

Unitary recording during movement and behavioural studies

Encoding of motor parameters by corticomotoneuronal (CM) and rubromotoneuronal (RM) cells producing postspike facilitation of forelimb muscles in the behaving monkey

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This paper compares the properties of corticomotoneuronal (CM) and rubromotoneuronal (RM) cells identified by postspike facilitation (PSF) of rectified EMG activity in the awake monkey. The postspike effects of CM and RM cells in flexors and extensors of the wrist and fingers have been determined, as have the discharge properties of these cells in relation to alternating ramp-and-hold wrist movements. The characteristics of postspike facilitation and postspike suppression (PSS) were similar for RM and CM cells. The magnitude of RM-PSF was weaker than CM-PSF and RM cells showed a stronger preference for facilitation of extensor muscles than CM cells. As with CM cells, the onset of discharge in RM cells preceded the onset of EMG activity in their target muscles. Tonic discharge related to static torque was more prominent in CM cells, whereas phasic discharge was more prominent in RM cells; however, many RM cells showed some tonic activity weakly related to static torque. We conclude that CM and RM cells share many common features; however, RM cells are concerned primarily with the dynamics of muscle contraction.

INTRODUCTION

Four major tracts descend from the brain to the spinal cord carrying efferent signals producing contraction of limb muscles: the corticospinal, rubrospinal, vestibulospinal and reticulospinal tracts². Lawrence and Kuypers^{18,19} divided these into two functional categories — a lateral and a medial descending system. The lateral system, consisting of the corticospinal and rubrospinal tracts, acts primarily on distal muscles, whereas

the medial descending system, consisting of the vestibulospinal and reticulospinal tracts, acts primarily on proximal and axial muscles. Since distal limb movements rely largely on lateral system neurons, their organization and the nature of the signals they transmit to motoneurons is essential to understanding the central control of movements at distal joints. Motor cortex and red nucleus both contain a multitude of different types of cells, of which only a fraction actually contact motoneurons synaptically — so-called cortico-

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motoneuronal (CM) and rubromotoneuronal (RM) cells. Yet it is specifically these cells that are of greatest relevance for understanding the descending control of movements at distal joints.

In previous work, we showed that both CM and RM cells can be identified in awake monkeys by their postspike facilitation in spike-triggered averages of rectified EMG activity^{5,11} (see also ref. 20). We also characterized the functional properties of CM cells in relation to active wrist movements against different external loads⁶, to passive wrist rotation and torque perturbations of active movement⁷. Currently, we are investigating the properties of RM cells using the same movement paradigms that were previously used to characterize CM cells. In this paper we compare the postspike effects and discharge properties of CM and RM cells in relation to similar ramp-and-hold wrist movements generated by the cell's forearm target muscles.

METHODS

Behavioral and recording methods

Monkeys were trained to generate two types of ramp-and-hold wrist responses: (1) auxotonic and (2) isometric. In both tasks, the monkey was seated in a primate chair with the forearms in padded restraints and the hand opposite the recorded cell clamped between a pair of padded plates attached to a torque motor. Auxotonic responses involved muscle shortening against elastic loads, which increased in proportion to displacement away from the zero position (hand aligned with the forearm). Isometric responses were obtained with the manipulandum locked at the zero position. The monkey was required to make ramp-and-hold torque trajectories alternating between flexion and extension target zones. In both tasks, responses were self-paced with a minimum hold time within the target zone of 1 s. Entry into a target zone was indicated by visual and auditory cues. Target zones were generally 10° or 0.04–0.08 nm wide and successful completion of the task required holding within the zone for a period of about 1 s. In the red nucleus experiments, the entire behavioral paradigm was controlled by a Commodore 64 com-

puter, which displayed the position and sizes of targets, and a cursor driven by wrist position or torque²¹. Monkeys typically worked for 3–5 h on this task for apple-sauce rewards on a variable ratio schedule.

