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Discharge Pattern of Reticular Formation Unit Pairs in Waking and REM Sleep

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Interactions between simultaneously recorded pairs of neurons in the magnocellular and gigantocellular fields of the reticular formation were studied in unanesthetized, unrestrained cats. Each cell pair was recorded during both waking and REM sleep. Dependencies in discharge between spike trains were observed visually and with cross-correlation analyses. These dependencies were present at both short-latency and long-latency intervals. Dependencies were observed with equal frequency in waking and REM sleep. Short duration (1 to 3 ms) interactions were found in 40% of significant cross correlations and were most common in adjacent cells with related behavioral correlates. Patterns of discharge in REM sleep were similar to those in waking. These results suggest that there is common synaptic input to a large proportion of adjacent reticular cell pairs during both waking and REM sleep. Synchronized firing in local cell clusters may be a way in which reticular formation contributions to complex motor behavior are synthesized.

INTRODUCTION

We previously showed that single units in the feline medial reticular formation (RF) discharge during waking in conjunction with specific movements (19-21). However, the pattern of discharge in populations of RF cells during waking movement is unknown. Understanding of this pattern could help explain how the RF is able to synthesize complex motor behaviors from units which relate to simple movements. RF cells also become

Abbreviations: CC—cross correlation, RF—reticular formation.

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active during rapid eye-movement (REM) sleep, and although discharge rates and interspike intervals are similar to those of waking (14, 22, 23), the organization of population discharge in this state has not been studied. Therefore, in the present study we examined the cross correlations (CCs) of pairs of RF cells in the intact, unrestrained cat in both waking and REM sleep. These data have been reported in preliminary form (24).

METHODS

Units were recorded in seven unrestrained cats, each implanted with two to six microwire bundles. Each bundle contained six 32-/um microwires. The bundles were moved by mechanical microdrives, as previously described (8, 22). Bundles were less than 200 /u*m* in diameter. Microdrives were advanced until two or more units could be recorded simultaneously. Unit signals were viewed on an oscilloscope to confirm the absence of noise and the stability of spike amplitude and waveform. All units had signal to noise ratios exceeding four to one. Signals from both cells in each unit pair were stable during recordings of at least 6 h which included periods of waking movement and a minimum of one REM sleep period. Sensori-motor electroencephalogram, electrooculogram, lateral geniculate nucleus activity, and dorsal neck electromyogram were used for sleep state identification. Polygraph records included pulse outputs from window discriminators monitoring the unit signal. The behavioral correlates of unit discharges were determined for eight units using previously described techniques (20, 21).

Computer analysis was done off line. The STAP-12 program (26), modified for use with the RK08 disk system on a PDF-12 computer, was used for data assimilation and analysis. Trigger accuracy and the uniformity of spike waveform were confirmed in every case by observing waveshape and refractory period after repeated spike-triggered sweeps on a storage oscilloscope, or by the use of the triggering waveform display program of the STAP-12 system. Procedures to ensure against the possibility of crosstalk between electrodes included long-term monitoring of the discharge of both units in each pair, and the observation of the independent discharges in each train.

Samples were selected for freedom from artifact, state continuity, and stationarity. The first three samples that fulfilled these criteria in each state were analyzed by computer. When possible, additional samples were taken. Adjacent, nonoverlapping samples as well as widely separated samples from different waking movement and REM sleep periods were used, as dictated by the cats' sleep patterns. No analyses were done on non-REM sleep

periods, as magnocellular and gigantocellular RF cells are inactive in this state (22, 23). Samples usually consisted of the STAP-12 system capacity of 2048 spikes.

Stationarity was determined by dividing each spike train into 30 segments and testing for linear trend with the Pearson product-moment correlation statistic. Samples in which either unit showed positive or negative linear trends equal to or exceeding the 0.05 confidence level were discarded or truncated and retested. A more fundamental assessment of both linear and nonlinear Stationarity was achieved by our examination of repeated samples in all units.

Autocorrelations and interval histograms were taken at bin widths of 1 and 64 ms for all units and at bin widths of 8, 16, and 32 ms for selected units. Cross correlations were taken at bin widths of 1 and 64 ms for all units and at 2, 4, 8, 16, and 32 ms for selected units. Graphic displays were scaled to approximately equal peak height and plotted out on paper using a Complot incremental plotter.

To provide an assessment of the significance of the dependencies between spike trains, the reference trains were shuffled and CCs were calculated between the shuffled and dependent trains (9) and compared with the originals. To quantify the magnitude of the CCs the method developed by Griffith and Horn (7) was used for calculating expected values and standard deviation of the central CC peak. We found that the values predicted by this procedure were similar to those derived from the shuffle method. Z scores exceeding ± 3.0 ($P < 0.003$) were used as the criterion for identifying strong relations. Our statistical analysis was restricted to CCs with 1 ms bin width. The methodologic and mathematical issues associated with CC analysis were discussed in detail elsewhere (3, 4, 7, 16).

