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Behavioral Organization of Reticular Formation: Studies in the Unrestrained Cat. I. Cells Related to Axial, Limb, Eye, and Other Movements

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SUMMARY AND CONCLUSIONS

1. We have recorded single-unit activity in medial reticular formation (RF) units in unrestrained, behaving cats. A total of 306 cells have been analyzed. Neuronal activity was observed during a variety of natural, spontaneously occurring behaviors, during rapid eye movement (REM) and non-REM sleep states, after sensory stimulation, and during elicited reflexes.

2. Most RF units discharged maximally in conjunction with a specific movement or group of movements. The companion paper (41) deals with cells related to movements of the facial musculature, while the present paper deals with all other cell types.

3. The most common RF cell types discharged during specific movements of the axial skeleton. Cells related to limb, respiratory, pharyngeal and laryngeal, jaw, and tongue movements were also observed. Reticular eye movement-related cells, previously investigated by others, were also seen in our unrestrained cats. A small percentage of cells were maximally activated by applied auditory, visual, vestibular, somatosensory, or proprioceptive stimuli.

4. Cells related to axial movement, which as a group constituted 38.2% of all RF cells, could be subdivided into cells related to neck extension, neck dorsiflexion, and ipsilateral or contralateral movement of the spine.

5. Cells related to active ipsilateral movement, constituting 19.3% of all medial RF cells, were the single most common cell type in the RF. Thirty-four percent of these cells did not respond to passive head movement, while 48% responded to passive head movement to the contralateral side and 18% to passive movement to the ipsilateral side. Neck proprioceptors contribute to the passive movement response in certain of these cells.

6. Cells related to limb movement constituted 6.9% of the cells encountered. Most were related to movement of the proximal portion of one limb. Cells related to movement of the distal portion of the limb were quite rare, constituting only 1.0% of RF cells.

7. While most RF cells were active only in relation to a single, directionally specific movement, we found a cluster of pontine RF cells, which discharged in relation to several limb and neck movements.

8. Cells related to several movements, eye movement, vestibular stimulation, and cells without spontaneous activity in sleep or waking were localized to restricted portions of the medial RF fields. Cells related to axial, proximal limb movements or somatic stimulation were intermingled throughout the entire region explored.

9. The unrestrained preparation allows the direct observation of the behavioral correlates of increased RF unit discharge. Most RF cells discharge in relation to a specific movement or group of movements of the axial musculature. Each movement-defined cell type has a different pattern of sleep, sensory and reflex activity, and anatomical localization. Anatomical intermingling of certain cell types may facilitate the synthesis of complex movement sequences from simpler elements commanded by individual RF cells.

INTRODUCTION

Unit-recording studies of cells in the brain stem reticular formation (RF) have produced a variety of often conflicting conclusions about their behavior role (32). Most of these studies have been conducted in restrained or anesthetized animals. The present papers (this paper and Ref. 41) report on the behavioral correlates of RF unit discharge in unrestrained, behaving cats. In previous studies we have found that RF cells discharge in relation to specific movements (33, 37, 38). We have hypothesized that these specific movement relations may underlie many of the previously reported correlations between RF unit activity and behavior (32). The present study extends our analysis throughout most of the medial RF of the brain stem. Our goals were 7) to identify by direct observation the major types of behavioral relationships seen in RF cells; cells were studied during a wide range of natural motor activities, sensory stimuli, reflex responses, and during sleep; and *2)* to determine the relative frequency and anatomical distribution of each cell type.

This paper describes cells that discharge during axial, proximal limb, and other movements. The companion paper (41) describes cells that discharge during facial movements.

METHODS

Recording techniques

Bundles of six 32-μm nichrome, Formvar-insulated microwires (California Fine Wire Co., Grover City, CA) protruding 5 mm from a 24-gauge support cannula were attached to a mechanical microdrive consisting of a screw threaded into a stack of nuts. Each microdrive held one, two, or three bundles of microwires. Two microdrives were implanted in each cat. Microwire bundles lowered rostral to AO or caudal to P8.5 were oriented in the coronal plane. Bundles lowered between AO and P8.5 were oriented at 30-40° to the coronal plane to avoid the bony tentorium. Sodium pentobarbital (Nembutal), 35 mg/kg, was used for all surgical procedures. After recovery from surgery the cat was placed in a recording chamber and each microwire scanned for discriminable unit discharge. Microwire bundles were advanced in 100-μm steps until one or more isolated units were located. Bundles were lowered over a total 5-mm excursion during the 3- to 5-mo survival periods. Signals were amplified with high-impedance preamplifiers and conditioned with high-pass 300-Hz filters to prevent interference from cable-movement artifact. Unit discharge during waking and sleep was routinely monitored with an oscilloscope to confirm the absence of movement artifact or injury discharge (39).

All cats had one pair of screw electrodes with 3-mm interelectrode separation implanted over sensorimotor cortex for electroencephalogram (EEG) recording and three electrodes in the orbital bone for electrooculogram (EOG) recording. Tripolar 30-gauge insulated wire electrodes with 1-mm separation of their bared sharpened tips were implanted at A+6, L10, H-2.0 to record lateral geniculate pontogeniculooccipital (PGO) spikes. Pairs of Teflon-insulated stranded stainless steel wires with 1 mm of insulation removed were implanted in the left and right splenius muscle in each cat. In two cats the sternomastoideus and longissimus dorsi muscles were also implanted. Integrated electromyogram (EMG) activity was printed out at 10- or 1-s intervals on an Anadex printer along with unit discharge counts and time code readings.

Behavioral tests

In our initial studies (37,38) we discovered that adjacent cells could have very different behavioral correlates. For example, cells relating to neck movement might be recorded near cells relating to tongue or facial movements. Specialized transducers could not adequately describe the variety of behavioral relations encountered in any RF region. Therefore, it was necessary to develop a behavioral testing procedure that would examine a wide variety of behaviors and that could be systematically applied to all cells. Our goal was to describe reliably the major behavioral correlates of increased unit discharge. Our test battery included a series of sensory stimuli as well as observations of spontaneous motor behavior and induced reflexes, as described below. Each observation was repeated a minimum of 5 times to assess the reliability of relationships. All cells were observed for at least 4 h. In every case the behavioral relationships were stable throughout this period. All behavioral tests were independently repeated by a second observer. In selected cases, results of the tests were further investigated by filming the cat and counts of unit discharge and performing a vector analysis of movement using a previously described procedure (36).

In order to compare our observations to previous studies, cell response latency to a stroboscopic visual stimulus and a discrete click or clap auditory stimulus (<90 dB, 0.5-ms rise time) repeated at 0.1-10.0 Hz was tested in most cells.

Somatic receptive fields were mapped with an esthesiometer (Rowan Products Co.), a calibrated "von Frey hair," to measure response thresholds to punctate pressure. All skin surfaces were also stimulated with deep pressure from fingers or blunt probes, since many cells not responding to strong punctate stimuli did show reliable responses and clearly delineated receptive fields to blunt stimuli. Somatic response latency was determined in responsive cells by applying 0.2-ms electric pulse stimuli through a pair of subcutaneous 27-gauge needle electrodes with 5 mm separation. Raster displays of unit activity occurring within 200 ms after discrete auditory, visual, and somatic stimuli were employed in all cells to document the occurrence and latency of sensory responses. To assess unit activity during arousing and/or painful stimuli, all units were monitored while the experimenter applied manual pressure to each forepaw up to a level sufficient to induce withdrawal or vocalization. Because a gentle approach was employed, cats tolerated all our test procedures well and maintained a playful interaction with the experimenter.

The tonic neck (magnus) reflex response was tested in all cells. To elicit these reflexes the head was held up, down, left, or right for at least 5 s while the cat was upright and while it was supine. The head was also twisted manually at accelerations varying from 90 to 360°/s in the horizontal and vertical axes. Positive responses on these tests were further analyzed by testing cell response with the head restrained with a rigid atraumatic restraint system attached to the head plug while the body was moved. This allowed us to discriminate between the contribution of neck and muscle proprioceptors and vestibular stimulation in producing unit activity. All limb joints were flexed and extended. The spinal column was passively raised, lowered, and turned right and left.

Eye movement-unit activity relations were routinely monitored by EOG recording. In addition, eye movements were visually observed with the cat's head restrained by hand pressure. Stimulation of each cornea with a cotton swab was used to test for unit discharge relationships to the nictitating membrane reflex.

The head-shake reflex is a rapid stereotyped torsional rotation of the head that serves to expel foreign matter from the face and canthus of the pinna. Sherrington (30) studied it in detail in the midbrain decerebrate cat in which it is nearly normal in vigor and threshold. This reflex can also be evoked in cats with brain stem transections just rostral to the abducens nucleus (J. M. Siegel, unpublished observations). Stereotyped pinna movement, eyelid closure, and other movements accompany the head-shake reflex. It is, therefore, a convenient way of reliably evoking this movement pattern. We elicited the reflex by placing a small pellet in either pinna.

