J. Physiol. (1985), **358**, *pp.* 527–549
With 1 *plate and* 11 *text-figures*
Printed in Great Britain

MAGNOCELLULAR RED NUCLEUS ACTIVITY DURING DIFFERENT TYPES OF LIMB MOVEMENT IN THE MACAQUE MONKEY

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(*Received 23 December 1983*)

SUMMARY

1. Three hundred and thirty-four neurones located in the magnocellular division of red nucleus (r.n.m.) were studied in three alert macaque monkeys. These cells had low discharge rates at rest and produced high frequency bursts during movement.

2. Single cells were selectively active for movement of one body part, and a motor somatotopy was evident. From dorsal to ventral we encountered cells related to movements of the face, contralateral upper limb, contralateral lower limb and, in one case, the tail. Free-form tests indicated that 76% of upper-limb cells were preferentially related to hand and finger movements, and 84% of lower limb cells were preferentially related to foot and toe movements.

3. Quantitative tests of movement relations were based on depths of modulation in discharge rate recorded while the monkeys operated several devices that served as manipulanda in a tracking task; each device elicited a different movement. We conducted 220 tests on eighty-one cells using eleven devices. The modulation in discharge rate exceeded a 50 pulses/s criterion level in seventy-nine cases; eleven were well related to proximal movements, twenty-two to movements of the digits and forty-six to a co-ordinated hand movement elicited by a device called the twister.

4. Both unidirectional and bidirectional patterns of bursting were frequent. A few cells showed reciprocal patterns consisting of a large increase in rate for one direction of movement and a small decrease for the other.

5. The bursts in discharge preceded movement onset (97% of 132 cases) by an average of 135 ms. Electromyographic activity in forearm muscles preceded movement by about 55 ms.

6. In some cases we recorded from a single cell while the monkey operated two, three or four devices. Depth of modulation on the twister device was twice that on a proximal device in nine cases whereas one case showed a proximal device preference; five cases showed overlap. Comparison between twister and digits yielded ten cases of twister preference, four of digit preference and twenty cases of overlap.

7. A directional preference was found for ten out of eleven cells responsive during active movement restricted to the metacarpo-phalangeal joints, and in all cases the preferred direction was extension.

8. Responses to natural somatosensory stimulation were weak or absent for the majority of cells. When present, sensory fields were confined to the same limb but were frequently out of register with motor fields.

9. Discrete extension movements of fingers or toes were elicited at low levels of electrical stimulation through the micro-electrode with more proximal movements being recruited at higher levels.

10. The results suggest that the magnocellular red nucleus is preferentially related to movements of the hand and foot. The presence of large bursts of discharge that begin before movement and the absence of appreciable responses to sensory stimuli is consistent with a role for this nucleus in the transmission of motor commands.

INTRODUCTION

The mammalian red nucleus is divided into a parvocellular and a magnocellular division (cf. Massion, 1967). The parvocellular division projects to the inferior olive, whereas the magnocellular division, which is the subject of the present study, is a source of long descending fibres to the spinal cord. The major inputs to the magnocellular red nucleus (r.n.m.) are from two motor centres, the cerebellum and the motor cortex, and the output fibres cross the mid line before descending as the rubrospinal tract (Brodal, 1969). Sites of termination in the spinal cord overlap those of the corticospinal tract. Rubrospinal fibres terminate among interneurones and laterally placed motor neurones (McCurdy, Hansma, Houk & Gibson, 1984) which in turn innervate distal muscles (Kuypers, Fleming & Farinholt, 1962). Stimulation within the r.n.m. causes discrete contractions of limb muscles acting about the shoulder, elbow, wrist and digits (Ghez, 1975; Larsen & Yumiya, 1980). These findings suggest that the r.n.m. might control limb movements, and this suggestion is supported by the results of lesion studies.

Monkeys with lesions that interrupt most of the descending pathways while sparing the rubrospinal tract are unable to control posture, but when propped up, they are able to use their arms and hands to retrieve food objects (Lawrence & Kuypers, 1968*b*). Conversely, section of either the pyramidal tract or the rubrospinal tract causes a loss of hand use which recovers over a period of time; however, section of both of these pathways leads to a permanent deficit in hand use (Lawrence & Kuypers, 1968*a*, *b*). Recent lesion studies in cats also support a role for the r.n.m. in the control of digit movements (Sybirska & Gorska, 1980).

There have been several micro-electrode studies of r.n.m. discharge during active movement, but in no case has an attempt been made to determine the type of movement to which r.n.m. activity is best related. In the monkey, neural discharge has been recorded during a button-pushing task (Otero, 1976), during wrist movements (Cheney, 1980) and during forearm rotation (Fromm, Evarts, Kroller & Shinoda, 1981). The majority of neurones were found to discharge after movement onset which prompted the suggestion that the r.n.m. controls movement termination rather than movement initiation (Fromm *et al.* 1981). In the cat, neural discharge has been recorded during elbow or whole limb movements. In the case of the elbow-movement task, discharge consistently led movement (Ghez & Kubota, 1977), whereas discharge usually lagged in the tasks involving whole limb movements (Padel & Steinberg, 1978; Otero & Lamas, 1982). We considered that these inconsistencies in timing relations might be related to the fact that neural discharge was being compared to different movements in the different experiments. However, this possibility is difficult to

evaluate since there has been no comparative study of the nature and extent of r.n.m. involvement in different types of limb movement.

The results described here provide a comparative analysis of r.n.m. unit activity for movements involving different proximal and distal joints. We sampled single cell discharge while monkeys made free-form movements to gain a qualitative impression of movement relations. However, our main innovation was to record discharge while the animals operated different manipulanda that exercised different forelimb movements. The results indicate that most r.n.m. neurones are preferentially related to movements of the hand and fingers as contrasted to movements about the wrist and more proximal joints, and discharge occurs in advance of movement. In the following paper (Gibson, Houk & Kohlerman, 1985) we describe detailed correlations that exist between the patterns of single cell discharge and the parameters of individual movements. Preliminary reports on these studies have appeared previously (Kohlerman, Gibson & Houk, 1980; Kohlerman, 1982; Kohlerman, Gibson & Houk, 1982).

METHODS

Subjects

Three male monkeys served as subjects for the single unit recording studies presented in this and the following paper. Monkeys F and H were rhesus (*Macaca mulatta*) and M was a cynomolgus (*Macaca fascicularis*). Electromyographic (e.m.g.) recordings were made in a fourth cynomolgus (subject T) trained in the tracking task but not used for the single unit studies described here.