RESULTS

Visual inspection of the polygraphic records suggested that discharge often occurred in close temporal relation in cell pairs. This could be seen in both waking and REM sleep (Fig. 1). Periods of independent discharge were also seen in both states. Waking discharge in each cell was associated with specific movements as described previously (20, 21). Although a general long-latency correlation of discharge in waking could be predicted on the basis of the relation of RF cells to correlated movements, we were surprised to find extremely short-latency temporal interactions between unit pairs. In some pairs, neuronal spikes from each cell would occur within the same 1 to 2 ms interval. Correlated discharge occurred not only in waking, but also in REM sleep (Fig. 2).

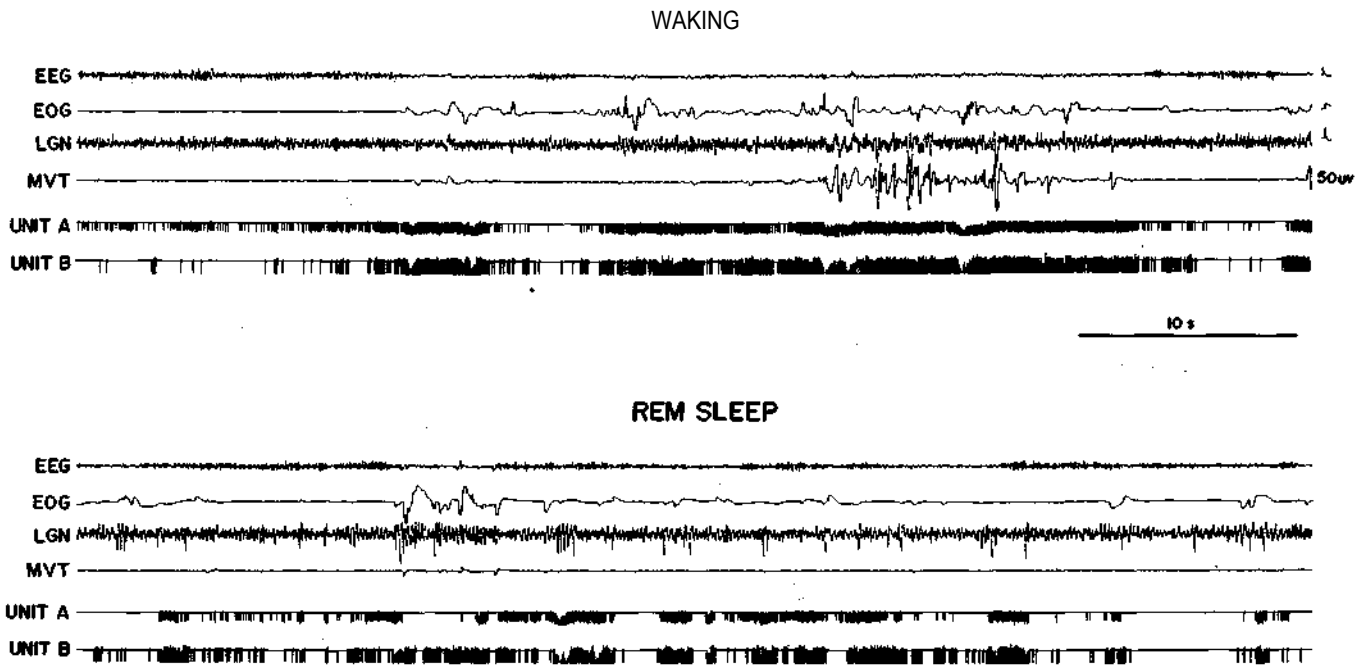

FIG. 1. Polygraph recording of unit pair in waking and REM sleep. These cells discharged together in both states, although periods of independent discharge were also visible. EEG—sensorimotor electroencephalogram, EOG—electrooculogram, LGN—lateral geniculate nucleus activity, MVT—head movement detected by a free wire, Unit A and unit B—pulse outputs of window discriminator monitoring unit activity.