A cotton swab was placed on the tongue. This induced rhythmic tongue and jaw movements. Jaw manipulation was used to dissociate jaw-tongue relations. All units were observed while the cat chewed and swallowed a Purina Cat Chow pellet placed on its tongue. All the cells had the complete series of behavioral tests administered. Therefore, the low percentage of some cell types, such as tongue movement-related cells, reflects their rarity in the population rather than selective testing procedures.

RF unit discharge relations to spontaneous behaviors were determined. All cells were observed during at least 10 spontaneous ipsilateral and contralateral head movements in the horizontal plane, at least 10 dorsi- and ventroflexions of the neck, and at least 5 neck extensions. Because of difficulty in quantifying the magnitude of relations obtained in this kind of analysis, we concentrated on ordinal ranking of magnitudes of unit activity during opposite movements, e.g., does the unit fire more during ipsilateral head movement than during contralateral head movement and does this movement increase or decrease discharge rates from base-line levels? These kinds of judgements were highly reliable when repeated by independent raters. In some units it appeared that lateral movement at cervical levels of the spinal cord produced greater increases in unit discharge than similar movement at lumbar levels. In other units the situation was reversed. However, because one could not always discriminate reliably between these situations, no attempt was made to identify routinely the spinal level of the optimal movement. Most cats also exhibited several of the following behaviors during the 4-h observation period: spontaneous eating, lapping, grooming, defecation or urination, spontaneous locomotion, quiet attentiveness and drowsy inattention, and a large variety of head, back, and limb movements. Unit rate changes during these behaviors were recorded.

Sleep studies

We routinely monitored sensorimotor EEG, EOG, lateral geniculate nucleus (LGN), and EMG and unit activity (using the pulse output of a window discriminator) on a Grass model 78 polygraph. All signals were recorded on a Vetter-Crown tape system. Lights in the chamber and home cages were synchronized on a 12/12 h light/dark cycle, with most recordings occurring in the light phase. The chamber had a litter box, water, and food cups. Cats adapted well to this environment and spent much of their time sleeping.

PGO spikes recorded in the lateral geniculate nucleus facilitated identification of REM sleep

and transitional states. We defined REM sleep onset as the point, after PGO spike onset, at which EMG suppression and EEG desynchrony are first present. Non-REM sleep was scored according to the usual criteria (39). The periods of slow-wave sleep (SWS) and REM sleep were identified and transition points correlated with time code readings. Sleep-state rates were determined by averaging unit counts in each state. During REM sleep we always scanned all microwires to determine if any new, possibly REM-selective, units appeared. This procedure is discussed in detail by Siegel et al. (42). As previously described (34, 39,42), three types of RF unit discharge during sleep were seen. Type 1 cells discharged in association with spontaneous or stimulus-evoked movements in waking and were otherwise silent. They had no appreciable spontaneous activity during quiet waking, SWS, or REM sleep, showing periods of at least 60 s of silence in each of these states. Type 2 neurons had high levels of tonic activity in quiet waking, SWS, and REM sleep. The defining characteristic of this cell group was a SWS discharge rate exceeding 4 spikes/s. Type 3 cells had a low level of spontaneous discharge in quiet waking and SWS (below 4 spikes/s). During REM sleep the firing rates in types 2 and 3 cells increased, most activity coming in phasic discharge bursts.

Histology

Electrode tracks were marked and units placed on summary plates (4), as previously described (39).

RESULTS

A total of 306 cells were recorded from 73 microwire bundles in 24 cats. All RF cells had higher discharge rates during "active waking" than during "quiescent waking" states. This was statistically confirmed by correlating integrated splenius EMG activity with unit counts over a 600-s waking interval in 40 randomly selected nonfacial RF units. In each unit, discharge rate and EMG level were positively correlated ($P < 0.01$, linear regression). This correlation was apparent in polygraph recordings of RF unit discharge and muscle activity (Fig. 1). Discharge rates during periods of waking without movement (based on 10-s samples) were 0.0/s in type 1 cells, 3.8/s in type 2 cells, and 0.4/s in type 3 cells. During movement, maximum rates were 34.9/s in type 1 cells, 52.7/s in type 2 cells, and 28.9/s in type 3 cells (38, 41). Because of the normally correlated occurrence of many different movements within active waking periods, it was not possible to discriminate between cells related specifically to neck movements and cells related to other movements with EMG correlation analysis. However, our behavioral analysis did allow us to make such distinctions. A number of cell types were identified. Each cell type discharged maximally in conjunction with a specific movement or family of movements. The companion paper (41) describes cell types related to facial and pinna movement. The remaining cell types are described below. Table 1 lists the major cell types identified by our behavioral analysis, x^2 tests over all cell groups indicated that movement-defined cell types differed significantly in the proportions having type 1, 2, 3 sleep activity patterns ($P < 0.001$), in the proportion of auditory ($P < 0.001$), shock ($P < 0.001$), and visual ($P < 0.02$) responses and in the presence of activity during the reflex head shake ($P < 0.001$). The locations of all recording sites at which either sleep or behavioral studies of units were completed are plotted in Fig. 2.

Sleep activity

The anatomical distribution of sleep types is shown in Fig. 3. Cells without spontaneous

FIG. 1. Polygraph recording of splenius EMG and unit activity in three simultaneously recorded RF units. Pen deflections are pulses triggered by window discriminators monitoring unit signals.

TABLE 1. *Frequency of cell types and sleep and sensory response*

Sleep Type									Head Shake
Behavioral Type	Percentage	*n*	1	2	3	Auditory	Shock	Strobe	
Facial specific	11.8	36	70.6*	5.9*	23.5*	0.0*	0.0*	6.9	81.5*
Facial multiple	2.9	9	ot	12.5t	87.5†	88.9*	77.8	0.0	12.5t
Eye movement	12.1	37	14.7	20.6	64.7	0.0*	0.0*	0.0	91.3*
Axial movement									
Extention	6.9	21	27.8	44.4	o ot	0.0	0.0	0.0	30.0
Dorsoflexion	3.9	12	50.0	0.0	50.0	22.2	25.0	0.0	o ot
Ipsilateral	19.3	59	I6.7†	24-l†	59.3t	35.6*	66.7	1.8	36.4
Contralateral	5.2	16	o ot	26.7†	73.3t	25.0	100.0	0.0	76.9
Miscellaneous axial	2.9	9	33.3	55.6	11.1	33.3	66.7	11.1	55.6
Limb	6.9	21	4.8t	61.9†	33.3t	27.3t	87.5	5.9	38.9
Tongue, swallow, jaw, respiration	4.9	15	53.3	33.3	13.3	0.0	33.3	0.0	50.0
Multiple movements	4.2	13	0.0	63.6	36.4	50.0*	58.3	20.0t	84.6t
Sensory	14.4	44	17.6	45.1	37.3	24.0	52.9	8.8	45.8
No conclusion	4.6	14	13.3	46.7	40.0	26.7	57.1	0.0	9.1
All cells	100	306	23.8	30.4	45.8	21.4	52.2	3.4	50.5

Each cell type had significantly different proportions of sleep type ($P < 0.001$, x^2). sensory ($P < 0.001$, x^2), and head-shake response ($P < 0.001$, x^2) in overall x^2 test. Numbers with footnote symbols indicate significant differences on individual x^2 tests comparing group to entire population. * Significant at 0.01 level. † Significant at 0.05 level.

activity (type 1 cells) were concentrated in the dorsal portion of the gigantocellular tegmental field (FTG) between P5 and P8. All the cells with spontaneous activity described in the present series had their lowest discharge rates in non-REM sleep and quiet waking periods. Rates increased in active waking and REM sleep, as has been reported previously (34, 38, 39, 42). We have also observed several "REM-off" cells in the region of locus ceruleus similar to those previously described (12). These cells and median raphe cells have behavioral characteristics that are quite different from those of medial RF cells (2, 11, 19, 46) and will not be described in the present papers. No cells that selectively increased activity in REM sleep were observed.

Eye movement cells

Cells related to eye movement (EM) (n = 37) constituted 12.1% of the total cells encountered. No EM cells were seen in the caudal medulla; all were located rostral to P7, referred to the Herman (4) atlas. Eye movement cells could be divided into three categories; those related to active ipsilateral movement of the eyes (n = 24), those related to active contralateral movement of the eyes (n = 2), and those related to active ventral eye movement (n = 11).