Behavioural control

The monkeys were initially trained to attend to a tracking display on an oscilloscope screen. They used a simple manipulandum to move a cursor into a target zone defined by two horizontal lines in order to receive a water reward. Next, they learned to follow moving targets, and, finally, they learned to use different manipulanda coupled to the same tracking display. The subjects received their daily water intake during training or testing. After each session, the animals were allowed additional water until they refused to drink. The monkeys consumed normal amounts of chow, showed growth throughout the testing period and never showed signs of dehydration.

The various manipulanda were designed to exercise different arm and hand movements (Fig. 1). Panel *B* shows a monkey operating a push–pull device that required co-ordinated movements of the whole arm involving shoulder, elbow and gripping hand movements. This particular device was servo driven by force feed-back and presented an inertial load several times greater than the equivalent inertia of the limb. The other devices were passive mechanisms that did not appreciably load the movements; all had a small amount of friction, and some had a weak elastic restoring force. The devices were designed to isolate movements behaviourally without the necessity of constraining the forelimb during task performance.

A shoulder–elbow device consisted of a lightweight extendable strut with a potentiometer mounted at the pivot point. Fig. 1*A* shows how the pivot point could be positioned so as to isolate relatively pure elbow movements. Repositioning the pivot point and lengthening the strut yielded a device for studying relatively pure movements about the shoulder joint. The handle for this device was freely rotating which permitted a steady grip that minimized hand movements.

A device we called the twister operated like a motor cycle throttle; it required a co-ordinated hand movement that involved motion about wrist and finger joints (Fig. 1*C*). During clockwise rotation of the twister, the wrist flexed. Another device (Fig. 1*D*) was designed to study relatively pure wrist movements; during operation of this device upper arm movements were minimized by providing a platform upon which the subjects rested their forearms. Hand and finger movements were minimized by the freely rotating handle design.

Several devices were used to study digit movements; in all cases the forearm was supported on a platform to minimize upper arm motion. Palmar squeeze and release were studied with a fluid-filled

rubber tube connected to a pressure transducer. Manipulatory movements of the fingers were studied by requiring the animal to operate a potentiometer knob. Co-ordinated movements of the four fingers in flexion (F) and extension (E) were studied with a depressable platform mechanism; another device isolated relatively pure movements about the metacarpo-phalangeal joints of the four fingers (Fig. 1*E*). A thumb device (Fig. 1*F*) yielded relatively isolated movements of that digit.

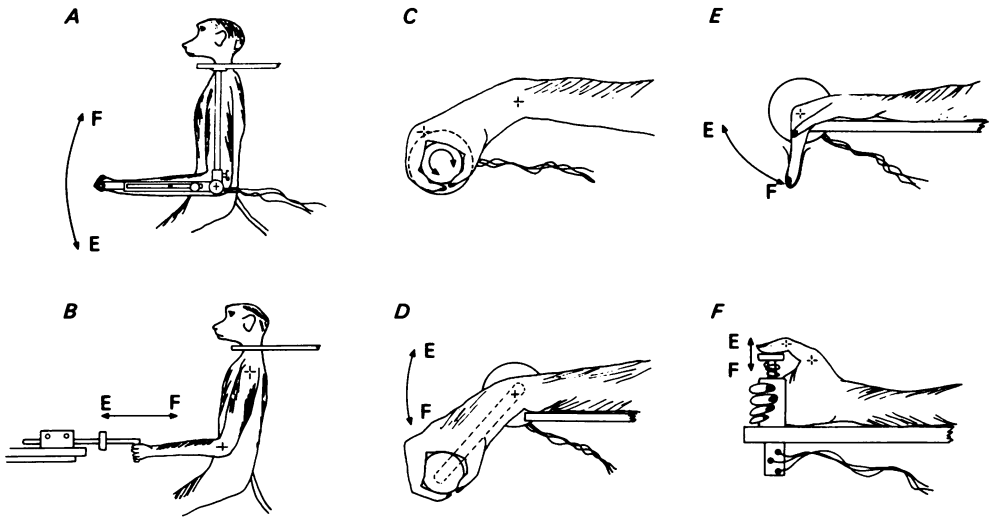

Fig. 1. Devices used as tracking manipulanda. *A*, relatively isolated movements about the elbow or shoulder joint were studied using the shoulder–elbow device; the arrangement shown is for elbow movement. *B*, the push–pull device required the monkey to make co-ordinated whole arm movements. *C*, the monkeys operated the twister similar to a motorcycle throttle using a co-ordinated hand movement involving wrist and finger joints. *D*, relatively pure wrist movements were studied on this wrist device. *E*, the metacarpal device isolated movements about the metacarpo-phalangeal joints of the hand. *F*, monkeys flexed and extended the thumb to operate the thumb device.

E.m.g. recording

The electrical activity of several forearm, back and chest muscles (biceps, triceps, wrist flexors and extensors, latissimus dorsi, pectoralis major and deltoid) were sampled while monkey T operated the twister. Pairs of 12 μm Teflon-coated, stainless-steel wires were inserted into the muscle bellies using 25 gauge hypodermic needles. The wires were bare for 1–2 mm at the tips. The signals were amplified differentially, filtered with a 50–500 Hz band width and sampled at 1 kHz along with movement records.

Micro-electrode recording and histological localization

Following training the animals were deeply anaesthetized with sodium pentobarbitone, and a Narishige chronic recording chamber was implanted under aseptic conditions over an opening in the skull (Evarts, 1968). The chamber was positioned about 6 mm anterior of Horsley–Clarke zero and angled off the mid-line vertical. The implant was fastened onto the skull using 0–80 stainless-steel machine screws covered with a cap of dental acrylic. Immediately after the implant, a daily routine of cleansing the skin margins and chamber interior, followed by application of povidone iodine (a non-irritating antiseptic), was begun. The animals were housed unrestrained in the standard monkey colony and showed normal behaviour and eating patterns within 48 h following surgery. The animals remained healthy throughout the course of testing and showed no evidence of any generalized infection.

