense arborizations and numerous terminal boutons were observed in the ventromedial, dorsomedial, and spinal accessory nuclei where motoneurons of dorsal neck extensor muscles, ventral flexor muscles, and lateral rotator muscles, respectively, are located (Abrahams and Keane 1984; Bakker et al. 1984; Brichta et al. 1987; Gordon and Richmond 1991; Rapoport 1978; Rose and Keirstead 1988; Richmond et al. 1978; Sugiu-uchi and Shinoda 1991). Stained MVST axons had boutons in close contact with large cell bodies in these nuclei (Fig. 3D). Monosynaptic projections of MVST neurons to neck motoneurons in the ventromedial (Rapoport et al. 1977; Uchino et al. 1988; Wilson and Maeda 1974; Wilson and Yoshida 1969), dorsomedial (Isu et al. 1988), and spinal accessory (Fukushima et al. 1979) nuclei have been documented electrophysiologically.

Many labeled axons terminated in more than one motor nuclei, suggesting that they synapsed on motoneurons of extensor, flexor, lateral flexor, and rotator muscles. This is consistent with previous anatomic studies that have shown vestibulospinal collaterals branching in multiple cervical motor nuclei (Donevan et al. 1992a; Isu and Yokota 1983; Shinoda et al. 1986a) and contacting different species of motoneurons (Shinoda et al. 1992).

Axon terminations in lamina VIII were probably connections to C1 interneurons. Intracellular recordings of lamina VIII interneurons in upper cervical segments have found disynaptic excitation after vestibular nerve stimulation (Bolton et al. 1993; Sugiu-uchi et al. 1992). Lamina VIII appeared to be the primary termination zone of several axons, most
Neurons with type II yaw responses and few terminals in the ventral horn. Same format as in Fig. 5. 

A: axon 8003, an i-V-C, neuron with gain in yaw of $-3.7$ spikes $\cdot$ s$^{-1}$ $\cdot$ deg$^{-1}$. Collaterals a and b are shown. Section containing the most proximal part of the primary collateral and the stem axon was lost.

B: axon 8006, a c-VO-C, neuron with gain in yaw of $-3.4$ spikes $\cdot$ s$^{-1}$ $\cdot$ deg$^{-1}$ and gain for rotation about the lac/rpc axis of 6.8 spikes $\cdot$ s$^{-1}$ $\cdot$ deg$^{-1}$. Collateral a shown.

Phaseolus vulgaris leucoagglutinin (PHA-L) labeling of MVST axons has shown numerous terminations in intermediate and dorsal horn laminae in the upper cervical cord (Donevan et al. 1990, 1992a,b). Some collaterals described here did become faint as they reached lamina VII, and a few branches projecting dorsal to the ventral horn were probably not detected. However, our results are in good agreement with the HRP studies of Donevan et al. (1992a) and Shinoda et al. (1992) in suggesting that secondary neurons do not contribute significantly to the MVST projection to cervical areas dorsal to lamina VII. It seems likely that nonsecondary vestibulospinal neurons, many of which have spatial properties different from those of secondary neurons (Iwamoto et al. 1996), are the source of these terminations.

Correlation of axonal morphology and spatial properties

The present study extends the work of Shinoda et al. (1988, 1992) by directly correlating the collateral morphologies of individual secondary MVST axons with their gross...
axonal projection patterns (VOC, VC, etc.) and responses to three-dimensional rotations. This analysis revealed a relationship between morphology and spatial properties, although there was variability in morphology from axon to axon and some neurons had terminal fields that were exceptions.

There was a clear trend for the terminal fields of neurons with responses suggesting excitatory input from afferents of a single ipsilateral canal to be different from those of neurons with responses suggesting additional convergence of primary vestibular signals. Most MVST neurons with type I yaw and roll responses and MADs suggesting input from only one semicircular canal pair had widespread branching within the C₁ ventral horn and dense projections to multiple motor nuclei, usually terminating in the dorsomedial, ventromedial, and spinal accessory nuclei. Only 2 of 11 neurons with this response pattern were clear exceptions. Neurons with responses suggesting input from more than one canal pair, with type II responses, or with spatio-temporal convergent behavior tended to have smaller terminal fields in C₁. Some of these axons terminated primarily in the ventral horn, but projections to the ventromedial nucleus were rare. Other axons had much sparser terminations in the ventral horn and targeted dorsolateral lamina VIII or lamina VII. Only 2 of 10 neurons with the more complex response patterns had widespread terminations that were clear exceptions to this trend.

Donevan et al. (1992a) made similar discriminations between narrow and widespread terminal fields for MVST axon collaterals. In their PHA-L and HRP study on C₂-C₇ collaterals, they reported that some neurons had “focused projections” to primarily one lamina, whereas others had “broad terminal fields” extending throughout the ventral horn. The present results suggest that these morphological classes of neurons had distinct spatial properties.