After training was complete, a stainless steel recording chamber was attached to the skull with Vitalium screws and dental cement. For motor cortex recording, the chamber was centered over the hand area — about 18 mm lateral to the midline along the central sulcus and at an angle tangential to the cortical surface. For red nucleus recording, the chamber was positioned at AP + 5 and at an angle of 30° to the sagittal plane. Task-related CM cells were found within a 2 × 5 mm area of the precentral gyrus; RM cells within a region of magnocellular red nucleus with chamber coordinates of about 1 × 1 mm. For red nucleus recording, the electrode was inserted through a 22-gauge cannula which penetrated the brain to within about 8 mm of the red nucleus. Several recording sites were marked with microlesions generated by passing 15–20 μA of anodal current for 15–20 s.

Identification of CM and RM cells using spike-triggered averaging (STA) of EMG activity

A full description of our spike-triggered averaging methods can be found in other papers^{8,11,17a}. Briefly, spikes of individual neurons were discriminated and used as triggers for computing averages of full-wave rectified EMG activity of forearm muscles. EMG activity of up to 6 coactivated flexor or extensor muscles was digitized at a rate of 4 kHz and averaged by a PDP 8e or PDP 11/73 computer. To eliminate redundant recordings through cross-talk, EMG-triggered averages were compiled; if a pair of muscles showed greater than 15% cross-talk, one muscle was eliminated as potentially redundant. Only spike events occurring during the phase of movement which engaged the activity of the muscles being averaged were accepted as trigger events. Since CM cells are largely inactive during the antagonist phase of movement, glutamate was used to sustain activity throughout the wrist movement cycle¹⁷. Spikes evoked by glutamate during the antagonist phase of movement were then used to compute averages of antagonist

muscles. RM cells showed a sustained background discharge throughout the wrist movement cycle, obviating the need for glutamate iontophoresis. All spike-triggered averages consisted of 2000 trigger events or more; the reproducibility of most postspike effects was confirmed by computing multiple consecutive averages from the same cell or by showing that the size of postspike effects continued to increase relative to noise with more trigger events.

RESULTS

The comparisons in this paper are derived from previously published work⁵⁻¹⁰ on a total of 118 CM cells recorded from 8 rhesus monkeys and on 23 RM cells recorded from 3 red nuclei in 2 rhesus monkeys. The RM cell data is previously unpublished except for a preliminary report⁵ which included two RM cells.

Properties of output organization

The central motor program must select the appropriate muscles to execute the intended movement. The sign and distribution of effects of a particular descending system neuron on different motoneuron pools places important constraints on the extent of that neuron's participation in different movements. STA of EMG activity from several task-related digit and wrist forearm muscles has provided estimates of the distribution and relative strength of synaptic effects from single corticospinal and rubrospinal neurons to motoneurons of agonist and antagonist muscles. We will refer to the muscles co-activated with the cell during a motor task as 'agonists' and those whose actions mechanically oppose the agonists as 'antagonists'.

Both CM and RM cells related to wrist movements show a divergent pattern of axon terminal organization with motoneurons of different wrist and digit muscles^{4,11}. We have used the term 'muscle field' to denote the muscles which a particular efferent neuron facilitates or suppresses^{11a}. The muscle fields of CM and RM cells were determined in the awake monkey using STA and are summarized in Table I along with the

properties of postspike facilitation (PSF) and postspike suppression (PSS) from these cells. The values in this table are based on recordings in which 5 or 6 synergist muscles were tested for postspike effects. The number of forearm agonist muscles facilitated by CM cells ranged from one to six, with a mean of 2.4 and 3.0 in two separate studies^{11,17a} (cf. ref. 4). We obtained a similar value of 3.1 for RM cells. The number of muscles per cell showing PSS were also very similar — 1.8 for CM cells^{17a} and 1.6 for RM cells.

The magnitude of PSF expressed as percent change from baseline was greater for CM cells (7.0%) than RM cells (5.1%). In contrast, the magnitudes of PSS using the same measure were nearly the same (4.1% for CM and 4.5% for RM). The mean onset latency of RM-PSF (5.2 ms) was shorter by 1.1 ms than the onset of CM-PSF (6.3 ms); RM-PSS (8.4 ms) was shorter by 0.9 ms. These differences are consistent with the differences in latency of hindlimb motoneuron postsynaptic potentials evoked from stimulation of motor cortex and red nucleus in the monkey²⁶ and can be largely attributed to differences in conduction distance of the descending tracts.