Recordings were made with Epoxylite-coated tungsten micro-electrodes. Impedances of 0·2–1 MΩ

seemed to offer the best compromise between selectivity and recording stability. Single units were held for 15 min to over an hour. Accurate stereotaxic co-ordinates were maintained by using an optical zeroing device that allowed us to cross-reference electrodes in three planes. The optical zeroing device consisted of a 50× microscope mounted on an electrode zeroing stand. The microscope tube could be swung between stops located 90 deg apart so that an optical reference (a cross-hair reticle) was available in both the A–P and M–L planes. After the desired electrode co-ordinates were set on the Narishige drive, it was positioned on a carrier mounted to a stereotaxic arm on the zeroing stand. The electrode tip was then centred on the cross-hairs and the stereotaxic co-ordinates of the arm were recorded. The stereotaxic co-ordinates provided a record of relative co-ordinates of all electrodes and allowed accounting for variations in micro-electrodes as well as co-ordinate settings.

Histological examination of Cresyl-Violet-stained frontal sections confirmed the accuracy of our recording sites. Before perfusion, the subjects were anaesthetized with a lethal dose of sodium pentobarbitone administered intravenously. After breathing had stopped and eye-blink reflexes were absent, the heart was exposed and the aorta cannulated. An initial flush of physiological saline was then followed by perfusion of 10 % formalin. An electrode was then positioned in the brain using the Narishige drive, and the brain was removed and blocked along the plane of the electrode. After storage in 30 % sucrose/formalin, the brains were frozen and sectioned at 40 μm.

In subjects F and H both red nuclei could be reached with the same chamber placement, as shown for H in the low-power photomicrograph of Pl. 1 *A*. Heavy gliosis is apparent along the electrode tracks that approach the r.n.m. at a 25 deg angle, and two lesions made by passing -10 μA for 20 s can be seen in the right r.n.m. The dorsal lesion (only faintly visible in this section) was placed where we recorded neural activity related to contralateral hand movements, and the ventral lesion was placed where we recorded activity related to contralateral foot movements. A total of 120 penetrations were made in subject H with the tracks being concentrated mainly in the caudal 2·5 mm of r.n.m.

In subject M, the first chamber did not allow us to reach both r.n.m., and a second chamber was mounted on the other side of the head. Plate 1 *B* shows tracks approaching at 30 deg angles from both sides and heavy gliosis at the cross-over point just dorsal to the oculomotor nuclei. A total of eighty-six tracks were run. Arm-related areas of the r.n.m. were preferentially studied in this subject, and heavier gliosis in the arm areas suggests an over-all stereotaxic accuracy better than 250 μm. Marking lesions were also recovered in the magnocellular region of this animal. No attempt was made to study the more anterior parvocellular regions of red nucleus in these monkeys.

In addition to stereotaxic co-ordinates, physiological landmarks along a penetration were quite distinctive and served as a guide to the recording site. Penetrations to the r.n.m. from the opposite side of the brain passed through the oculomotor nucleus (o.c.n. in Pl. 1) which has characteristic burst–tonic discharge related to eye movements. For about 1 mm beyond the o.c.n. there was relative quiet with occasional eye movement related cells. The r.n.m. was then entered and was easily identified by the vigorous activity elicited as the subject reached for food or other objects. The depths at which various nuclei were encountered could be predicted to about 100 μm accuracy from the optical zero calibration of the electrode. In penetrations where the ipsilateral r.n.m. was targeted, we relied mainly on stereotaxic depth, though saccade-related bursting was sometimes recorded just before entering the r.n.m.

Data collection and analysis

Target shifts, data collection and the delivery of reward were co-ordinated by a PDP-11 computer (Digital Equipment Corporation). Each trial was preceded by a foreperiod the duration of which was randomly varied from 1·0 to 1·5 s. The procedure effectively eliminated anticipatory responses as verified in the behavioural records. The foreperiod also served to establish a steady base line of activity at the starting position, and, if the monkey moved out of the target zone, a new foreperiod was initiated. Data collection began 0·5 s before a change in target position, and usually continued for an additional 3·5 s. Manipulandum position was sampled at 100 Hz and the interspike intervals of a single unit were recorded with 0·1 ms accuracy. Drops of water were delivered as a reward after the monkey successfully responded to the stimulus by moving to the new target position within a prescribed response time (typically 1 s) and holding that position for 400 ms. On most trials, the monkeys made prompt and rapid movements, though they were not required to do so.

Fig. 2 provides an example of data collected during an individual trial. The second trace shows an extracellular recording. The larger of the two units was discriminated with a level detector, the output of which triggered a programmable clock that timed interspike intervals. The plot of instantaneous discharge rate (upper trace) was generated from the interspike interval record. The integrated spike plot shown as the third trace was also derived from the interspike interval record.

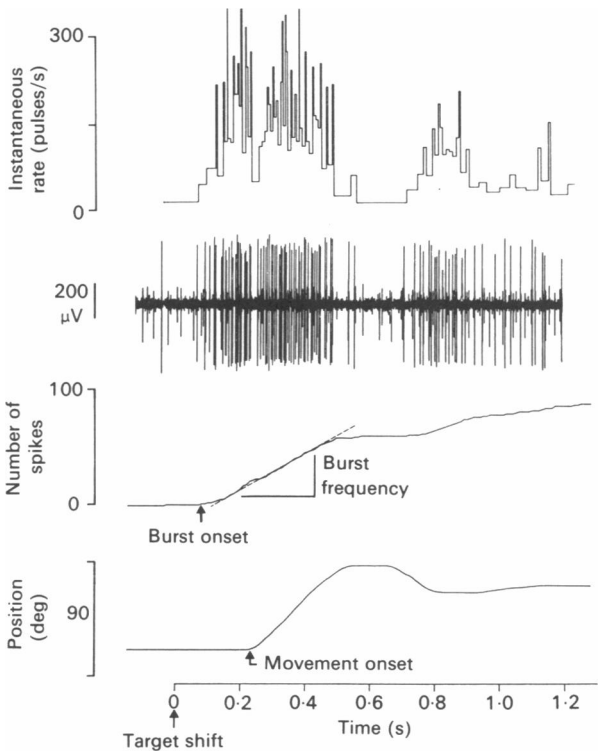

Fig. 2. Example of data collected during a single trial, showing activity of cell H120 during anticlockwise twister movement. Second trace shows a micro-electrode recording of action potentials; the large unit triggered a programmable clock that generated computer records of interspike interval. These records were stored and used later to produce plots of instantaneous discharge rate (top trace) or integrated spike plots (third trace). The latter, which are simply cumulative counts of the number of spikes, facilitated the measurement of burst onset (inflexion point) and average burst discharge rate (slope) from individual trial data records. The bottom trace shows a record of movement derived from the output of a potentiometer attached to the twister. The tracking target shifted to a new position at time zero, a burst of r.n.m. discharge began 90 ms later and the movement began after a 240 ms reaction time.