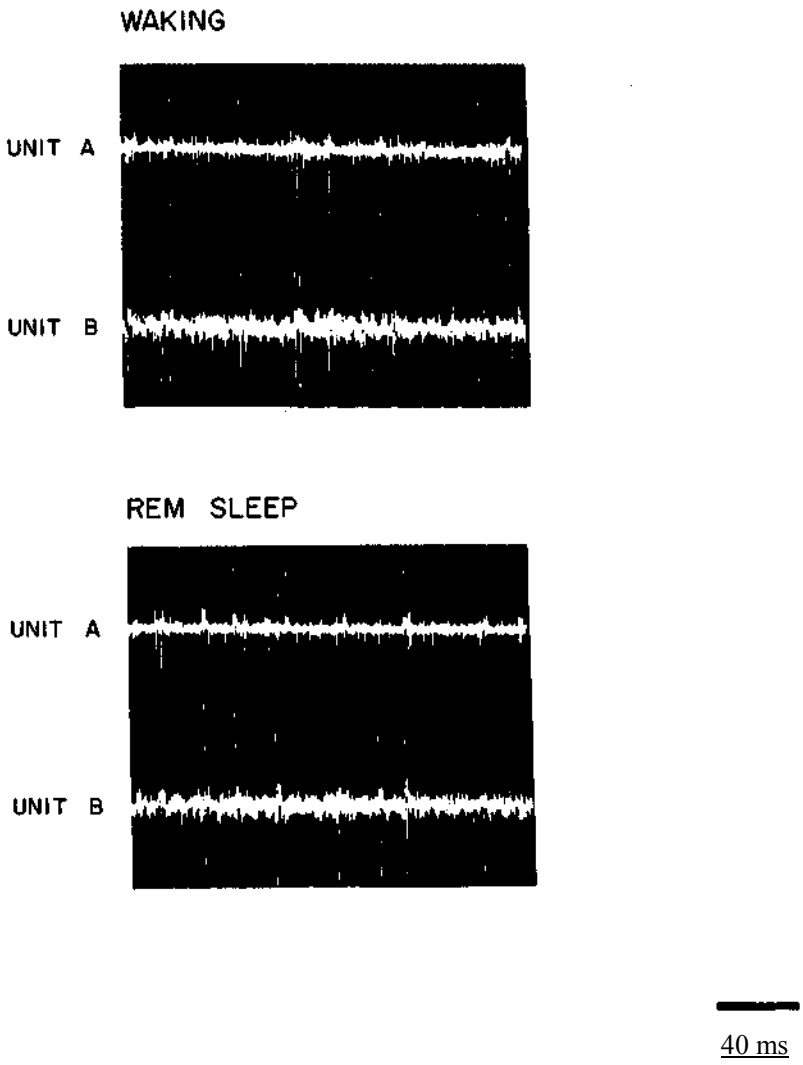

FIG. 2. Oscilloscope display of pair of neurons in waking and REM sleep. Note correlated discharge of units in both states.

To describe and characterize these relations more precisely, cross correlations were computed. To assess the stability of CCs, multiple samples were taken in both waking and REM sleep. A total of 116 samples were derived from 20 unit pairs.

Figure 3 illustrates the types of relations seen in 64-ms bin width CCs in waking and REM sleep. The first unit pair showed a large central peak indicating a strong CC in REM sleep but only weak, long-latency inter-

WAKING

SECONDS

FIG. 3. Representative cross correlations of four separate unit pairs in waking (left) and REM sleep (right) computed with 64-ms binwidth. Standard deviation and mean predicted under the null hypothesis are indicated to the right of each CC.

actions in waking. The second pair had dependencies, in the 1 to 2 s range which were larger in waking than in REM sleep. The third unit pair showed dependencies in both states but the fourth unit pair had no significant interaction in either state. The shapes of significant CCs tended to be similar in waking and REM sleep. Note particularly the skewed peak of the second unit pair in both states. The form of the 64-ms CCs computed in waking were a function of the behavioral relations in the units. Units that related to similar movements showed large central peaks in their CCs. Units that related to mutually exclusive movements often had shifted peaks.

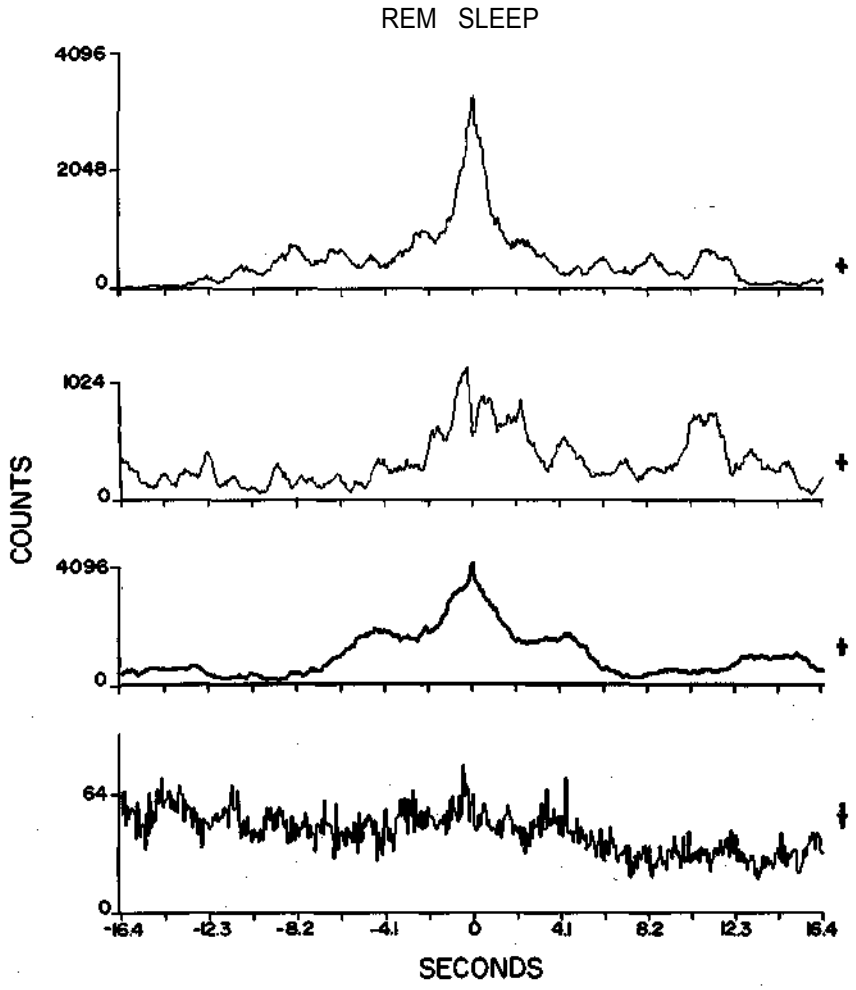

FIG. 3 (*Continued*)