All cells related to ventral eye movement were located rostral to P4 and between 1.2 and 1.6 mm from the midline in the FTG and central tegmental (FTC) fields. Cells related to ipsilateral eye movement were located between P2.5 and P7 and were between 1.2 and 2.3 mm from the midline, in the FTG field. The dorsal cluster of these cells was in the abducens nucleus. The location of feline reticular ipsilateral eye movement cells seen here overlaps with those reported in a recent study (14), although our recording sites were somewhat more lateral (Fig. 4).

All EM cells responded to passive head movements that would be expected to elicit compensatory slow-phase EMs in the units on-direction. Thus, the cells related to ipsilateral EM all discharged during passive contralateral head movement and the cells re-

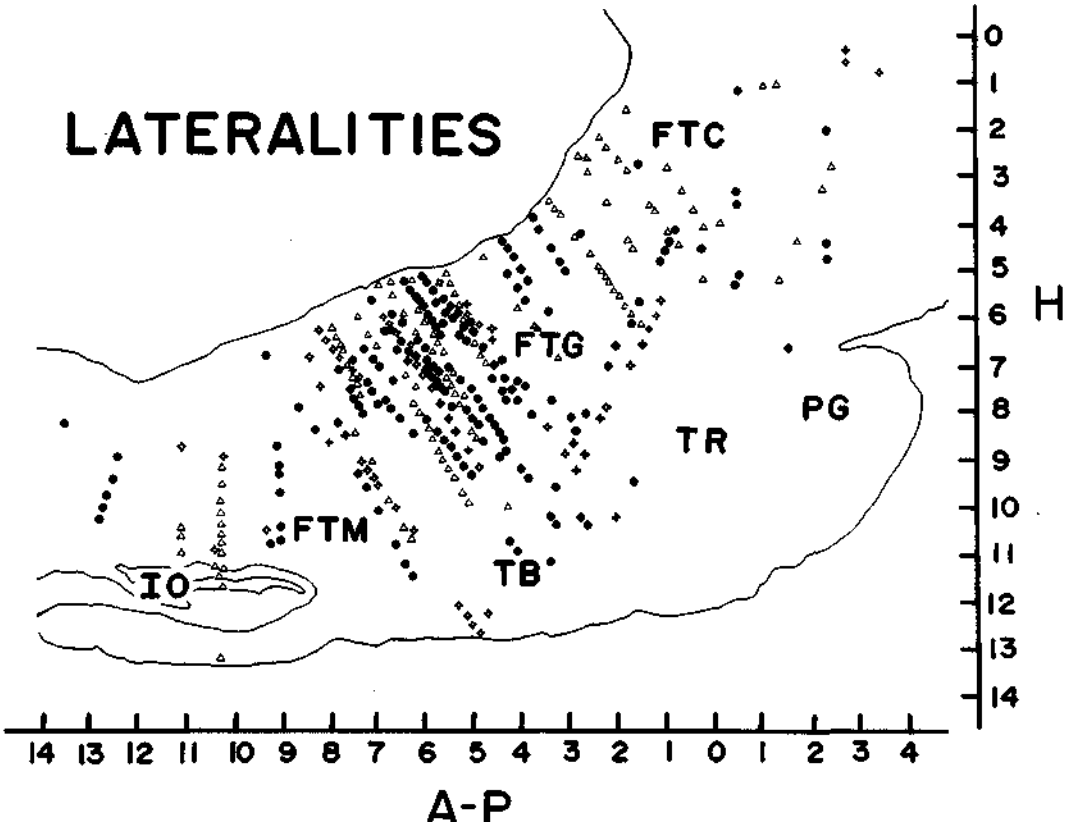

FIG. 2. Locations of all recording points. Between one and five units were recorded at each point. Circles, recording points between 0.5 and 1.4 mm from midline; triangles, recording points between 1.4 and 2.1 mm from midline; crosses, recording points between 2.1 and 2.5 mm from midline. Abbreviations: FTG, FTM, FTC, gigantocellular, magnocellular, and central tegmental fields; IO, inferior olive; TB, trapezoid body; TR, tegmental reticular nucleus; PG, pontine gray.

lated to ventral spontaneous eye movement all discharged during passive dorsiflexion of the head. The unit response to passive head movement did not attenuate even with rapid (90 Hz) and prolonged (60 s) stimulation. This was in distinct contrast to most non-EM cell types, whose response to passive head movement habituated after fewer than five repetitions. No attempt was made to analyze EM latencies in relation to activity in these units; however, it is likely that these cells correspond to the burst tonic and medium- and long-lead bursters that others have described in the RF of the monkey and cat.

In addition to their relation to EMs and passive head movement, these cells shared the following characteristics that distinguished them from adjacent non-EM-related RF cells: 7) Of 23 EM cells tested, 21 were activated during the reflex head shake response. This contrasts with non-EM cells (n = 268), only 28% of which were activated during this same movement. This difference was significant ($P < 0.001$, x^2)- *2)* None of the 34 EM cells tested responded during discrete auditory stimulation, while 22% of non-EM RF cells tested (n = 298) responded to this stimulus ($P < 0.01$, x^2)- Similarly, none of the 34 EM cells tested responded to stroboscopic visual stimulation. None of the seven EM cells responded to electric pulse stimulation of torso or facial region ($P < 0.05$ x^2). No EM cells responded to punctate somatic stimulation with an esthesiometer or to manually applied pressure on any body surface. *3)* One might reasonably expect that cells related to eye movements would also be active during the rapid EMs occurring in

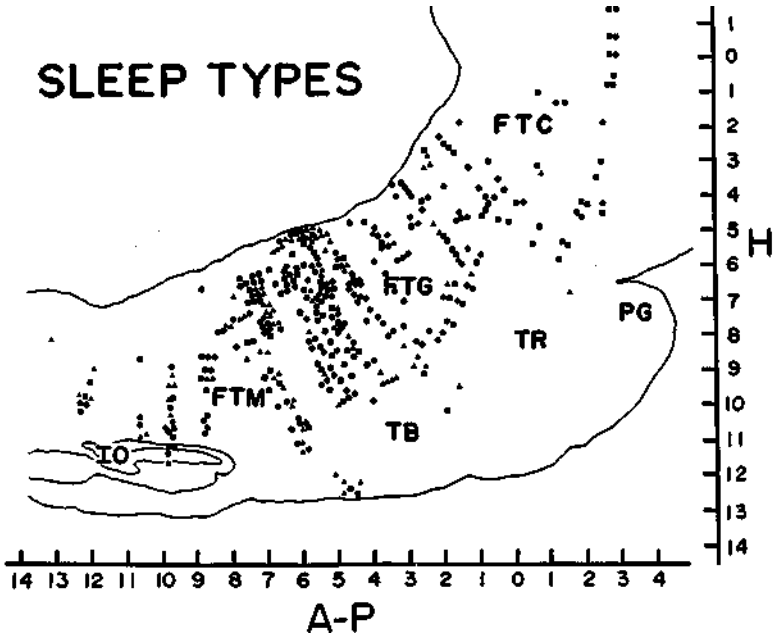

FIG. 3. Anatomical distribution of sleep types. Triangles, type 1; squares, type 2; circles, type 3.

REM sleep and, indeed, most were. However, we were surprised to find that 5 of the 37 EM cells studied (14%) had little or no activity in REM sleep, meeting our criteria for type 1 cells (i.e., having no spontaneous activity in quiet waking or slow-wave sleep

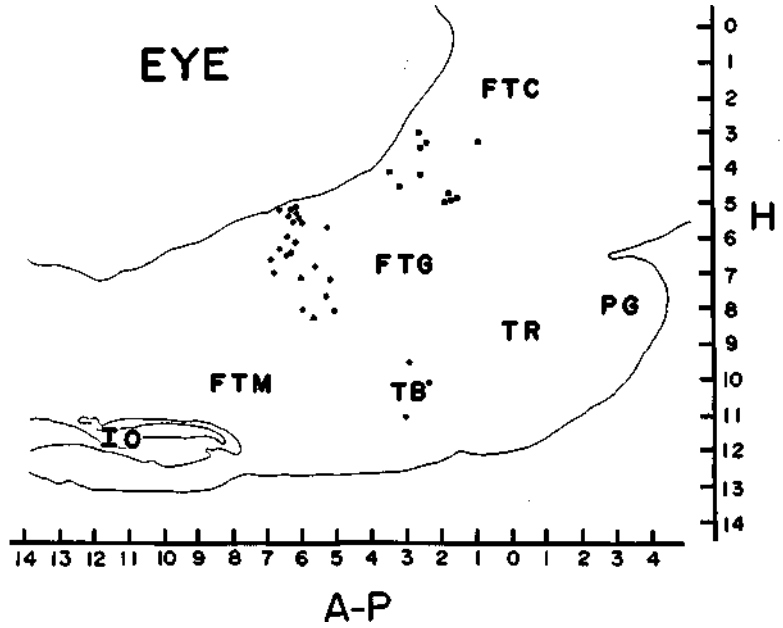

FIG. 4. Location of eye movement cell types. Circles, cells related to ipsilateral eye movement; triangles, cells related to contralateral eye movement; squares, cells related to ventral eye movement.

and >60 s of silence in REM sleep). Indeed, the proportion of type 1 cells among EM cells was not significantly less than in the general population. The lack of activity in many of these cells in REM sleep can be related to their lack of activity during much of waking EM activity. These cells discharged only during particularly rapid EMs in waking. We have previously reported that RF cells' discharge rates in active waking and REM sleep are positively correlated (39, 42).