It is simply a cumulative count of the number of spikes *versus* time; this calculation adds no distortion while effectively smoothing out spike-to-spike variations in interspike intervals thereby facilitating the analysis of single trials. The slope of the integrated spike record provided a reproducible measure of the average firing rate during bursts of discharge that occurred in association with movement (Fig. 2). The onsets of bursts of activity were readily estimated from inflexion points in the integrated spike records (Fig. 2). Movement onsets were estimated in a similar manner from inflexions in position traces and subtracted from burst onsets to determine values of lead time.

The measurements of discharge rate were used to calculate two additional parameters. The depth

of modulation, which is the difference between discharge rate during movement and the resting rate in the pre-stimulus interval, was used as an index of the strength of the relation between cell discharge and a particular movement. For the majority of cases, the mean values of depth of modulation were calculated from five trials on a particular device. Though this procedure disregards the dependence of discharge rate on movement velocity documented in the following paper (Gibson *et al.* 1985), this is unlikely to have caused much error. Trials in which the movement was slow or small in amplitude were not used to estimate depth of modulation. An index of directional specificity was calculated by dividing the depth of modulation in the non-preferred direction by

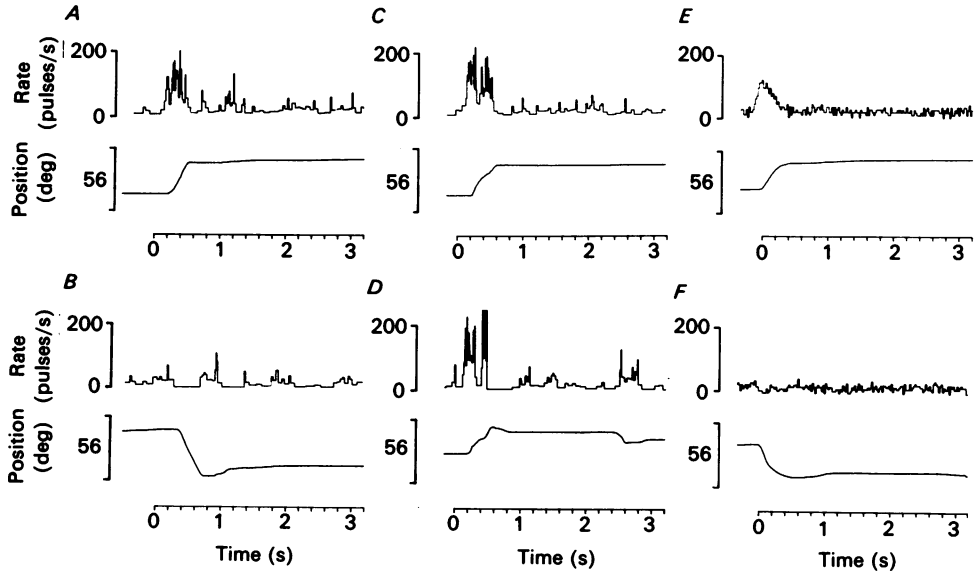

Fig. 3. Comparison of individual and averaged trial data for cell H60. In each panel instantaneous frequency records are shown at the top and movement traces at the bottom. Individual trials in panels *A*, *C* and *D* show bursting activity related to anticlockwise twister movement. One trial (panel *B*) shows a cessation of activity related to twister flexion. In *C* and *D*, note the correspondence between segmented components of movement and bursting activity. Average responses calculated from six anticlockwise and eight clockwise trials are shown in panels *E* and *F* respectively.

that in the preferred direction and subtracting the resultant value from 1. A value of 1 indicates that the cell fired in one direction of movement only, a value of 0 signifies equal discharge in both directions and a value >1 indicates a reciprocal relation, an upward modulation in one direction and a small decrease or cessation of activity in the other. Cells with indices $>0{\cdot}5$ were considered to show directional specificity, whether unidirectional or reciprocal.

Average responses were calculated from data files that contained a number of similar movements. An interactive display program was used to align a cursor to movement onset, and this information was inserted as a synchronization point into the record header. An averaging program then sorted the processed trials according to category, formed peristimulus time histograms aligned to movement onset and calculated the corresponding averages of analog records. Panels *A*, *C* and *D* in Fig. 3 show three trials of anticlockwise twister movement and the bursts in r.n.m. activity that preceded each movement. Note that the segmented movements in panel *C* and *D* are associated with a corresponding segmentation in the discharge pattern of the cell. Panel *B* shows a single trial of movement in the opposite direction and the decrease in discharge that preceded it. Panels *E* and *F* show the average responses in the two directions for the cell.

Electrical stimulation

A relay in the pre-amplifier stage allowed us to switch between record and stimulate modes. Cathodal pulse trains (10–120 μA, 50–200 μs pulses, 100–500 Hz) lasting between 40 ms and 2 s were delivered to the red nuclei of two monkeys (H and M) in the course of twenty penetrations. The number of stimulus pulses varied from 4 to 800. Current levels were monitored using a current probe.

Responses to stimulation were corroborated by at least two investigators. Positive responses were observed most readily if the monkeys were relaxed and motionless before stimulation. Threshold currents were determined for all positive repeatable responses. To normalize for variations in pulse width, frequency and duration of the stimulus train, as well as stimulus intensity, the total charge (in μC) delivered to the tissue was calculated and used as an index of stimulus strength. After stimulating, the pre-amplifier was switched to record mode to verify (by recording normal extracellular action potentials) that no tissue damage had occurred at the site of stimulation.

RESULTS

A total of 334 neurones were studied that were located within or near the anatomical boundaries of the magnocellular portion of the red nucleus (r.n.m.), determined histologically as described in the Methods. Since all large cells in r.n.m. send their axons to the spinal cord (Kneisley, Biber & LaVail, 1978; Castiglioni, Galloway & Coulter, 1978; Hayes & Rustioni, 1981), we presume that most of these units were rubrospinal neurones. A few may have been cerebellothalamic fibres which are known to course directly through the r.n.m., but this number is likely to have been small since most units tuned over large distances (50–200 μm) and had large action potentials (0·4–2 mV) with the characteristic negative–positive or positive–negative configurations that are typical for cells (Walsh, Houk & Mugnaini, 1971; Humphrey, 1979). Single units were distinguished by a constancy of their wave form.