Figure 4 is an example of a CC taken from a pair of units, one of which related to dorsal head movements while the other related to ventral head movement. The figure was taken during the repetitive movements of grooming, resulting in a rhythmic interaction with a shifted central **CC** peak.

Figure 5 presents samples of CCs computed at 1-ms bin width. As with 64-ms CCs, strong correlations were seen either in REM sleep (Fig. 5, pair one), waking (pair two), both states (pair three), or neither (pair four). Peaks disappeared when the reference train was shuffled. Significant central peaks were often broad, although short-duration central components were apparent in many samples (pair two in waking, pair one in REM sleep).

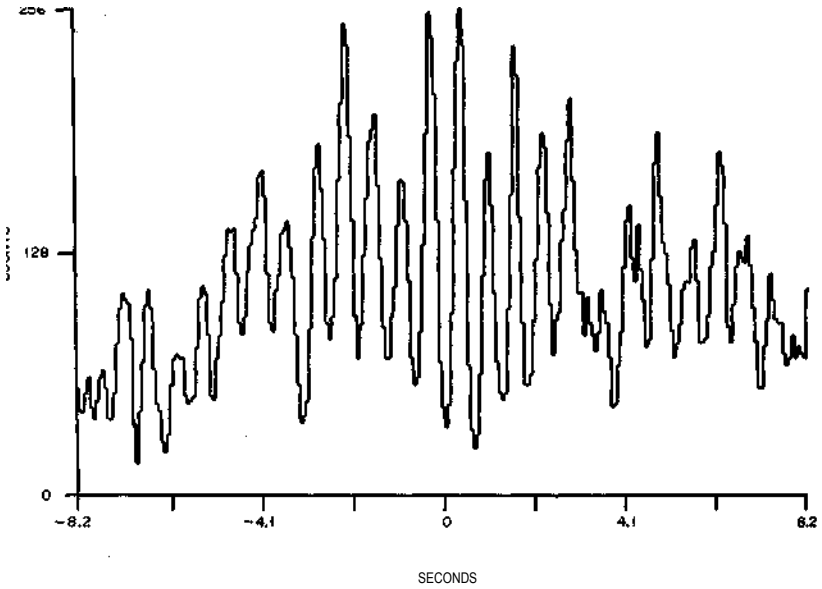

FIG. 4. Cross correlation during grooming. Note shifted central peak and rhythmic nature of interaction. Bin width is 64 ms.

Table 1 presents the statistical analysis of 1-ms bin width CCs for each of the samples. Mean Z scores for each unit pair in each state were calculated by averaging the sample values. There was no significant difference between the mean central bin Z scores of waking and REM sleep *(P*

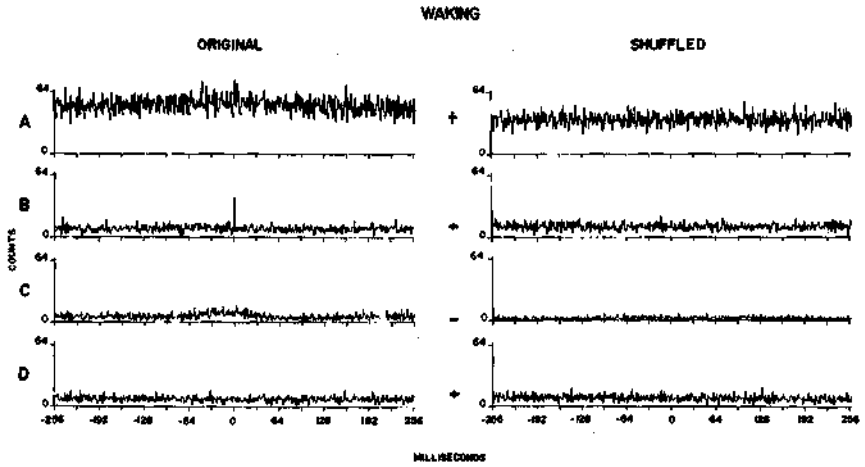

FIG. 5. Representative cross correlations of four unit pairs computed with 1-ms bin width. Sharply peaked CCs are visible in pair A in REM sleep and pair B in waking. Broad peaks are visible in both states in pairs A and C. Second and fourth columns present CCs computed after shuffling data in original CCs; CCs disappear after shuffling.

> 0.2, Wilcoxon test) although the mean Z scores in REM sleep were somewhat higher. Five of the unit pairs had significant mean CC Z scores in waking and an overlapping group of five pairs had significant CC Z scores in REM sleep.