Axial movements

Cells related to active movement of the axial skeleton constituted 38.2% *(n* = 117) of the total. They could be subdivided into two groups: cells with laterally symmetrical movement relations, i.e., cells that discharged equally during ipsilateral and contralateral movements, and cells with laterally asymmetrical movement relations, i.e., cells that discharged during movements to the ipsilateral or on the ipsilateral side of the body at rates that differed from the rates during corresponding movements to the contralateral or on the contralateral side of the body. The group with laterally symmetrical movement relations *(n* = 33, 10.8% of total) could be further subdivided into two groups; cells related to extension of the spinal column and cells related to dorsiflexion of the spinal column.

LATERALLY SYMMETRICAL. *Extension Cells.* Cells related to active extension of the spinal column *(n* = 21, 6.9% of total) had the following defining characteristics: *a)* they showed no asymmetry in their discharge during active ipsilateral versus contralateral movement and *b)* they responded maximally during head extension. Active dorsiflexion or lateral flexion of the head and neck was not correlated with maximal discharge in these cells. But active extensions, both with the neck horizontal and with ventroflexion produced high discharge rates. One behavior that consistently produced maximal discharge was approaching food or water bowls placed on the floor of the cage or eating from these bowls. That the relation was to the posture rather than the consummatory act could readily be demonstrated by presenting food in such a way as to produce lateral head movement. No discharge occurred during approach or consumption if this lateral flexion posture was maintained. Conversely, sniffing of the floor or investigation of a novel object placed on the floor would also produce tonic-enhanced unit discharge as long as the extended posture was maintained.

None of these cells responded to auditory stimuli *(P* < 0.05, x^2) or visual stimuli. Two were tested for response to shock stimulation; neither responded. Three of the 13 cells tested responded during the head-shake response, not significantly different from the general population. Similarly, the distribution of sleep types did not differ from the general population. None of these cells had any consistent response to skin stimulation or to passive head movement. Acceleration of the entire body rostrally after lifting the cat was also without effect. These cells were dispersed throughout a large portion of the area explored, ranging from PI3.0 and A2.5 and from L0.8 to L2.3 (Fig. 5).

Neck dorsiflexion cells. A second subgroup of cells had laterally symmetrical movement relations. The defining characteristic of these cells *(n* = 12, 3.9% of total) was maximal discharge during active dorsiflexion of the neck. None of these cells were active during the reflex head shake *(P* < 0.05, x^2)- These cells did not differ from the general population in their sleep, auditory, or shock responses. Four of these cells responded during passive ventroflexion of the neck, and the remaining units had no response or inconsistent response to passive head movements. The dorsiflexion cells were scattered over a wide area, from P10 to P0.5 and from 1.2 to 2.3 mm from the midline (Fig. 6).

Additional cells. We have identified an additional nine cells (2.9% of total) as related to nonlateralized active movement of the axial musculature. These cells responded maximally during specific movements that did not fall into any of the above-described categories. For example, two cells responded only during active ventral movement of the lumbar vertebrae; others discharged only during thoracic or abdominal movements.

LATERALLY ASYMMETRICAL. *Ipsilateral head movement cells.* Cells related to ipsilateral flexion of the spinal column *(n* = 59, 19.3% of total) were the most commonly encountered cells in the RF. Their defining characteristic was maximal discharge during

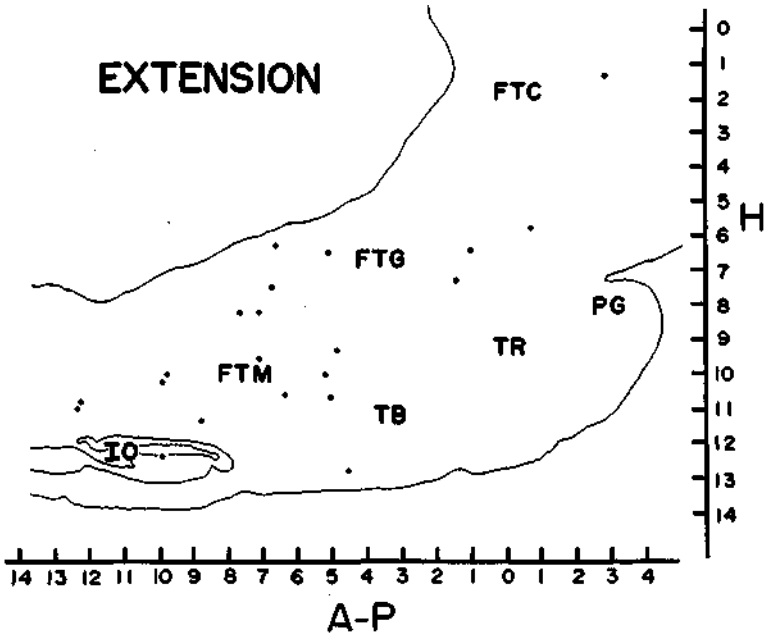

FIG. 5. Location of cells related to extension.

active flexion of the cervical, thoracic, or lumbar vertebrae to the ipsilateral side. Vector analysis (36) of the correlation between unit activity and movement was performed in 10 cells behaviorally identified as ipsilateral head movement cells. Head movements

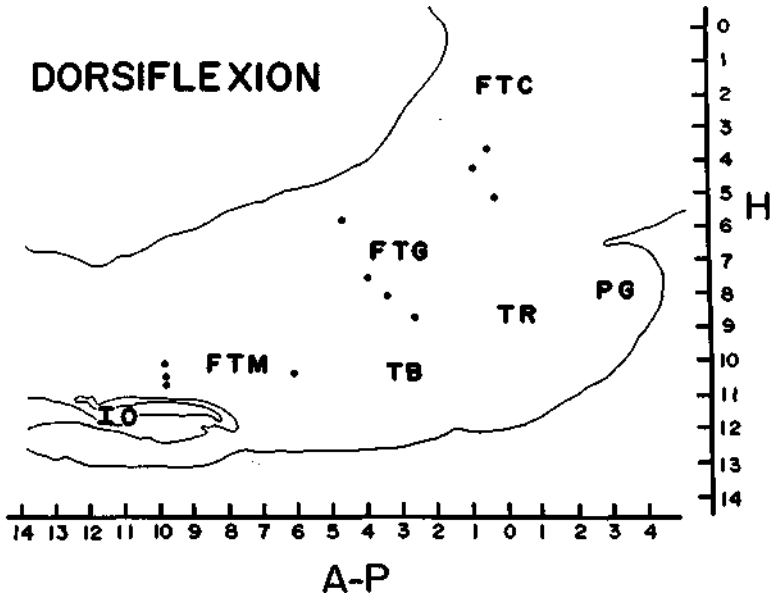

FIG. 6. Location of cells related to dorsiflexion. The most dorsally located dorsiflexion cell, found at A1, C2.3, H+2.0, is not plotted.

to the ipsilateral side were found to occur within 56 ms of the onset of unit discharge. Active movement to the contralateral side either reduced or had no effect on the spontaneous activity of these cells. Tonically maintained ipsilateral flexion postures were associated with tonically elevated discharge rates in a minority of cells. Most cells achieved their maximal discharge rates during the movement with the discharge rate returning to base line if the posture was held. Operant reinforcement of increased activity in these cells produced repetitive ipsilateral head movement (5). In addition to their maximal discharge during active ipsilateral movement, 15 of these cells also discharged at lower rates in relation to other active movements. Ten of these increased rate during ventroflexion of the cervical vertebrae, while only one was active during dorsiflexion of this region. Four cells were active during extension of the spinal column.

Fifty-six of these cells were tested for response to passive head movement. Nineteen did not respond to this stimulus. Of the remainder, 27 responded to contralateral passive movement, while 10 responded to ipsilateral passive head movement. To define further the role of neck proprioception in these responses, we restrained the head to prevent vestibular stimulation and moved the body. We studied five cells in each group. *a)* Cells responding to contralateral passive head movement. Three of the five cells tested also responded to passive neck flexion to the contralateral side with the head restrained. The remaining two cells had no response to this stimulus, *b)* Cells responding to ipsilateral passive head movement. None of the five tested cells responded to passive ipsilateral neck flexion. However, three of these cells responded to contralateral neck flexion.