The general search procedure was to advance rapidly to within approximately 1 mm of the nucleus, and then to advance slowly while the monkey worked on one of the manipulanda. We frequently interrupted the task to have the monkey make reaches for bits of food. Most units discharged at spontaneous rates of 15 ± 10 pulses/s when the animals sat motionless and showed dramatic increases in discharge rate during active movements. These features facilitated the isolation of units and made it likely that our population sample was representative.

Relations derived from free-form tests

Early in the course of these experiments it became obvious that r.n.m. neurones fired well during some phase of reaching for food with the contralateral limbs. We then attempted to design free-form tests that separated movements into proximal and distal categories. Distal movements were elicited by having the subjects work food out of small wells or grooves similar to those used by Brinkman & Kuypers (1973). Proximal movements were elicited by blocking the return of the food to the mouth so that the monkey would have to make evasive arm movements while holding the food in the hand. A typical r.n.m. neurone fired in high frequency bursts during the distal test and returned to low spontaneous rates during the proximal test. Similar tests were implemented for movements of the foot and leg. Movements of the jaw were observed during chewing, but these could not be dissociated from tongue and facial movements. At least two observers were present during testing, and discharge

was judged by listening to unit activity on an audio monitor. Some of the tests were recorded on video tape and reviewed in slow motion.

Of 235 cells recorded in the forelimb zone of r.n.m., 179 (76%) were judged to be related to the hand or fingers, and the remaining 56 (24%) were judged to be related to movements about more proximal joints of the contralateral limb. These figures probably underestimate the percentage of hand-related units since our earliest observations, particularly for subject F, were sometimes designated arm without sufficient attempt to distinguish proximal and distal categories; these ambiguous cases were included in the proximal category. Of the 68 cells recorded from the hindlimb zone, 57 (84%) were judged to be related to the foot or toes, and the remaining 11 (16%) were related to contralateral knee or hip movements. Mouth or facial relations were seen for twenty-eight neurones, tail for one and trunk for one.

The correlation of recording depth with the results of free-field testing indicated rather clear separations between different somatotopic zones of the r.n.m. In eighty-four out of eighty-five penetrations in which both forelimb and hind-limb zones were encountered, the former was dorsal to the latter. Another frequent sequence was mouth–forelimb seen in forty-eight penetrations; in nine of the latter, forelimb units were also encountered dorsally yielding a forelimb–mouth–forelimb sequence. A complete mouth–forelimb–hind limb sequence was seen in twenty-eight penetrations. The single tail unit was found below a hind-limb zone.

Discharge during tracking

Initial training and testing in the manual tracking task for subjects F and H was with the push–pull device (see Methods). Previous studies had reported r.n.m. discharge in relation to various arm movements (Otero, 1976; Ghez & Kubota, 1977; Burton & Onoda, 1978; Fromm *et al.* 1981), and since push–pull operation required movement about both elbow and shoulder, we anticipated that many r.n.m neurones would fire well with this task. Instead we found few cells that modulated consistently during tracking. Visual inspection of the hand that held the manipulandum handle revealed that vigorous bursting often occurred when the monkey adjusted its grip on the handle in the absence of overt arm movement. Free-form testing usually confirmed our impression that activity was better related to hand and finger movement than to movement about the shoulder and elbow joints.

It was at this stage of our study that additional devices were constructed to serve as manipulanda and subject H (and later M) was trained to track with them (see Methods; Fig. 1). In this manner we tested for relations between r.n.m. activity and a variety of movements about both distal and proximal joints. Fig. 4 shows examples for three cells of individual trial records that were obtained during performance on three of the eleven devices used in these experiments. Discharge generally occurred in high frequency bursts that began and ended before movement onset and offset respectively (Fig. 4*A* and *E*). Cell activity never changed in relation to target movement alone. For a few units the elevation in rate trailed on into the holding phase of the movement before decaying back to base-line levels (Fig. 4*C* and *F*). We found no significant tonic changes in rate associated with different holding positions.

The average depth of modulation of unit activity (see Methods) was used as one

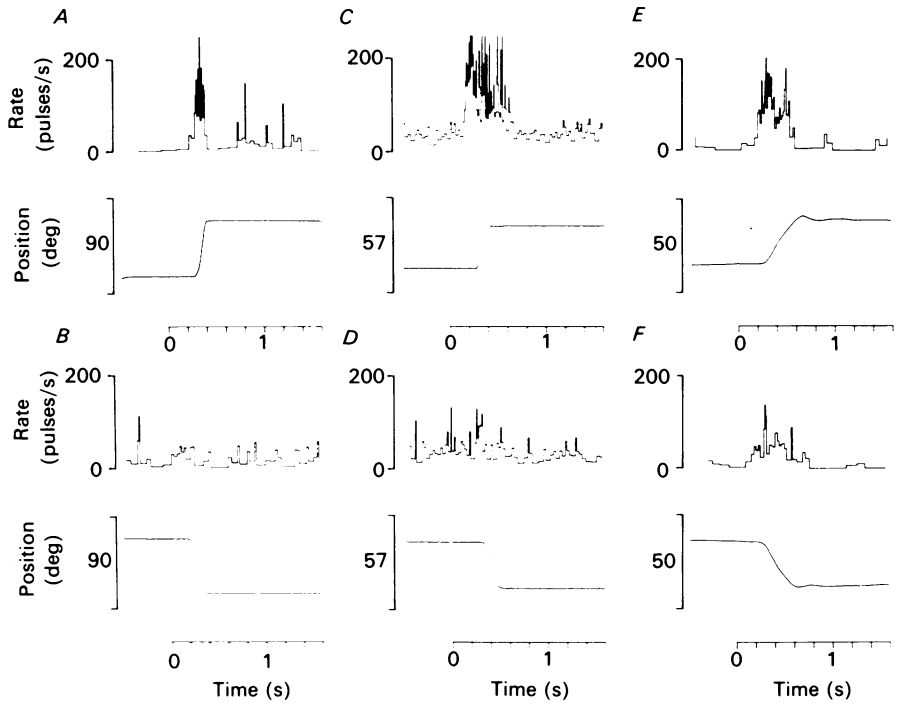

Fig. 4. Examples of discharge patterns observed during individual tracking movements. *A* and *B*, unit H106 showed a unidirectional pattern; it fired preferentially to extension of the metacarpal device. *C* and *D*, unit M37 was also directionally specific (clockwise twister motion), but its burst trailed into the holding phase of the movement. *E* and *F*, unit H83 discharged in a bidirectional pattern; it was one of the few units which showed consistent relations to movements on the elbow device. A reciprocal pattern of discharge is illustrated in Fig. 3*A* and *B*.