Ten of the unit pairs were derived from units on the same side of the brain and seven of these from units on the same microwire bundle. Of those recorded on the same side of the brain, eight had significant mean (averaged overall samples) Z scores (four in REM sleep and four in waking). Only two of the six pairs recorded on opposite sides had significant mean CCs (one in REM sleep and one in waking).

The magnitudes of the short-duration CC peaks were calculated by determining the number of standard deviations by which the counts in the central bin exceeded the mean of the preceding and following bins in the 1-ms bin width CCs. Of the 30 samples with significant 1-ms CCs, 12 had central bin counts more than three standard deviations greater than the mean of adjacent bins. Three of these CCs were derived from units on opposite sides of the brain, and one had its units on the same side but on different microwire bundles and eight had units which were both on the same microwire bundle. The largest short-duration CC peaks occurred in units recorded on the same bundle.

The behavioral correlates of discharge were examined in four pairs of cells recorded from adjacent microwires on the same microwire bundle. Two of the pairs had significant short-latency CCs and the other two pairs did not have significant CCs. The units in the two pairs that had significant short-latency CCs had related, but not identical, behavioral correlates. In

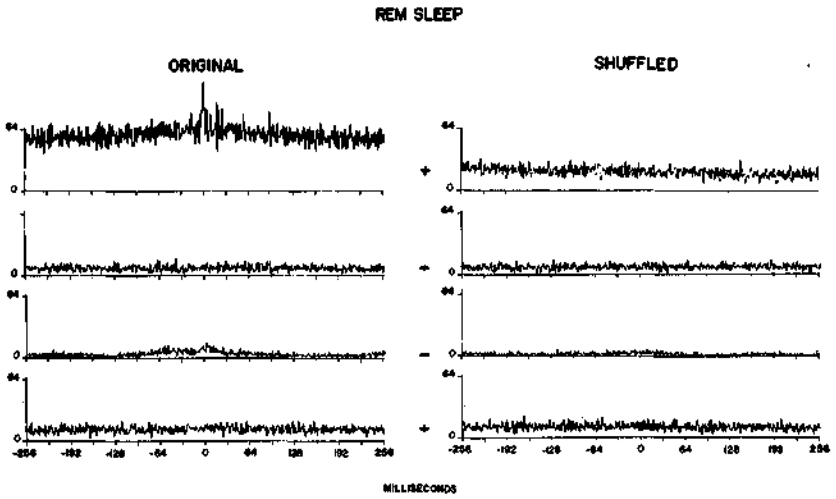

FIG. 5 (*Continued*)

TABLE 1 Cell Pair Statistics for All Samples at 1-ms Bin Width[a]

Waking					REM sleep			
Experiment	Sample	Train A rate	Train B rate	Z score	Sample	Train A rate	Train B rate	Z score
X5-2-56	a	2.6	3.1	0.9	a	6.9	6.0	12.7
	b	2.8	1.2	2.3	b	11.5	7.3	12.3
	c	2.2	0.6	-0.7	c	7.3	3.1	22.7
A36-11-14	a	4.7	1.1	3.8	a	11.6	7.3	7.2
	b	10.3	10.3	-1.6	b	3.9	2.5	13.8
	c	9.1	15.7	1.0	c	7.6	3.0	8.7
A36- 12-64	a	33.5	40.6	6.7	a	9.0	13.5	37.0
	b	9.3	12.1	6.1	b	19.0	30.4	11.3
	c	7.7	3.4	5.1	c	16.0	34.3	19.9
	d	13.2	31.2	5.8				
P39-1-13	a	10.2	44.7	9.0	a	11.1	25.0	-0.5
	b	15.0	68.9	7.4	b	27.8	19.4	0.7
					c	35.2	27.2	2.1
					d	40.0	26.5	2.0
P40- 10-61	a	9.1	9.7	1.3	a	17.7	18.3	1.1
	b	7.7	7.5	-0.6	b	17.3	23.8	1.3
	c	9.1	43.7	-0.5	c	50.1	63.7	0.8
P43-5-36	a	1.1	1.5	3.4	a	0.5	9.4	0.9
					b	0.6	9.4	1.2
R56- 10-63	a	52.3	7.4	-3.1	a	41.2	8.7	1.2
	b	50.1	12.6	-0.3	b	16.8	18.7	-3.7
	c	42.6	3.2	-2.0	c	56.1	40.1	2.9
X5-1-17	a	21.4	4.6	2.8	a	5.5	2.6	7.5
	b	9.3	3.3	11.6	b	22.7	3.1	11.0
	c	7.4	2.6	. 15.4	c	6.7	2.2	8.8
P46-8-57	a	20.8	3.2	0.9	a	6.8	2.2	1.4
	b	11.2	1.8	2.1	b	9.1	2.6	3.0
					c	7.0	2.1	2.4
R56-9-56	a	7.8	7.9	-1.2	a	22.7	15.6	2.0
	b	8.6	1.8	0.5	b	48.2	8.2	-0.6
	c	12.6	2.0	1.7	c	18.6	7.5	2.3
X5-1-13	a	27.0	7.3	-1.8	a	5.7	3.2	-0.4
	b	11.1	6.5	-1.4	b	22.1	7.7	2.4
	c	6.3	4.0	5.9	c	8.6	2.8	-0.8
X5-1-73	a	3.8	6.6	-1.6	a	2.9	3.2	-3.9
	b	3.2	5.2	0.0	b	3.9	5.6	0.8
	c	2.8	4.6	0.2				