Responses to passive head or body movement were unvarying in sign in all cells tested, regardless of the size of the acceleration or displacement applied. However, larger or more rapid displacement always produced more unit discharge. The magnitude of the response to passive head movement was also a function of the cats behavioral activity. Response attenuation superficially resembling "habituation" occurred when the cat began to struggle and make a variety of movements during the testing procedure. No attentuation of RF unit discharge occurred during repetitive active movements, such as those occurring during grooming (37).

Ipsilateral movement cells were significantly more likely than the general RF population to respond to auditory stimulation *($P < 0.005$, x^2)*. Three of the 53 ipsilateral movement cells tested responded to stroboscopic visual stimulation. Ipsilateral movement cells did not differ from the general population in response to electric pulse stimulation. Forty-seven of the 57 tested (82%) did not respond to punctate somatic stimulation of up to 1.5 g or to manually applied pressure. The eight that responded to somatic stimulation did so at pressures of less than 0.2 g. Three of these responded to stimulation of the ipsilateral neck and one to stimulation of the contralateral neck. Four cells responded in a nonspecific manner to somatic stimuli presented to any part of the animal. The response of these cells was similar to that which we have described in the nonspecific facial cells (41). Like the nonspecific facial cells, these four cells all had auditory and electric pulse responses, and three of them were located within the same RF region that contains the nonspecific facial cells. The sleep cycle properties of ipsilateral movement cells differed significantly from those of the general population *($P < 0.025$, X^2)*, with type 3 cells being overrepresented and type 2 cells underrepresented.

Cells related to active ipsilateral head movement were found throughout the RF regions studied. They comprised a somewhat higher proportion of cells encountered between P4 and P7 in the FTG field. Figure 7 shows their location and the distribution of subtypes with different passive head movement responses. Cells related to ipsilateral passive movement were restricted to the dorsal portion of the area explored. In an attempt to determine if any other variables might reveal a more restricted anatomical grouping of units, we have also determined the distribution of ipsilateral movement cells that respond to auditory stimuli, shock stimuli, and the head-shake reflex. Ipsilateral head-movement cells of each sleep type have been plotted. We have mapped the distribution of cells that also discharged during

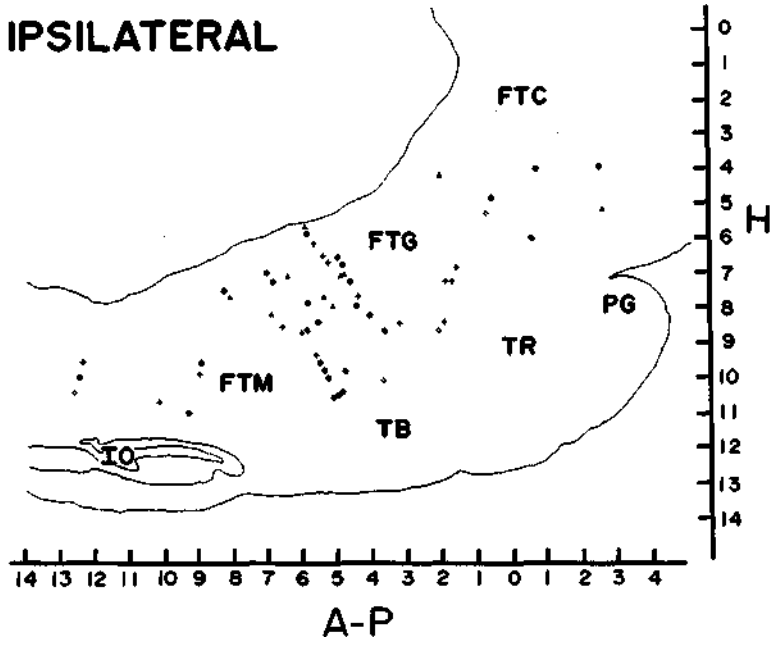

FIG. 7. Location of cells related to active ipsilateral movement. Cells are subdivided into those responding to passive contralateral movement (circles), passive ipsilateral movement (triangles), and those with no response to passive movement (open diamonds).

active ventroflexion of the neck. None of these maps revealed any further concentration of cells in a particular RF nucleus or field.

Contralateral head movement cells. Cells related to active contralateral flexion of the spinal column (n = 16, 5.2% of total) were considerably less common than cells related to active ipsilateral movement. In addition to their maximal discharge during contralateral movement, four of these cells also discharged at somewhat lower rates during active dorsiflexion of the neck and two discharged during active neck ventroflexion.

All of these cells were tested for response to passive head movement. Seven did not respond to this stimulus. Of the remainder, six responded to passive ipsilateral head movement, while three responded to passive contralateral movement. The pattern of habituation of activity in these cells during repetitive stimulation was similar to that seen in ipsilateral movement cells.

Contralateral movement cells did not differ from the general population in their response to auditory, somatic, or visual stimulation. Six of the 13 cells tested responded during the reflex head shake, which was also not different from the general population. Like ipsilateral movement cells, the sleep-cycle properties of contralateral movement cells differed significantly from that of the general population ($P < 0.05$, x^2), with type 3 cells overrepresented and type 1 and 2 cells underrepresented. Contralateral movement cells were distributed throughout the region explored with a concentration in caudal pontine regions (Fig. 8).

Limb movement

Cells related to limb movement constituted 6.9% of the total (n = 21). Nine cells were related to active movement of the ipsilateral forepaw, seven to movement of the contralateral forepaw, three to movement of the contralateral hindlimb, one to movement of the ipsilateral hindlimb, and one to ipsilateral forelimb and hindlimb movement. A striking finding was the rarity of cells related to distal limb movement. Only three of the limb-movement cells were related to active movement of the distal portion of the limb (elbow or forearm joints). All of these cells

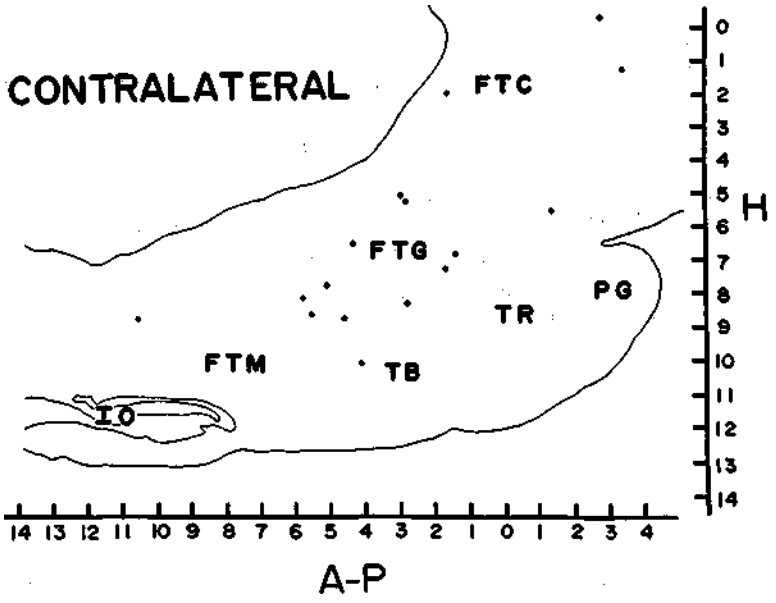

FIG. 8. Location of cells related to active contralateral movement.

were localized to the midbrain FTC field, caudal to the red nucleus and between 1.9 and 2.3 mm from the midline. All the pontine and medullary limb movement-related RF cells discharged maximally in conjunction with movements of the proximal portion of the limb that involved the scapula or pelvis.

In 13 limb-related cells, movement relations were analyzed to determine if the cells discharged during active flexion or active extension of the limb. Nine of these cells discharged during extension, while four discharged during flexion.

Eight of the nine limb movement cells tested responded to electrical pulse stimulation of the related limb. However, these cells also responded when this same stimulus was applied to the torso or any other limb (Fig. 9). Seven of the 22 cells tested responded to discrete auditory stimulation. The frequency of auditory and electric pulse responses did not differ significantly from those of the general population. Seven of the 19 cells tested responded during the reflex head shake. The sleep-cycle patterns of limb movement cells differed significantly from those of surrounding cells ($P < 0.05$), with type 1 cells underrepresented and type 2 overrepresented.

These cells were distributed throughout the medial RF from P10 to A3, L1.2 to 2.5. Apart from the cells related to distal limb movement being restricted to the midbrain, the anatomical segregation of the different limb movement relations was limited (Fig. 10).