A remarkable difference between CM and RM cells is the strong preference exhibited by RM cells for extensor muscles of the forearm. Of 23 RM cells, 18 (78%) facilitated forearm extensor muscles exclusively; only 2 RM cells facilitated flexors exclusively and the magnitude of their facilitation was less than that for the extensors. Three cells co-facilitated flexors and extensors; in two, PSF of extensors was stronger, in one flexor PSF was stronger. This extensor preference of RM cells cannot be easily explained by incomplete sampling from the red nucleus, since histological reconstruction showed penetrations throughout the magnocellular division. Similarly Gibson et al.^{13,14} also found that neurons in the hand area of magnocellular red nucleus were predominantly related to wrist extension.

CM cells also showed effects favoring extensor muscles^{11,17a}. A higher percentage of wrist extension related cortical cells were CM cells than flexion-related cortical cells. Moreover, CM-PSF of extensor muscles was stronger than

TABLE I

Summary of wrist related CM and RM cell properties

	CM [†]	RM
<i>Postspike effects</i>		
Onset latency (ms)		
PSF	6.3 ± 1.6	5.2 ± 1.2
PSS	9.3 ± 2.3	8.4 ± 3.6
Peak magnitude (% of baseline)		
PSF	7.0 ± 6.6	5.1 ± 1.9
PSS	4.1 ± 2.4	4.5 ± 2.4
Number muscles with PSF/cell	3.0	3.1
Number muscles with PSS/cell	1.3	1.5
<i>Discharge properties for active movement</i>		
Pattern in relation to ramp-and-hold movement		
Phasic-tonic	59%	52%
Tonic	28%	9%
Phasic only	0	30%
Phasic-ramp	8%	0
Ramp	5%	0
Suppression or unmodulated	0	9%
Onset relative to target muscle EMG	- 54 ms (- 71, - 63, + 5, + 101)*	- 96 ms
Tonic component of activity		
% of tonic cells with relation to static torque	100%	100%
Rate-torque slope		
Extension	480 Hz/nm (140-800)	128 Hz/nm (72-346)
Flexion	250 Hz/nm (60-500)	22 Hz/nm (1 cell)
Phasic component of activity ^{††}		
Number cells tested	16	15
Relation to dT/dt	50%	27%
Relation to velocity	?	27%
Unrelated	50%	27%
<i>Discharge properties for passive movement</i>		
Number cells tested	19	13
Number activated at short latency	17 (90%)	11 (85%)
Unidirectional	10 (53%)	0
Bidirectional	7 (37%)	11 (100%)
Best response for stretch of target muscles	7 (70%)	1 (9%)

[†] Data from refs. 6 and 11.

^{††} Relations to velocity were not systematically tested for CM cells. Percentages for RM cells are based on parameter to which activity was best related.

* Mean onset times for phasic-tonic, phasic-ramp tonic and ramp cells respectively.

that of flexors, and muscle fields of extensor CM cells tended to be larger.

CM and RM cell output organization was also categorized according to the cell's postspike effects on antagonist muscles. The most common

patterns of output organization for both CM and RM cells were: (1) reciprocal, and (2) pure facilitation^{17a}. Reciprocal cells facilitate the agonist muscles and simultaneously suppress the antagonists. Fig. 1 illustrates one reciprocal RM