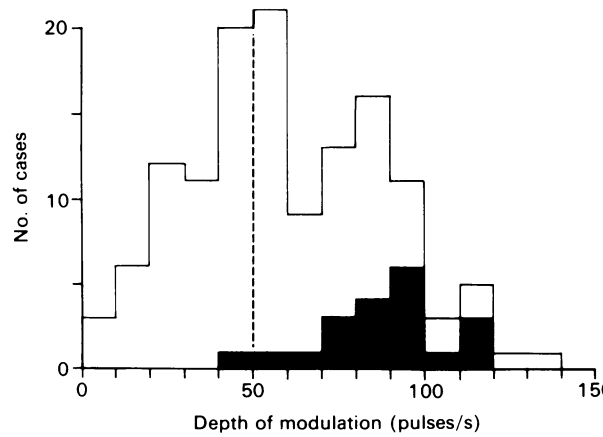

Fig. 5. Distribution of mean values of depth of modulation. The histogram summarizes the results of 132 cases in which a cell responded during performance on one of the eleven tracking devices (Table 1). Only values for the preferred direction of movement are included in this histogram. Filled areas represent observations obtained from the top twenty cells based on parametric correlations with movement (Gibson *et al.* 1985). The dashed line indicates the 50 pulses/s criterion for well relatedness.

indicator of the degree to which a neurone was related to the particular movement being studied. Fig. 5 shows the distribution of depths of modulation in 132 cases studied for 81 neurones. Each case represents the average response of one cell studied on one device (some cells were studied on more than a single device). A depth of modulation in excess of 50 pulses/s was used as a conservative criterion for considering a cell to be 'well related' to the task.

TABLE 1. Responsiveness of r.n.m. cells studied during different types of forelimb movement

Device	*n*	>50 pulses/s	<50 pulses/s	Unresponsive cells
Push–pull	19	6	4	9
Shoulder	6	2	1	3
Elbow	13	3	7	3
Wrist	12	0	3	9
Total proximal	50	11	15	24
Twister	97	46	19	32
Knob	5	3	0	2
Squeezer	8	2	0	6
Finger	23	10	7	6
Phalangeal	6	1	3	2
Metacarpal	22	6	5	11
Thumb	9	0	4	5
Total digits	73	22	19	32

Columns: tracking device used to elicit movement; number (*n*) of cells studied on each device; number of cells with a depth of modulation exceeding 50 pulses/s; number of cells with modulation less than 50 pulses/s; number of unresponsive cells. Cells tested on more than one device will be included in more than one row.

Table 1 summarizes device relations of r.n.m. neurones based on the 50 pulses/s modulation criterion. The 220 total cases are divided into three main movement categories: (i) performance on devices requiring movement about the wrist and more proximal joints (shown at the top of the Table); (ii) performance on devices requiring movement of the digits (shown at the bottom of the Table), and (iii) performance on a particularly successful device called the twister (shown in the middle). Operation of the twister required a co-ordinated movement that involved both wrist and fingers. We therefore listed it at an intermediate point in the proximal to distal gradient in Table 1. For seventy-nine cases in which modulation was in excess of 50 pulses/s, forty-six (47 % of the cells tested) occurred with the twister, twenty-two (30 %) with devices requiring movements of the digits and eleven (22 %) with devices requiring movements about more proximal joints.

Some units discharged only for one direction of movement (Fig. 4*A–D*), others showed bidirectional patterns (Fig. 4*E* and *F*) and a few showed reciprocal patterns with upward modulation in one direction of movement and a small decrease or cessation of activity in the other direction (Fig. 3*A* and *B*). We did not encounter cells with high resting rates and graded downward modulation except in one case that was attributed to damage discharge. Fig. 6 shows the distribution of directional

indices (see Methods) calculated for the 132 responsive cases represented in Table 1. A value of 0 represents a symmetrical bidirectional response and 1·0 indicates a purely unidirectional response. The large number of cases lying between 0 and 1 represent partially bidirectional responses and the few above 1 represent reciprocal responses showing a large upward modulation in the on direction and a small decrease in the

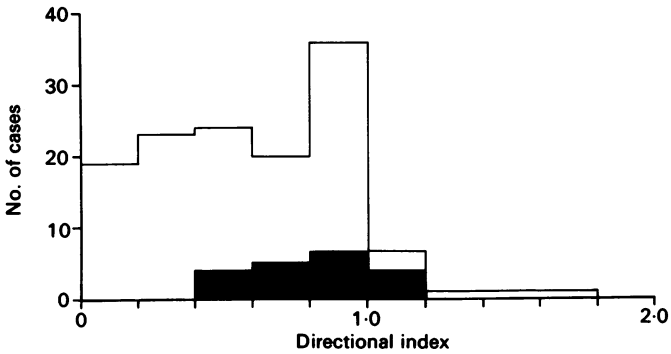

Fig. 6. Distribution of directional selectivity for the 132 responsive cases illustrated in Fig. 5 and Table 1. Filled areas represent observations obtained from the top twenty cells based on parametric correlations with movement (Gibson *et al.* 1985).

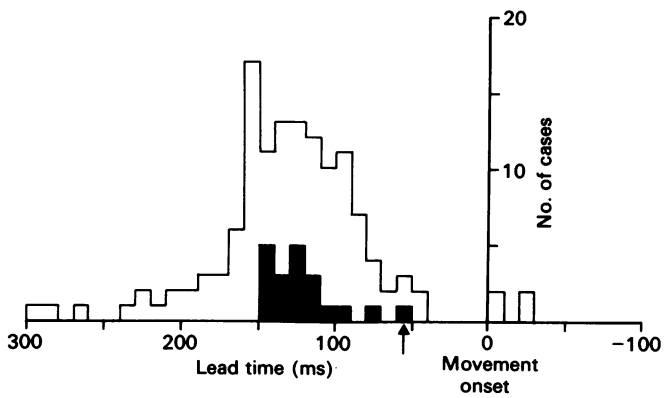

Fig. 7. Distribution of mean lead times for the 132 responsive cases illustrated in Figs. 5, 6 and Table 1. The arrow marks the onset of forearm e.m.g. activity as recorded during performance on the twister. There were only four cases in which burst onset lagged movement onset (negative values on abscissa). Filled areas represent observations obtained from the top twenty cells based on parametric correlations with movement (Gibson *et al.* 1985).

off direction. The sample of well-related cases had higher directional indices than did cases in which modulation was less than 50 pulses/s ($0{\cdot}67 \pm 0{\cdot}30$ *versus* $0{\cdot}54 \pm 0{\cdot}41$, $P < 0{\cdot}05$). When the observations were further subdivided into proximal, twister, and digit categories, well-related twister observations stood out as having the largest directional indices ($0{\cdot}73 \pm 0{\cdot}31$). The other groups were indistinguishable and had index means in the range 0·5–0·59.