Cells related to several neck and forelimb movements

Cells related to several neck and forelimb movements constituted 4.2% of the total ($n = 13$). The defining feature of these cells was that, in contrast to all other nonfacial cells, they increased rate during any of a number of neck and forelimb movements. These cells increased discharge rate during neck extension, ipsilateral and contralateral flexion of the neck, and rapid adduction of either forepaw. There was no detectable difference in discharge evoked during movement of the left and right forepaws or left and right neck movement. However, these cells did not respond during hindlimb movement or during movements of the caudal axial musculature. Also, in contrast to the nonspecific facial cells discussed in the companion paper, these cells did not increase discharge rate during any facial or pinna movements. They had no consistent response to passive limb or neck

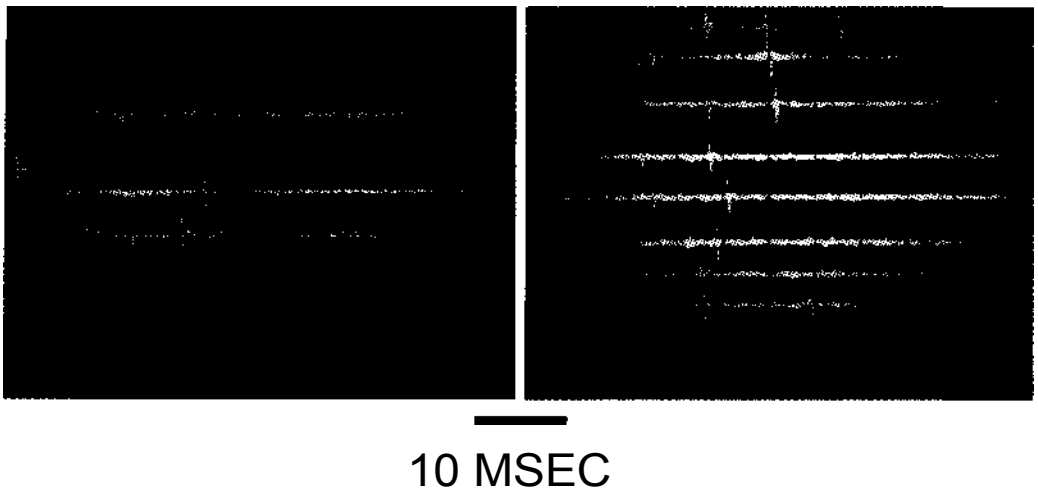

FIG. 9. Response of limb movement-related cell to electric pulse stimulation of left proximal scapula (right) and right proximal pelvis (left).

movement. These cells were significantly more likely to respond to auditory ($P < 0.001$, X^2) and visual ($P < 0.05$, x^2) stimuli than the general cell population. They were also more likely to respond during the head-shake reflex ($P < 0.05$, x^2)- These cells were restricted to a relatively small portion of the area explored. All were located rostral to P5 and caudal to PO. The most caudal cell was 2.3 mm lateral to the midline, while all the others

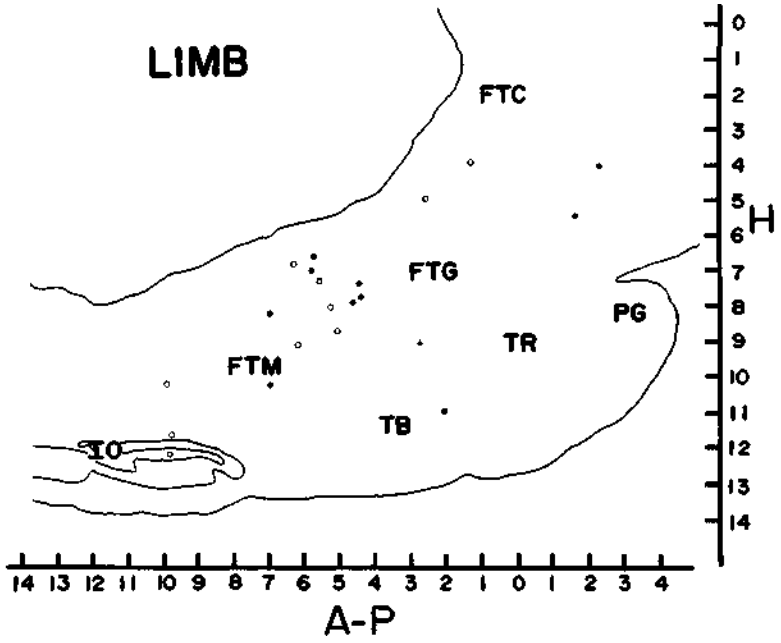

FIG. 10. Location of cells related to active limb movement. Cells are subdivided into those discharging during movements of the ipsilateral forelimb (filled circles), contralateral forelimb (open circles), ipsilateral hindlimb (filled square), contralateral hindlimb (open squares), or both ipsilateral limbs (filled triangle).

were between 1.0 and 1.7 mm from the midline in the FTG and FTC fields (Fig. 11).

Cells related to other movements

A small number of cells discharged in relation to one of a variety of other specific movements. As a group, these cells constituted 11.8% of the total number studied. Three cells discharged specifically in relation to tongue protrusion. All these cells were type 1 in their sleep discharge pattern. None responded to gustatory or other sensory stimulation. One cell was located just medial to the interstitial hypoglossal nucleus. The other two cells were in the dorsal FTG field at P3 and P7, far rostral to the hypoglossal complex.

Two cells discharged only during swallowing. Neither responded to auditory or somatic stimuli. One cell had a type 1 sleep discharge pattern, while the other had a type 3 pattern. Both were located in the ventral medulla above the inferior olive between P9.5 and 10.5, in the region of the nucleus ambiguus.

Six cells were related to jaw movement. They discharged maximally during strong jaw-closure movements associated with the crushing of food pellets. They were not active during the rhythmic chewing of ground meat or other soft foods. Tooth and gum afferents, as well as muscle proprioceptors may be involved in activation of these cells. There were two type 1, two type 2, and two type 3 jaw cells. Jaw movement cells were located in medial pontine regions between P4.5 and 6 and in midbrain regions between Al and A3. Several of the cells described above as neck- and back-movement cells were weakly correlated with respiratory activity. This correlation could be explained by the back movement common to both behaviors. However, four cells had a stronger correlation with respiration than with any head or back movement. Two of these "respiratory cells" discharged during both peak inspiration and peak expiration while the other two discharged during peak expiration only. Three of the four had type 2 sleep patterns, the remaining cell having a type 1 pattern. None of these cells had auditory, visual, or shock responses. Respiratory cells were found in midbrain and pontomedullary regions. The high proportion of medial RF respiratory-related cells reported by others (47) may be due to the involvement of axial musculature as accessory respiratory muscles (31) as well as

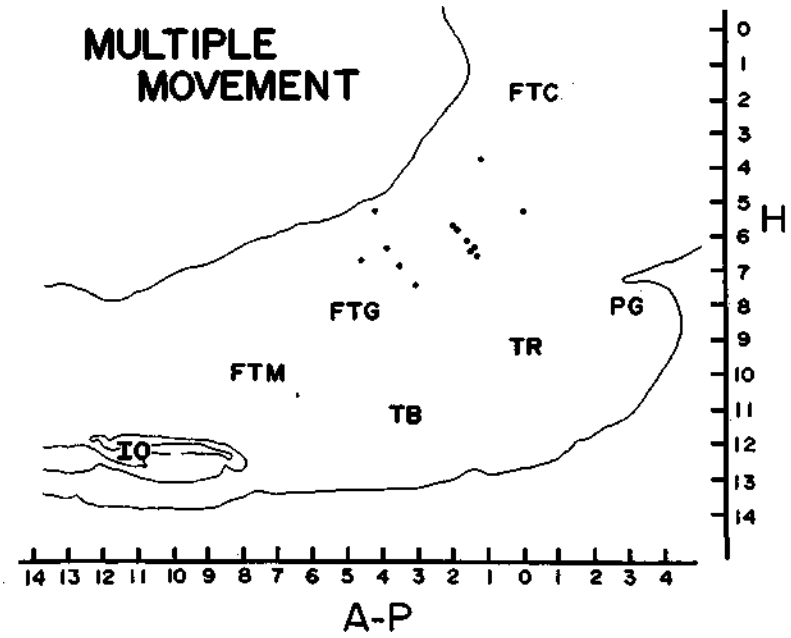

FIG. 11. Location of cells related to multiple forelimb and neck movements.

problems with the computer algorhythm used to determine respiratory relationship (22).

Sensory cells

Of all encountered sensory cells, 14.4% discharged maximally to applied sensory stimuli. Included in this group were cells responding to vestibular, auditory, visual, somatic, and proprioceptive stimuli.

VESTIBULAR CELLS. Cells were defined as vestibular if they had the following characteristics: *1)* response of similar magnitude to active and passive head movements in the same direction, 2) no response to active or passive neck movements with the head restrained, *3)* no activity during saccadic or pursuit eye movements when the head was restrained, and *4)* no variation in response amplitude to repeated passive head movements.