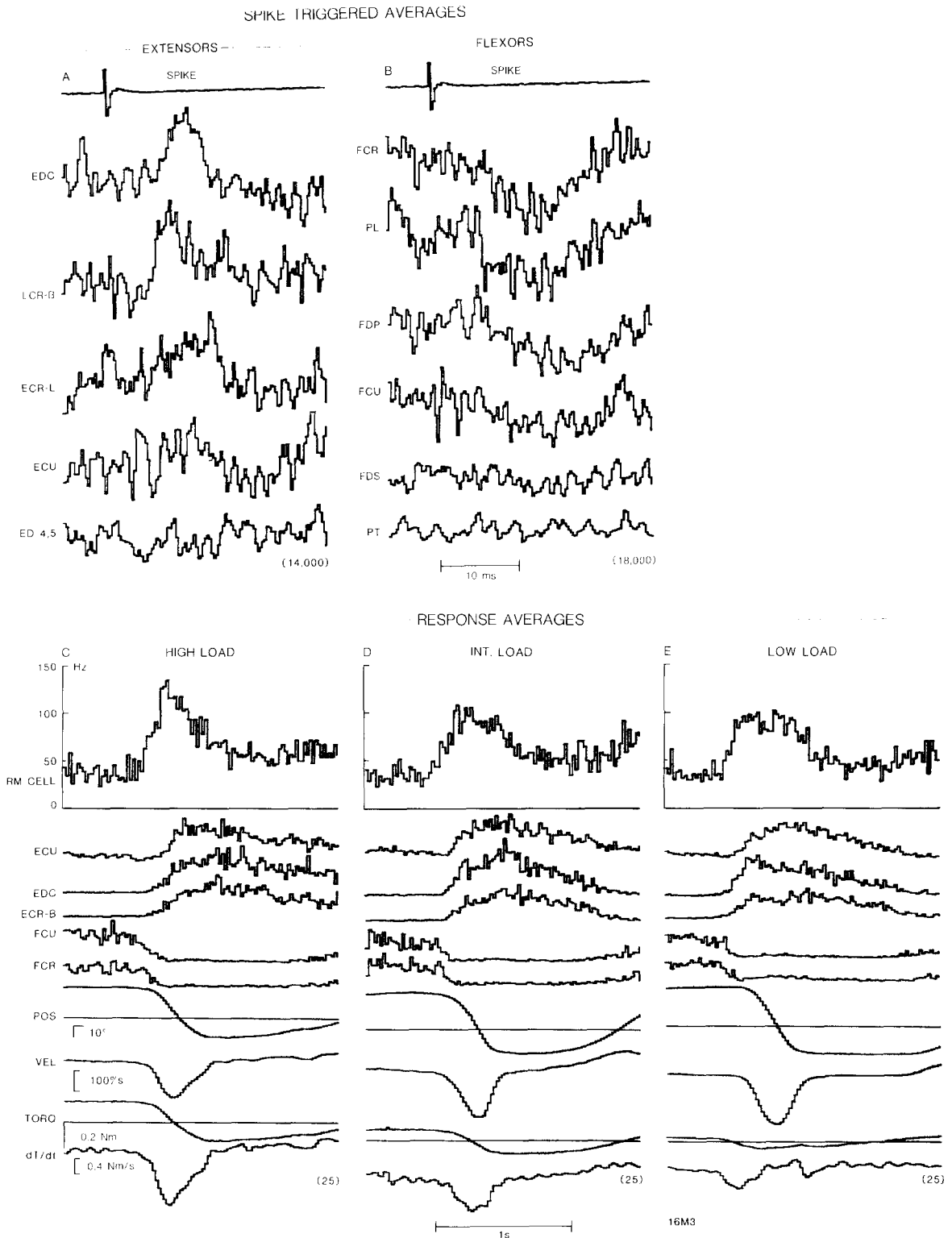


Fig. 1. RM cell spike-triggered averages and discharge histograms in relation to 3 different loads opposing wrist extension. Numbers in parentheses represent the number of events averaged. Note reciprocal output pattern: PSF of multiple extensors (A) and suppression of multiple flexors (B). Response averages show a phasic-tonic pattern for this RM cell. Phasic component for flexion not shown. Note that tonic component is related to static torque and phasic component is best related to dT/dt .

cell which facilitated 4 extensor muscles (agonists) and suppressed 4 flexors. Response averages show that the cell discharged in a phasic-tonic pattern for wrist extension and had a sustained tonic discharge during flexion. Pure facilitation cells facilitated their agonist muscles but had no detectable effects on the antagonists. The remainder of the output cells produced either mixed postspike effects in different agonist muscles (unpublished observations), pure suppression of antagonists⁹ with no effect on agonists, or, paradoxically, reverse effects⁹: facilitation of the antagonists or suppression of agonists. Although no CM cell facilitated both extensor and flexor muscles, we did find 3 RM cells whose output effects were best characterized as co-facilitation of agonists and antagonists. These effects were relatively weak, however, and this category must remain provisional until more convincing examples are documented.