The onset of bursting began in advance of the movement for the vast majority of

units, as is the case for those examples illustrated in Fig. 4. Fig. 7 shows the distribution of mean lead times measured for the 132 responsive cases represented in Table 1. Most of the values lie in the 80–170 ms range. There was no significant difference between the lead times of well-related cases and those cases in which modulation was less than 50 pulses/s (135±45 *versus* 119±58 ms, $P > 0{\cdot}05$). When different movements were compared for the well-related cases, the longest lead times were found for performance on proximal devices (170±59 ms) and the shortest for digit devices (116±34 ms). The lead found for the twister was 135±41 ms.

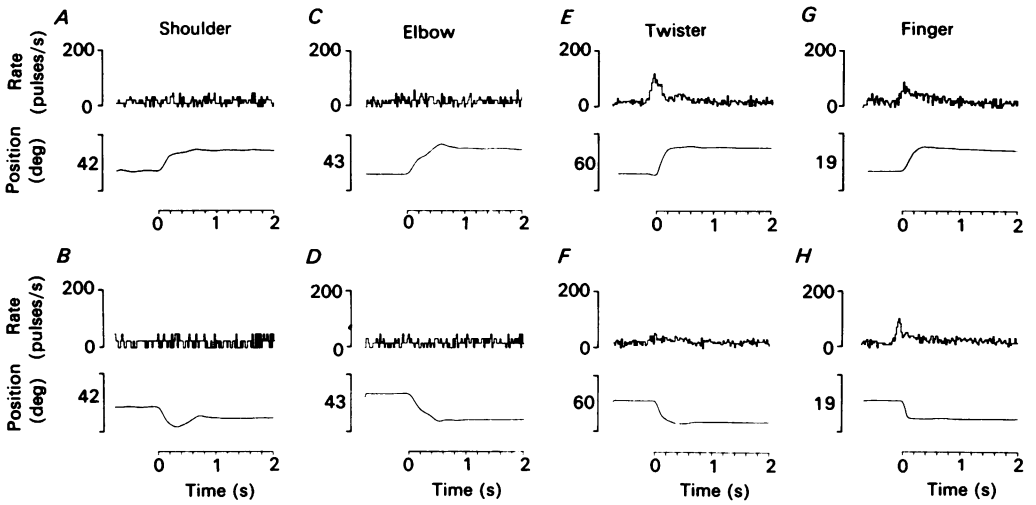

Fig. 8. Averaged responses of a cell (H77) that was studied on four devices. In each panel, the top trace is the averaged discharge rate, and the bottom trace is the averaged movement record. Two directions of movement are illustrated for each device. This cell was inactive during performance on the shoulder (*A*, *B*) and elbow (*C*, *D*) devices. It fired in a unidirectional pattern (clockwise preference) on the twister (*E*, *F*) and it was also active during finger flexion (*G*) and extension (*H*). (Number of trials in averaged records *A*–*H*: 4, 2, 4, 3, 9, 10, 8, 6.)

Device comparisons

In some cases we were able to record from the same neurone while the monkey operated more than a single device. The data collected for a cell that was studied on four devices are summarized in Fig. 8 by histograms aligned to movement onset. There was essentially no modulation in discharge rate during movements of the shoulder and elbow in either flexion or extension, nor was there modulation during anticlockwise twister motion. The largest modulation occurred with clockwise twister motion (80 pulses/s), and there was also a bidirectional response during performance on a finger device. Only three cells were held sufficiently long for testing on four devices, but twenty were tested on three devices and forty-three on two.

From the group of twenty-three cells tested on three or four devices, fourteen were suitable for a three-way comparison of activity on a proximal device, the twister and a digit device. Among these, nine showed appreciable activity on at least one of the tested devices, and the depths of modulation for these cases are listed in Table 2. Five

cells (36 %) were not active on any of the devices, though all fired vigorously during free-form tests. For this comparison, the push–pull device was excluded since hand and finger involvement along with the shoulder and elbow was frequent, as noted earlier. Similarly, we excluded results with the knob from the digit category since this device was not as effective as the other in isolating movements of the digits.

TABLE 2. Depths of modulation for cells tested on three or four devices

Cell no.	Shoulder	Elbow	Twister	Finger
H83	70	100	10	20
H78	—	70	120	70
H76	—	40	30	70
H97	—	30	50	20
H73	—	30	40	20
H80	0	20	80	40
H72	20	—	40	30
H82	—	10	30	110
H77	0	0	80	80

Numbers in the Table represent mean values of depth of modulation calculated from at least five movement–response pairs. The values were then rounded to the nearest 10 pulses/s.

TABLE 3. Movement preferences based on depths of modulation during performance on two devices

Proximal preference	Overlap cases	Twister preference
1	5	9
Digit preference	Overlap cases	Twister preference
4	20	10

The preference entries indicate cases in which the depth of modulation was at least two times greater during performance on the preferred device.

Though the sample is small, the entries in Table 2 echo the preference for twister and digit relations seen earlier in Table 1. These results further suggest specificity in the movement relations of a given neurone. Only one cell (H78) showed a large modulation for all three categories – proximal, twister and digit. One cell was relatively specific for proximal movement, two for digit movement and three for performance on the twister. The remaining two were quite active on both twister and digit devices and relatively inactive on proximal devices.

The degree of specificity between proximal and twister relations and between twister and digit relations was more fully analysed by including additional cells studied during performance on two devices. In Table 3 the 'preference' entries indicate cells for which the depth of modulation was at least two times greater during performance on one of the two devices, whereas the 'overlap' entries represent cells for which depths of modulation were large on both devices. The proximal–twister comparisons indicate a clear tendency for twister preference, with a minority of overlap cases. Digit–twister comparisons instead show a majority of overlap cases, and the preferences are distributed in both digit and twister categories.