TABLE 1 *(Continued)*

	Waking				REM sleep			
Experiment	Sample	Train A rate	Train B rate	Z score	Sample	Train A rate	Train B rate	Z score
X5-2-52	a	2.5	2.8	-0.5	a	6.0	4.8	2.0
	b	2.8	2.5	0.1	b	10.0	7.5	2.5
	c	2.0	2.8	-1.1	c	6.3	8.3	-6.4
X5-2-62	a	3.0	2.7	2.5	a	5.0	5.0	2.2
	b	1.2	2.5	2.4	b	6.7	7.2	1.9
	c	0.6	0.6	6.1	c	2.9	7.9	4.7
X5-7-51	a	9.9	22.1	-0.3	a	20.8	6.8	1.4
	b	5.8	2.4	0.9	b	40.3	5.9	-1.6
	c	16.2	6.1	3.6	c	8.9	12.2	2.1
A36-10-56	a	17.1	26.6	3.7	a	9.6	23.8	0.5
	b	3.0	20.4	0.0	b	100.7	42.7	-0.9
	c	19.1	25.3	1.3	c	26.6	21.5	1.2
R56-10-26	a	46.2	51.8	1.0	a	10.3	41.9	0.9
	b	12.3	58.6	1.4	b	16.8	15.2	2.2
	c	24.8	43.2	0.4	c	13.9	40.2	0.6
R56-10-23	a	26.3	6.3	-0.5	a	16.4	6.5	0.8
	b	15.7	1.5	2.6	b	20.4	20.8	2.8
	c	16.5	2.5	-0.2	c	16.1	27.1	-4.3
R56-9-35	a	25.2	7.5	-0.3	a	43.6	28.6	-2.9
	b	47.7	8.6	0.1	b	19.5	45.0	-2.0
	c	59.8	7.5	-2.3	c	32.9	26.6	-1.9
R56-9-36	a	28.0	5.7	-1.3	a	33.0	20.7	-0.7
	b	58.9	1.9	-1.9	b	24.8	12.5	0.7
	c	61.7	2.1	-2.0	c	28.7	52.1	-0.7

" Train rate given in spikes per second. The first seven unit pairs were derived from the same microwire bundles, the next three pairs from the same side of the reticular formation but different bundles, and the remaining pairs from opposite sides of the brain.

one pair, one unit discharged maximally during active movements of the ipsilateral scapula while the other discharged maximally during active ipsilateral flexion of the neck. In the other pair, one unit discharged maximally during active dorsoflexion of the neck, and the other discharged maximally with active extension of the neck. The two adjacent cell pairs without significant short-latency CCs had less closely related behavioral correlates. In one pair, one unit discharged only during contralateral facial stimulation, and the other discharged in relation to ipsilateral neck movement. In the second pair, one unit responded maximally when the cat

extended its forepaws bilaterally to support its weight, and the second responded maximally during ipsilateral neck flexion. A more detailed description of the behavioral correlates of discharge in these cells will appear elsewhere.

The location of the highest count in the cross correlation relative to the central bin was determined for all signficant 1-ms CCs. There was no consistent pattern of peak shift, most peaks being in the central bin. Two unit pairs had repeated significant peaks in both waking and REM sleep. In one (A36-12-64), three of the four waking samples and all three REM sleep samples had peaks in the central bin. The remaining waking CC peak was shifted 2 ms. In the other (X5-1-17), all three REM samples were shifted 2 to 8 ms in the same direction. One waking sample was also shifted in this direction by 2 ms and the two other waking samples were shifted 9 and 18 ms in the reverse direction. Two unit pairs had more than one sample with a significant CC peak in REM sleep. In one pair (X5-2-56) all three were shifted 5 ms in the same direction, indicating that one unit consistently led the other. In the other (A36-11-14) all three samples had peaks in the central bin.

Autocorrelations at 1- and 64-ms bin widths were calculated on all samples. Figure 6 presents autocorrelation data on the units shown in Fig. 5. The shape of the autocorrelation function was characteristic of the unit and similar in waking and REM sleep. Multiple peaks, indicating rhythmic discharge, were visible in a few units in both waking and REM sleep at 64-ms bin width but most autocorrelation functions were unimodal.

Units subjected to computer analysis were histologically localized to the magnocellular and gigantocellular tegmental fields of the medial pontomedullary reticular formation. The positions of the unit pairs are given in Fig. 7.