It is possible that a finer resolution of morphophysiological specialization exists for secondary MVST neurons. For example, the collateral morphologies of four neurons with type II yaw responses could be divided into two dissimilar types that might be correlated with other aspects of the neurons’ response properties (e.g., both neurons with widespread terminations in C₁ were activated by nose up rotations in the plane of the ipsilateral posterior-contralateral anterior canal pair). However, our sample was not large enough to determine the extent of the correlation between morphology and spatial properties. We stained too few neurons with the same canal inputs, often only one or two per physiological group, to draw any conclusions about distinctions between terminal fields for neurons within the “simple” and “complex” response categories.

In the preceding paper, we reported a relationship between the gross anatomic projection pattern (e.g., VOC) and spatial properties of secondary MVST neurons (Perlmutter et al. 1998). The responses of VOC, VC, and V-C₆ neurons suggested different patterns of input from the semicircular canal pairs. In the present study, we found that a neuron’s projection pattern was also predictive of its collateral morphology. Neurons that were activated antidromically from C₆ had far fewer collaterals in C₁ than those that terminated in the upper cervical segments (Fig. 2). In addition, four of six C₆-projecting axons had C₁ collaterals that terminated primarily in dorsolateral lamina VIII and lamina VII and gave off few branches in the motor nuclei, unlike most VOC and VC neurons. These findings support the suggestion that most C₆-projecting neurons do not play a large role in the vestibulocollic reflex (Perlmutter et al. 1998).
Although the distribution of terminals in C₁ was correlated with the gross projection pattern of MVST axons, there appeared to be a stronger relationship between a neuron’s terminal field distribution and its response properties. This conclusion is based on a comparison of the terminal fields of neurons with similar spatial properties or similar projection patterns (Table 1). For example, although axons 8601 and 5605 had similar MADs and terminated in similar regions of the ventral horn, one was an i-VC neuron and the other was an i-V-C₆ neuron. This is also true for axons 8605 and 5811. The same argument is made by comparing axons with the same projection pattern, like c-VOC neurons 8102, 5809, and 8103. Axons 5809 and 8102, with MADs suggesting inputs only from lac/rpc, had widespread terminations in the dorsomedial and ventromedial nuclei. Axon 8103, with a MAD suggesting input from lhc/rhc as well as lac/rpc, had a smaller terminal field with no projections to the ventromedial nucleus. In conclusion, our study suggests that a neuron’s termination pattern in C₁ is best correlated with its physiological characteristics.

Spatial transformations in the vestibulocollic reflex

The preceding paper (Perlmutter et al. 1998) reported that the relative sensitivity of some MVST neurons to horizontal and vertical rotations is similar to that of particular neck muscles (Banovetz et al. 1995). We hypothesized that projections to neck motoneurons from two groups of neurons that received convergent input from horizontal and vertical semicircular canal pairs could account for part of the signal that drives these muscles during the vestibulocollic reflex.

The first group of MVST neurons exhibited type I responses with MADs 180° away from the MADs of the dorsal extensor muscles (shaded vectors in Fig. 7C of Perlmutter et al. 1998). One neuron (6209) with such
spatial properties was stained in the present study. This neuron’s response was suitable for providing inhibitory input to the occipitocapularis and rectus capitis posterior major muscles. It projected to dorsolateral lamina VIII, apparently targeting interneurons and not motoneurons. This is not consistent with our hypothesis that neurons with spatial properties like those of neck muscles project primarily to motoneurons. However, the convergence onto lamina IX of signals with diverse MADs indicates that the secondary MVST projection is not organized in a strictly reciprocal pattern. It is likely that reciprocal activation of muscles during head rotation is generated by a fine balance of excitatory and inhibitory vestibular inputs, with a wide range of spatial properties, to motoneurons. Divergent vestibulospinal pathways can also endow the vestibulocollic reflex with a rich capacity for adaptation.

Projections to other motor nuclei of neurons with MADs aligned with the contralateral horizontal canal pair vectors are more difficult to interpret. For example, c-VOC neurons with MADs aligned with the ipsilateral anterior/contralateral posterior canal pair vector (e.g., Fig. 5) had terminals in the dorsomedial, as well as the ventromedial, nucleus. Because c-VOC neurons are probably excitatory (see DISCUSSION in Perlmuter et al. 1998), this suggests that these neurons produced EPSPs in neck flexor, as well as extensor, motoneurons. This connection is not consistent with the compensatory vestibulocollic reflex.

It is possible that axonal branches projecting to motor nuclei that are inconsistent with normal reflex behavior do not synapse on motoneurons but on nearby interneurons. However, the convergence onto lamina IX of signals with diverse MADs indicates that the secondary MVST projection is not organized in a strictly reciprocal pattern. It is likely that reciprocal activation of muscles during head rotation is generated by a fine balance of excitatory and inhibitory vestibular inputs, with a wide range of spatial properties, to motoneurons. Divergent vestibulospinal pathways can also endow the vestibulocollic reflex with a rich capacity for adaptation.

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