Timing of discharge onset

The discharge of pyramidal tract neurons is well known to precede the onset of movement and agonist muscle EMG activity²⁵. We also measured CM and RM cell onset times, from response averages of EMG and force, during self-paced movements (10 ms time resolution). The timing of CM cell discharge relative to target muscle EMG was different for cells with different discharge

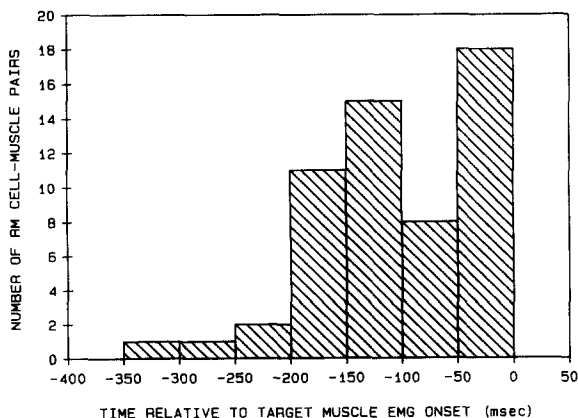


Fig. 2. Timing of discharge onset relative to onset of target muscle EMG activity for 19 wrist movement-related RM cells yielding 56 RM cell-PSF muscle pairs. Mean onset time was -96 ms. Measurement resolution was 10 ms.

patterns⁶. The mean onset times for phasic-tonic, tonic, phasic-ramp and ramp cells were -71 , -63 , $+5$ and $+101$ ms respectively (Table I). The overall mean onset time of all CM cells was -54 ms, considerably greater than the PSF latency. The onset of RM cell discharge also preceded the onset of target muscle EMG activity as illustrated in Fig. 2. The discharge of all RM cells either preceded (91%) or was coincident with (9%) the onset of target muscle EMG activity; the mean onset time was -96 ms.

Patterns of cell activity in relation to ramp-and-hold wrist responses

Four patterns of cell discharge in relation to ramp-and-hold wrist movements were found for CM cells: (1) phasic-tonic (59% of CM cells); (2) tonic (28%); (3) phasic-ramp (8%); and (4) ramp (5%)⁶. For a given cell, these patterns were the same during both auxotonic and isometric responses. Characteristic features of CM cell discharge included a clear, load-dependent, static component of discharge associated with the hold phase of wrist movement, and no sustained background discharge in the absence of movement or during the antagonist phase of movement. No pure phasic CM cells were found.

In contrast, RM cells showed more prominent phasic patterns. The types of response patterns of RM cells in relation to ramp-and-hold movements were: (1) phasic-tonic (52% of RM cells); (2) pure phasic (30%); (3) tonic (9%); and (4) unrelated or suppression (9%) (Table I). Five of the six pure phasic cells were bidirectional; only one was unidirectional. The phasic component of all phasic-tonic cells was bidirectional. Of the 17 bidirectional cells, only one had equal phasic components for both flexion and extension. The remainder were preferentially active for movements produced by their target muscles (15 for extension and one for flexion).

Relations to static torque

A prominent characteristic of CM cells is the presence of a load-dependent tonic firing rate in association with the hold phase of the task. Cheney and Fetz⁶ found that all CM cells exhibited a range over which their discharge rate

was linearly related to the static torque to which the cell's target muscles contributed. The mean rate-torque slope for extension-related CM cells (480 Hz/Nm) was about twice that of flexion-related CM cells (250 Hz/Nm).

A total of 63% of the RM cells had a significant tonic component of discharge (Table I) and in all these cases the tonic firing rate increased with increasing static torque (9 extension cells and 1 flexion cell). One of these cells is illustrated in Figs. 1 and 3. Relations to static torque were determined from response averages of unit firing rate and torque such as those in Fig. 1. Representative averages are shown for 3 different load levels. These records illustrate that as the monkey

generated greater static torques toward extension, the tonic discharge increased. This is clearer in Fig. 3A which plots the tonic firing rate, against static torque measured during the torque plateau. Both parameters were measured as the mean over a 0.5 s segment of the record beginning 0.5 s after the peak of movement. The rate-torque slope of this cell was 139 Hz/Nm.