DISCUSSION

The results of our spike train analyses on RF unit pairs are consistent with what is known about behavioral correlates of their activity in waking. These cells have been found to discharge in conjunction with specific movements (21). The most common cell type discharges in conjunction with ipsilateral head and back movement, with other cell types related to specific limb, facial, and other movements (20). The similarity of behavioral correlates in homolateral cells would cause the broadly peaked positive CCs we have seen. The variability and peak shifts seen in CC relations with repeated samples are also seen to result from the behavior pattern occurring during each sample. For example, during the rapid ipsilateral movement that occurs in grooming the ipsilateral hindquarters, the majority of cells

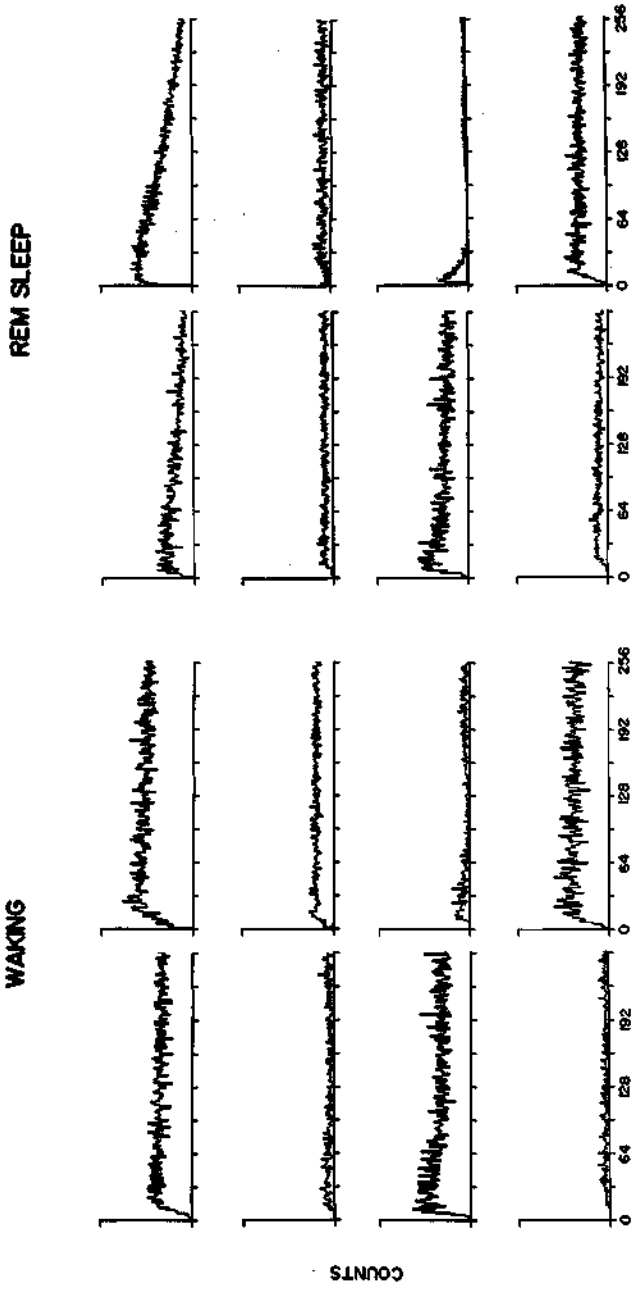

FIG. 6. Autocorrelations at 1-ms bin width of units in Fig. 5.