A total of 14 cells, 4.6% of the total, were classified as vestibular. Seven of these cells responded to contralateral head movement and seven to ipsilateral head movement. In addition to their vestibular response, these cells had the following characteristics. None of them responded to auditory stimuli *($P < 0.025$, x^2)*. None of the four tested responded to stroboscopic visual stimuli. None had any response to somatic stimulation. Their sleep types did not differ from the general population.

Vestibular cells were concentrated in a relatively restricted region of the rostral portion of the prepositus hypoglossi nucleus and the adjacent FTG field. Those cells related to ipsilateral movement were concentrated in a still more circumscribed portion of that region (Fig. 12).

SOMATOSENSORY CELLS. As has been discussed above, many cells that discharged in relation to active movement also responded to specific somatic stimuli. The cells described in the present section, while having somatic response, had no active movement correlate. There were a total of 21 cells (6.9% of total) in this category. These cells could be divided into two general categories: *1)* cells with unilateral or laterally asymmetrical receptive fields and 2) cells with bilaterally symmetrical receptive fields. Cells in the first group *(n = 13)* had receptive fields that ranged in size from 0.5 cm^2 to the entire side of the animal. The most common type (n = 9) responded to stimulation of a large portion (>9 cm^2) of the head region, with the remainder responding only to stimulation of the torso or proximal limb. Two responded

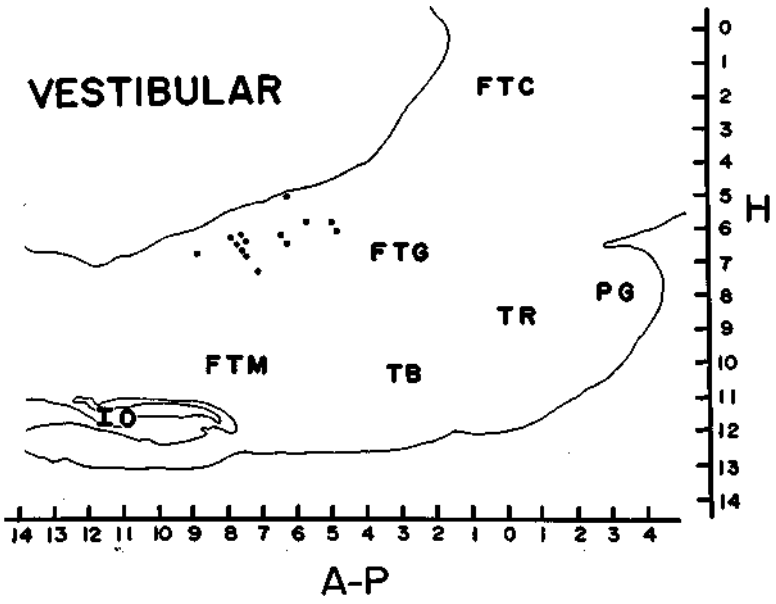

FIG. 12. Location of cells related to vestibular stimulation. Cells related to ipsilateral head acceleration are indicated with circles, while cells related to contralateral acceleration are indicated with squares.

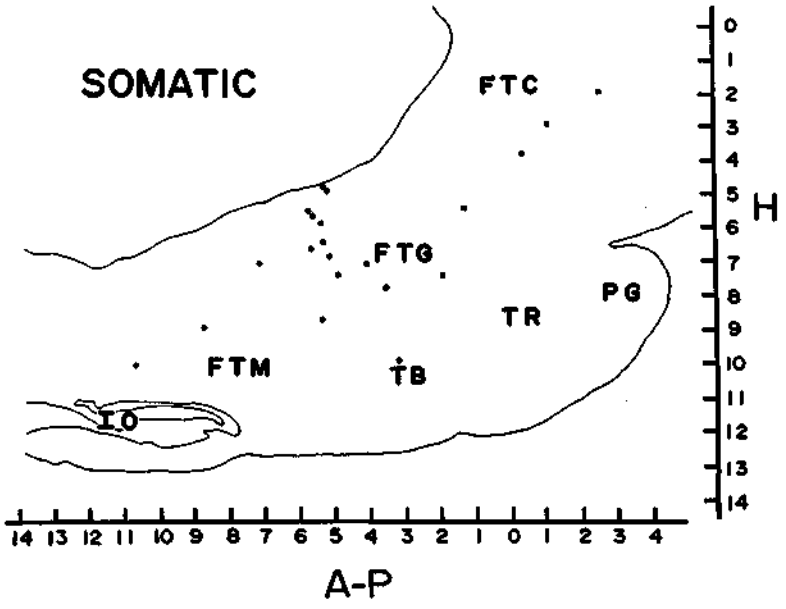

FIG. 13. Location of cells related to somatosensory stimulation. Cells with unilateral or laterally asymmetrical fields are indicated with circles, while cells with bilaterally symmetrical receptive fields are indicated with squares.

to contralateral stimulation, the rest to ipsilateral stimulation. While some cells responded briskly to punctate stimulation of less than 0.2 g, others were only activated with deep manually applied pressure in the receptive field. Cells with bilaterally symmetrical receptive fields *(n* = 8) responded to stimuli applied to half or more of the torso. The dorsum was the most sensitive region. Only one cell with a receptive field including distal portions of the limbs was found.

Contrary to what one might have expected, these cells were no more likely than the general population to respond to electric pulse stimulation. All were tested with stimuli applied to the center of the receptive fields. Conversely, most cells in the general RF population that did respond to shock stimulation had no somatic receptive field defined by punctate stimulation or even by manually applied deep pressure. Somatic cells did not differ from the general population in their response to auditory stimulation, in their sleep types, or in their anatomical localization (Fig. 13).

Other sensory cells

Two cells were identified as auditory. These cells responded to a variety of sound inputs, discharging tonically during human speech, scratching noises, and other stimuli, and at short (<27 ms) latency to click stimuli. Two cells responded only to visual stimuli moving in specific directions, having no discharge during active eye movements. Five "proprioceptive" cells responded similarly to active and passive movements of particular neck or limb movements but had no response to vestibular stimulation induced by acceleration of the body unless joint movement occurred.

DISCUSSION

Behavioral techniques

Before discussing the results it is necessary to consider the strengths and limitations of the behavioral observation techniques we have employed. The present results are a description of the behavioral correlates of activity in RF cells. The correlations between unit activity and spontaneous movement that we observe should not be taken by themselves as demonstrating a premotor role for RF cells. In some cells, observed relations between unit discharge and movement could have resulted from proprioceptive feedback from joint or muscle receptors or somato-

sensory stimulation. In other cases, as discussed below, a sensory explanation is clearly inadequate to explain the pattern of unit activity. However, the inadequacy of the simple sensory explanation does not necessarily indicate a premotor role for these cells. Cell activity may function as a reafference discharge, as an error signal in autonomic adjustments, or in other interneuronal information processing. In many systems it may not be possible or profitable to distinguish between sensory and motor cells. No attempt was made in the present studies to relate the latency of changes in unit discharge to movement onset. Therefore it is not possible to say if discharge in a given unit preceded or followed the onset of the observed movement. Photographic studies have shown a close temporal relation between RF unit activity and movement (36). However, even "simple" limb movements are preceded by a variable sequence of postural movements (6). Most RF units discharge primarily in relation to such axial movements. Identification of the muscles involved and accurate measurement of onset time of movements will be necessary to allow the analysis of unit-latency relations to this activity.

Behavioral studies can eliminate many hypotheses of cell function. By observing a wide variety of natural behaviors it is possible to identify the major variables affecting cell activity. One can also determine which classes of behavior do not have a major effect on cell activity. For example, in the present study we have observed all RF cells during food and water consumption, grooming, during arousal caused by noxious stimuli, and during sleep. We saw no units whose activity was selectively enhanced or diminished by any of these activities. In every case it was the movements that the animal made, and not the behavioral context in which they were executed, that were correlated with changes in unit activity. RF cells could be divided into those relating to facial, axial, or a number of other mutually exclusive movement categories. Once a movement to which cell discharge related had been identified, it was possible to distinguish cell groups that relate to directionally specific movements from those that relate to any movement of the identified body part. In every case we have observed unit activity during equivalent movements of body parts ipsilateral and contralateral to the cell. In most cells there was a consistent difference between activity during these movements. There were at least two classes of cells not showing any detectable directional or laterality difference, nonspecific neck/paw movement cells and nonspecific facial movement cells (41). However, even these cells were selectively active as a function of whether rostral or caudal muscular groups were activated. Therefore, activity in most RF cells is not a simple function of generalized arousal, pain, attention, or even movement. Any explanation of RF function in such terms must account for the specificity of the movement relations observed in the behaving animal.