Although the tonic discharge of phasic-tonic and tonic RM cells, like CM cells, was related to static torque, it should be emphasized that the mean RM cell rate-torque slope was only about half that of comparable CM cells (Table I). Also, the variability of data points in these plots was generally greater than for CM cells. The cell

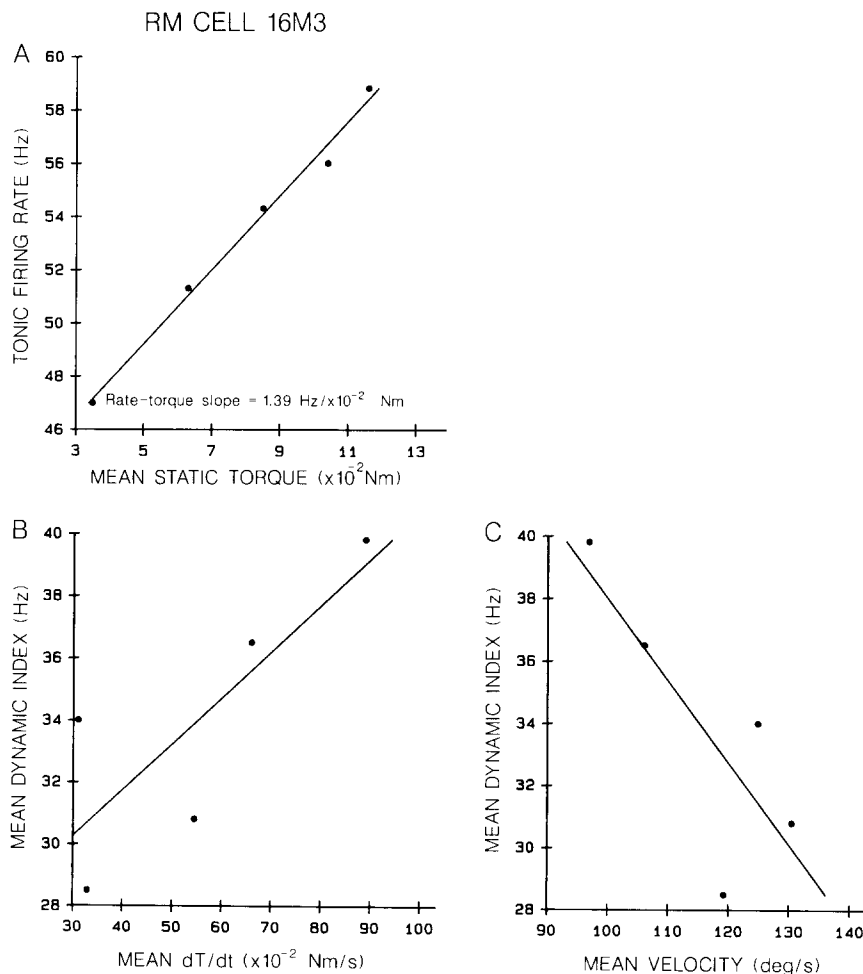


Fig. 3. Parametric relations for RM cell illustrated in Fig. 1. All measurements were from response averages such as those in Fig. 1. A: plot of tonic discharge rate against static torque ($r = 0.97$). B: plot of dynamic index (mean phasic firing rate minus tonic firing rate) against mean rate of torque change (dT/dt) ($r = 0.55$). C: plot of dynamic index against movement velocity ($r = 0.65$).

illustrated in Fig. 3 was exceptionally clear with a correlation coefficient of 0.97.

Relations between phasic discharge and movement dynamics

Movement dynamics in the auxotonic task were characterized by measuring both the velocity of movement and the rate of change of torque (dT/dt). Of course, for a given external load under auxotonic conditions, velocity and dT/dt will covary. Consequently, it is necessary to systematically change the external load to determine whether a neuron's phasic discharge is better related to velocity or dT/dt . We previously found that the phasic discharge of 50% of CM cells tested was related to dT/dt . The possibility that these cells or the unrelated cells might have encoded movement velocity was not specifically examined; however, this seems unlikely, since the phasic component of discharge was undiminished during isometric responses, in which movement velocity was negligible or zero.