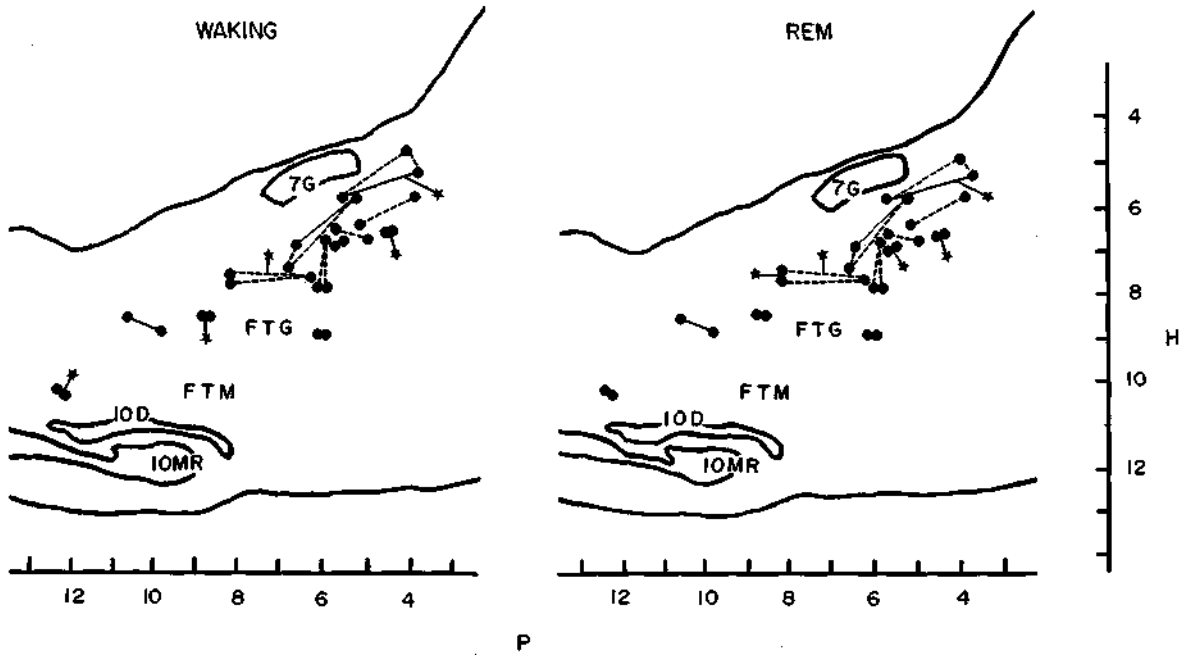

FIG. 7. Sites of cell pairs on sagittal section of cats' brain stem. Cell pairs recorded from the same or adjacent wires are represented by overlapping circles and other pairs are connected by lines. Broken lines indicate cells on opposite sides of midline. Cross correlations that were significant at the 1-ms bin width are indicated by stars. 7G—genu of the facial nerve, FTG—gigantocellular tegmental field, FTM—magnocellular tegmental field, IOD—dorsal accessory nucleus of the inferior olive, IOMR—medial accessory nucleus of the inferior olive, rostral division.

with ipsilateral head movement relations would show synchronous burst discharges. However, when other behaviors with a weaker horizontal component occurred, only those cells with lower movement thresholds would be activated and fewer significant CCs would be observed.

A similar variability was present during the REM sleep state, suggesting that a wide range of motor programs are expressed during this state. Discharge rates (22), interval histograms (14), autocorrelations, and cross correlations of RF unit pairs are similar in waking and REM sleep. The similarity of discharge in medial RF cells in waking and REM sleep is consistent with the idea that they reflect or cause some aspect of the motor activation common to both states (19). It was hypothesized that RF cells discharge synchronously in REM sleep but only in an isolated, uncorrelated manner in waking (13). The present observations do not support this idea. Synchronous discharge of RF cells is not restricted to the REM sleep state.

Some differences do exist between waking and REM sleep spike train parameters. Maximum REM sleep rates are 47% higher than maximum waking rates (22, 25), modal interspike intervals are somewhat shorter (14), and CC peaks are somewhat higher in REM sleep, although there is considerable overlap between the waking and REM sleep values of all these variables. On balance these findings suggest that REM sleep motor activation is somewhat more intense than waking activity. Much of this difference may result from the rather limited range and intensity of waking motor activities observable in the caged cat compared with the cat's complete behavioral repertoire. These differences may also be a consequence of the motoneuron inhibition of REM sleep. This inhibition, by preventing most motoneuron discharge, also blocks the usual proprioceptive feedback of movements. One may speculate that this feedback limits RF unit activity in waking and that its absence in REM sleep results in faster, more synchronized discharge.

The presence of spike for spike synchronization in some neuronal pairs, illustrated in Figs. 2 and 4, suggests that a powerful common synaptic linkage is driving them during certain behaviors. Because in most cases there does not appear to be any consistent phase difference in the discharge of cells pairs, an input shared by both cells is the probable source of their synchronized excitation. The cell pairs with shifted peaks could also share a common input or could be synaptically interacting with each other (16). Two previous studies of a smaller number of midbrain RF cell pairs reported no significant short duration CCs in adjacent RF cells (1, 12). Those studies used restrained or paralyzed cats. In such preparations, not only is proprioceptive feedback blocked, but it is reasonable to assume that the patterns of commanded motor activity are abnormal and perhaps diminshed in rate and intensity, making detection of CCs less likely. The frequency

with which we detected sharp central CC peaks, in adjacent cells, suggests that many localized colonies of cells are being driven synchronously during waking and REM sleep. Short time scale correlations have also been seen in the pneumotaxic area of the pons (9) and an analogous synchronous activation of medullary respiratory and cyclically active midbrain RF neurons in waking, paralyzed animals has also been described (6, 11). The dendritic and axonal fields of reticular formation cells, which often extend over large portions of the brain stem tegmentum (17), are a possible anatomic substrate for the short-latency interactions seen in neighboring cells. Groups of dendrites are sometimes packed into bundles or complexes and within these bundles the membranes of pairs or trios of dendritic shafts can run parallel to each other for considerable distances, frequently without any intervening structures (18). Cerebelloreticular (5) or descending systems (10, 15) might also be involved.

Synchronously activated cell clusters may be the functional units of the reticular formation, analogous in function to the columns seen in cortical regions. Whereas individual RF cells discharge in relation to simple movements or stimuli (20, 21), the RF as a whole appears to be capable of organizing complex sequences of motor activity (19). The simultaneous activation of local subpopulations of RF cells each related to a separate motor element of a complex movement pattern could be the way in which descending or intrinsic systems integrate simple RF unit motor relations into coordinated movements. A shift in the cells constituting these populations may be a mechanism for altering the pattern of muscle activation during behavior.

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