At a further level of analysis one can distinguish between *a)* cells with similar active and passive movement relations, *b)* cells responding in opposite ways to active and passive movements, and *c)* cells responding only during active or only during passive movements. Each pattern of activity can eliminate certain functional roles for the unit. Thus cells with similar active and passive movement relations may be hypothesized to be driven by joint proprioceptors, while such a hypothesis cannot deal with the activity patterns of cells with no passive response or cells with opposite active and passive movement relations.

Cell types

Cells related to active ipsilateral head and neck movement were the single most common cell type in the RF. In the majority of cases the responses to passive neck or head movement were incompatible with a simple sensory explanation. Responses to passive movement were in a direction opposite to that which would explain discharge during spontaneous movements. A similar response pattern has been seen in cells recorded in the rabbit rhombencephalon (7). Furthermore, the unit response habituated to repetitive passive movements but not during active movements. During atraumatic head restraint, unit discharge continued if and only if the neck muscles were active (38, 39). One may hypothesize that the responses of these cells to passive head and neck movement are related to the reflex motor response to such stimuli. This interpretation is consistent with

studies in the acute decerebrate preparation showing that activity in reticulospinal neurons responding during vestibular stimulation parallels the neck muscle response to such stimuli (24).

A surprising feature of the data is the rarity of cells related to limb movements and especially to distal limb movement. This is in contrast to cortical sensory and motor systems where limb and particularly distal limb movements are proportionately overrepresented. Our unit-recording data indicates that the medial RF is primarily related to control of the axial and proximal limb musculature. Lesions placed in this same region have been shown to prevent spontaneous ipsilateral head movements (43) as well as disturbing other axial movements (15).

Most RF cells were related to directionally specific movement of the spinal column or of a single joint, but two fascinating cell types, nonspecific neck/forelimb cells, and nonspecific facial cells (41) discharged at equal rates during several movements. These cells may either be involved in facilitating a number of pools of motoneurons or may convey a relatively nonspecific reafference discharge to other regions. Each cell's action appears to be restricted to certain levels of either the spinal or trigeminal and facial system.

We have mapped the anatomical distribution of all behaviorally defined cell types. Several of the types of facial movement-related cells discussed in the companion paper (41) were clustered in relatively small portions of the medial RF regions explored. Similarly, the cells related to nonspecific forelimb and neck movements described in the present paper were relatively localized. These functional groupings do not correspond to any previously described reticular subnuclei. Other cell types had a somewhat less restricted localization. For example, cells related to head extension were concentrated in medullary areas and were relatively rare in pontine and midbrain regions. However, the most striking feature of the distribution of most cell types was the lack of anatomical localization. Even adjacent cells recorded with the same microelectrode usually had very different movement, sensory, and sleep-cycle discharge correlates. While it remains possible that other parameters will allow one to identify cell clusters within specific regions of the medial RF, it appears likely that, in fact, it is the mixing of different cell types within the RF that is functionally significant. Adjacent RF cells having different behavioral relations often synaptically interact (40). The mixing of cell types may therefore allow the RF to synthesize complex motor patterns out of simpler elements. This could be more readily performed if the cells responsible for the different elements of complex movements were adjacent than if a precise mapping of the body's muscles caused the anatomical separation of cells that participate in coordinated movements.

Synaptic mechanisms

Our behavioral findings are consistent with anatomical, physiological, and lesion studies showing direct projections from caudal RF areas including the nucleus gigantocellularis to motoneurons controlling axial musculature (9, 13, 16, 25, 26, 45). Individual RF neurons can project monosynapti-cally to several levels and both sides of the spinal cord (25). This projection pattern would allow a single RF unit to facilitate several groups of motoneurons participating in coordinated movement of the axial skeleton (31). However, one cannot assume that monosynaptic projections to motoneurons underlie all the motor relations seen in RF units. Only a small proportion of the medial RF cells in the more rostral RF areas examined in the present study have direct projections to the spinal cord (44). Furthermore, even those regions with direct projections to motoneuronal pools exert their most potent effects through polysynaptic pathways (23). However, despite the probable involvement of multisynaptic pathways in some cells, our studies do demonstrate a high degree of specificity in the relation between the activity of individual RF units and movement.

Responses to discrete sensory stimuli

One of the first observations made on RF units was their response to discrete auditory and somatic stimuli. This occurs in anesthetized, paralyzed, and decerebrated animals (1,3, 28, 29). We have confirmed these observations in our unrestrained cats, finding a similar proportion of responsive cells and similar response latencies. We found that re-

sponses to discrete auditory and somatic stimuli were significantly more common in cells related to neck and back movement and completely absent from units related to specific eye and facial movements. The response to such stimuli along with sleep-activity patterns and anatomical location can therefore serve as markers of behavioral subtype probability in acute preparations.

We found that cells responding to auditory clicks do not respond to weak (<75 dB) or slow-onset auditory stimuli, including the vocalizations of other cats, human voice, and a variety of other laboratory noises. Similarly, cells responding to electric pulse stimulation of the skin often did not respond to punctate pressure with a von Frey hair or to brushing of the skin surface. In no case did we find that the effectiveness of electric pulse stimulation was restricted to one region of the skin surface. Rather, cells responding to, for example, stimulation of the right neck region, would also respond, at a 1- or 2-ms greater latency, to stimulation of right or left hindlimb. Cells responding to electric pulse stimulation of the skin were significantly more likely to respond to discrete auditory stimulation ($P < 0.001$, x^2)- These observations suggest that both auditory and somatic responses are tapping a common pathway. Both kinds of stimuli could be expected to trigger a startle response. Lesions in the medial RF have been shown to interfere with this response (10, 17, 18). Therefore, the units responding to such stimuli may form part of the startle-response pathway. We may hypothesize that behavioral subtypes responding to rapid-onset stimuli are those that participate in the startle reflex, while those not responding are related to movements not elicited during startle.

Sleep activity

Virtually all medial RF cells discharge at their slowest rates in non-REM sleep and at their highest rates either during waking movements or in REM sleep. Waking and REM sleep rates are positively correlated, so that those cells with the highest REM sleep discharge rates also have the highest waking discharge rates. Different behavioral subtypes show distinctive patterns of activity during the sleep cycle. For example, cells related to head movement in the horizontal plane were significantly more likely than adjacent cells with other behavioral relations to be type 3 in their discharge pattern, i.e., to have little or no tonic activity in non-REM sleep and to fire in high-frequency bursts during waking movements and REM sleep. Cells related to proximal limb movement were significantly more likely to be type 2 in their discharge pattern, i.e., to have substantial levels of tonic activity in quiet waking and slow-wave sleep, while discharging in bursts during waking movements and REM sleep. Cells related to specific facial movements, discussed in the companion paper (41), were significantly more likely to be type 1 in their discharge pattern, i.e., discharging in bursts during waking movement and otherwise silent. In general, cells related to rapid-onset, high-velocity movements tended to have type 1 or 3 sleep discharge patterns.

During REM sleep the brain generates a complex series of motor activities whose expression in skeletal musculature is normally blocked by hyperpolarization of peripheral motoneurons (8, 20, 21). If this atonia is disrupted by pontine lesions, a variety of well-coordinated motor activities can be observed (27). Motoneuron hyperpolarization prevents the normal feedback from proprioceptors. Therefore, the REM state can be viewed as a natural experiment in which external sensory feedback is blocked. As such it indicates that such feedback is not essential in the activation of most RF cells, which show similar activity patterns in waking and REM sleep. This would be consistent with a motor hypothesis of RF activation. REM sleep activation could also be seen as resulting from a sensory efferent signal or reafference discharge. However, it is not consistent with the idea that RF activity is mediated by an external sensory loop. Our preliminary studies showing RF unit activity bursts in waking paralyzed cats suggest that sensory feedback is also not required for activation in RF cells during waking (35).

Concluding remarks

The principal finding of these studies is that most RF cells discharge in relation to a specific movement or group of movements. A number of cell types have been identified. Each cell type has a characteristic profile of sensory and sleep cycle response in addition

to its defining movement relation. Certain cell types are localized to specific regions within the RF, while others are intermingled over a wide area. The synaptic inputs and projections of each cell type remain to be determined. We hypothesize that the synaptic interaction of clusters of adjacent cell types related to different aspects of coordinated movement patterns may allow the RF to synthesize complex movement sequences from simpler elements.

A number of behavioral functions have been ascribed to medial RF cells, including arousal, sensory integration, REM sleep control, respiratory control, pain perception, conditioning and habituation processes, and modulation of emotional states. These conclusions were derived largely on the basis of studies in restrained animals. An analysis of the anatomical distributions and frequencies of these cell types indicates that the data underlying these conclusions are to some extent in conflict (32). It was hypothesized that RF cell discharge during simple movements may be the common element in RF activity reported after a variety of behavioral manipulations. The present data support this hypothesis.

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