The phasic discharge of RM cells was examined by plotting both mean and peak velocity and dT/dt , measured from response averages at different external loads, against corresponding values for mean and peak RM cell discharge rates. The phasic component of the cell illustrated in Fig. 1 was best related to dT/dt . Going from low loads to high loads, the velocity records in Fig. 1 show a clear decrease, and dT/dt a clear increase. The firing rate histograms of the RM cell show that the phasic component of discharge also increased with load; hence it was directly related to dT/dt but inversely related to velocity. These relationships were confirmed by plotting the dynamic index of the cell (mean phasic discharge minus the tonic discharge) against mean velocity and dT/dt (Fig. 3). The same result was obtained using peak phasic activity. These relationships were further confirmed in scatter plots of RM cell dynamic index versus peak velocity or dT/dt measured from 50–200 individual trials.

If the phasic component of discharge of some RM cells is genuinely related to movement velocity, then it should be absent or greatly reduced during isometric responses. Indeed both cells tested in this way showed substantial reductions in the phasic component of activity during isometric responses.

In summary, while it is true that most (85%) wrist-related RM cells have a clear phasic component of discharge in relation to auxotonic movements, the dynamic parameter (velocity or dT/dt) to which this component of discharge is best related seems to differ for different cells. From our analysis, 4 of 15 cells (27%) with a phasic component of discharge were best related to movement velocity; 4 were best related to dT/dt , and the remainder did not correlate reliably with either velocity or dT/dt .

Responses to passive wrist movements

Sensory input to CM and RM cells was examined by using the torque motor to move the wrist passively through ramp-and-hold displacements with the monkey inactive. The absence of muscle contraction was confirmed in averages of EMG activity. Most CM cells (17 of 19) responded at short latency (<30 ms) to passive movements which stretched the cell's target muscles⁷. Of the responsive cells, 10 were unidirectionally sensitive and 7 were bidirectionally sensitive. Two cells were unresponsive to these passive wrist movements (although they facilitated wrist muscles).

The majority of RM cells also responded to passive wrist movements (11 of 13). However, in sharp contrast to CM cells, all 11 RM cells were bidirectionally responsive. Six cells showed responses of similar magnitude for passive extension and flexion, and 5 responded more strongly for passive extension. The extensors were the target muscles for all of these RM cells. Although 3 RM cells showed PSF in both extensors and flexors and were tentatively classified as co-facilitation cells, in 2 of these 3, PSF in extensors was stronger than flexors. Thus, we conclude that RM cells tend to respond best to passive movements which shorten their target muscles, whereas CM cells tend to respond best to passive movements which stretch their target muscles.

DISCUSSION

Postspike effects

Postspike effects from RM cells were similar to those of CM cells in most respects. Reciprocal and pure facilitation patterns of output organization were the most common. The number of

muscles facilitated or suppressed were comparable for both RM and CM cells, and the onset latencies of RM and CM postspike effects were similar after adjusting for differences in conduction distance. The mean RM-PSF was weaker than the CM-PSF, but the magnitudes of PSS were virtually the same. The most striking differences between CM and RM postspike effects was the strong preference of RM cells for extensor muscles. A total of 87% of RM cells facilitated extensor muscles exclusively or most strongly; whereas 53% of CM cells facilitated extensors. This strong preference of RM cells for extensor muscles was also evident in the output effects observed with stimulus-triggered averaging^{8,9}. At 12 of 14 (96%) extensor RM cell sites where single pulse intrarubral microstimulation was applied, facilitation was exclusively or predominantly of extensor muscles. At 2 sites where the RM cell facilitated predominantly flexors, poststimulus facilitation was still largest in extensors. Nevertheless, at present, we cannot completely rule out the possibility that a focus of flexion RM cells was 'missed' in our penetrations. This bias toward extensor cells is consistent with the findings of Gibson et al.^{13,14}; 90% of their magnocellular red nucleus cells related to active movements at the metacarpal-phalangeal joint were related to extension.

Timing of activity relative to target muscle EMG

Although existing reports of motor cortex cell onset time differ quantitatively, all seem to agree that the average onset of discharge precedes the onset of movement and the onset of agonist muscle EMG activity²⁵. This is true of motor cortex cells in general, as well as identified pyramidal tract cells and identified CM cells^{6,12,25}.

In contrast, studies of the timing of red nucleus cell activity in relation to active movement have yielded less consistent results. Padel and Steinberg²⁴ reported that red nucleus cell discharge began 30–160 ms after the onset of forepaw movement in contact-placing in the awake cat. Otero et al.²³ reported that 78% of cat red nucleus cells related to a ballistic forelimb extension movement changed their firing rate after

the onset of EMG activity in task-related muscles. On the other hand, Ghez and Kubota¹⁶ and Ghez and Vicario¹⁵ found that cat red nucleus cells began discharging before the first increase in force in an isometric elbow extension task; the mean onset time was –34 ms. Amalric et al.¹ also found that red nucleus cell discharge leads the onset of movement in a reaction time task in the cat. The reasons for these discrepancies remain unclear although task differences could certainly be a factor.

Onset times obtained in monkey studies are also conflicting. Fromm et al.¹² report that the majority of red nucleus neurons start discharging at the onset of large movements or later, whereas Otero²² and Gibson et al.¹⁴ found that the discharge of most magnocellular red nucleus neurons (97% in Gibson et al.) preceded the onset of movement. In our sample, the mean onset of RM cell discharge led the onset of target muscle EMG activity by 96 ms (Fig. 2), comparable to the time of 80 ms reported by Gibson et al.¹³. Although the late onset times reported by Fromm et al.¹² remain puzzling, it seems reasonable to conclude that most rubrospinal and certainly most RM cells begin discharging before the onset of activity in their target muscles.

Relation to static torque

Most authors have noted the phasic nature of rubral cell discharge. Ghez and Vicario¹⁵ reported that only 2 of 24 neurons in the cat showed tonic activity related to static load and Fromm et al.¹² found only 3 of 79 such neurons in the monkey. Gibson et al.¹⁴ found no cells that were clearly influenced by increasing the load against which the monkey worked. Our results indicate that this phasic bias is also characteristic of rubromotoneuronal cells: 63% of RM cells had a significant tonic component of activity in relation to the hold phase of the task, whereas all CM cells showed a clear sustained discharge during the static hold. Although the tonic component of discharge of these RM cells was related to static torque, the rate-torque slopes were only 10% (flexion cells) and 26% (extension cells) of CM rate-torque slopes (Table I). Therefore, our data are consistent with those of others in showing that

RM cells are much less involved in the specification of sustained, constant muscle contraction than are CM cells.

Relation to dynamic aspects of movement

Although most experimenters agree that the discharge of red nucleus neurons is best related to the dynamic features of movement, it remains unclear which parameter is the best descriptor of discharge. Ghez and colleagues^{15,16} studied an isometric task in the cat and concluded that red nucleus discharge is related to dF/dt . In contrast, Burton and Onoda³ found that the discharge of elbow flexion-related red nucleus neurons in the cat correlated best with velocity. Similarly, Gibson et al.^{13,14} studied non-isometric movements in the monkey and concluded that the best descriptor of magnocellular red nucleus discharge was velocity. However, Fromm et al.¹² noted that their red nucleus cells discharged most intensely with the acquisition of small targets requiring small but very accurate movements. This was true even though the velocity of the small movements was much lower than that of large movements, so that their cell discharge was actually inversely related to velocity. In none of these studies, however, were both movement velocity and torque (or force) systematically measured or independently varied. Using auxotonic movements against different loads, we were able to test relations to both velocity and torque. In our sample, RM cells were equally divided between those whose discharge was best related to velocity and those best related to dT/dt . About half of the RM cells tested did not show a consistent relation to either velocity or dT/dt . In two cases, we examined the discharge in relation to isometric contractions (in which velocity was minimal) and found that in both these cases the phasic discharge of the RM cell was greatly reduced, confirming a component related to velocity. The range of velocities available from our average records was relatively small, raising the possibility that with a larger range, the results would more clearly favor velocity. Nevertheless, measurements of velocities from many individual responses have yielded a 3–5-fold range of velocities and the results of this analysis have supported the conclusions derived from

average records. Therefore, we conclude that the phasic activity of the RM cell population is clearly related to the dynamics of movement but is a mixed signal in which some neurons encode velocity and others encode dT/dt .

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