Twister and finger relations

The previous sections show that many of the strongest relations between r.n.m. activity and movement were seen with the twister device. We therefore sought to analyse the individual joint motions contributing to twister movement and to explore r.n.m. relations to isolated movements about the contributing joints.

Operation of the twister appeared to involve motion at wrist and finger joints (Fig. 1*C*), with a lesser involvement of the elbow and shoulder. Electromyographic recordings obtained in monkey T (Fig. 9) showed large phasic activity in forearm

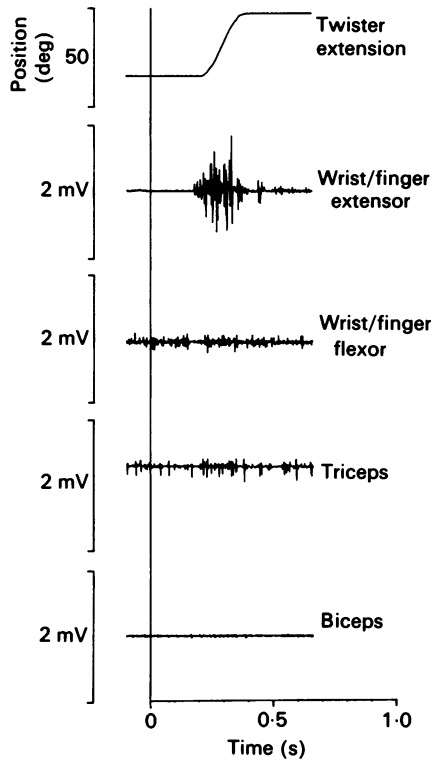

Fig. 9. E.m.g.s recorded from four muscles in monkey T during anticlockwise movement of the twister. Wrist/finger extensors in the forearm were activated 55 ms before movement onset. Neither the triceps nor the biceps showed phasic patterns of activity. Vertical line at time zero marks the onset of the target shift.

flexor and extensor muscles which contribute to both wrist and finger movement. In contrast, very little task-related activity was present in biceps, triceps and several shoulder, back, and chest muscles that were sampled (see Methods). Evidently motion about proximal joints was passive. The phasic bursts in forearm muscles occurred approximately 55 ms in advance of our estimate of movement onset, as illustrated in Fig. 9. This time is also marked by the arrow in Fig. 7 for comparison with lead times of r.n.m. cells. It appeared that the strong relations of r.n.m. activity to twister performance might be correlated with wrist or finger movements, or both.

The relation of r.n.m. activity to relatively pure movements about the wrist was assessed using the wrist device (Fig. 1 *D*; see Methods). During trials with this device there was a striking absence of any task-related activity of either single units or of background multi-unit activity, yet vigorous activity occurred when the monkey reached for food. We did manage to find three cells that showed some modulation (Table 1), but the largest was only 32 pulses/s. The example in Fig. 10 compares the large modulation of an r.n.m. cell on the twister with the lack of any significant modulation on the wrist device.

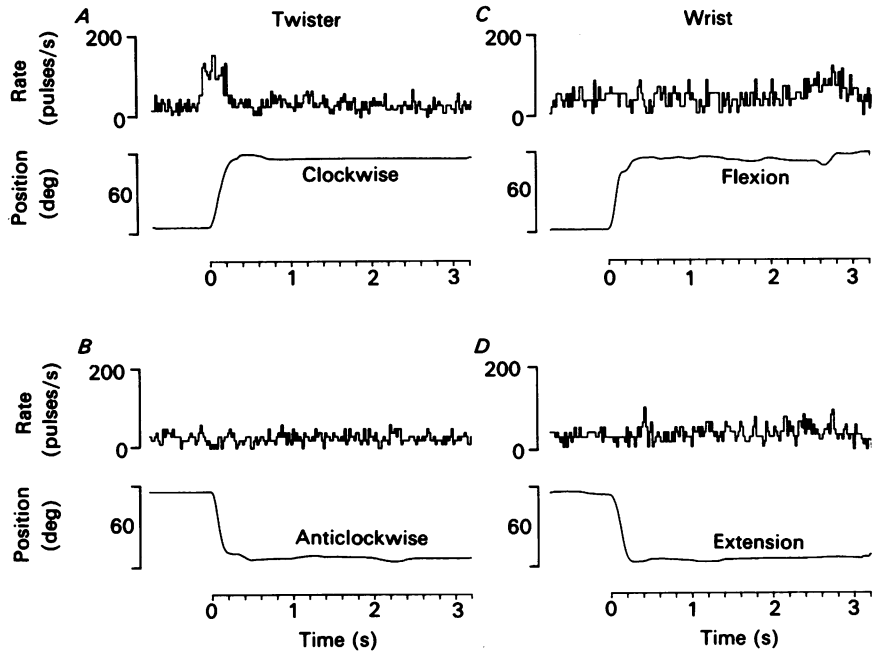

Fig. 10. Comparison of responses of cell H104 during performance on the twister and on the wrist device. All panels show average responses that were synchronized on movement onset (time zero). A large burst of discharge preceded clockwise twister movement (*A*) whereas no appreciable modulation occurred during isolated wrist movements (*C*, *D*). (Number of trials in averages *A*–*D*: 5, 5, 3, 4.)

The relation between r.n.m. activity and movement of the digits was studied using six different devices as listed in Table 1 and described in the Methods. Each of these devices was more successful in eliciting r.n.m. discharge than was the wrist device. The example in Fig. 11 compares the large modulation of an r.n.m. cell on the metacarpal device, which elicited movement about the metacarpo-phalangeal joint, with the much smaller modulation observed during performance on the wrist device (the largest response we saw using this device).

One of the most successful digit devices was the one designated 'finger' in Table 1. It elicited co-ordinated opening (extension) and closing (flexion) movements involving the metacarpal and phalangeal joints of all four fingers. Based on our sample of twenty-three cells studied on this device, 43% had depths of modulation above

50 pulses/s, 31 % showed smaller modulations and only 26 % were unresponsive. Five of the ten cells that modulated above 50 pulses/s showed strong directional preferences (directional index > 0·5), and for all of these, extension was the preferred direction. For two of the latter, performance on the twister was also directionally selective, and the preferred direction was clockwise rotation.

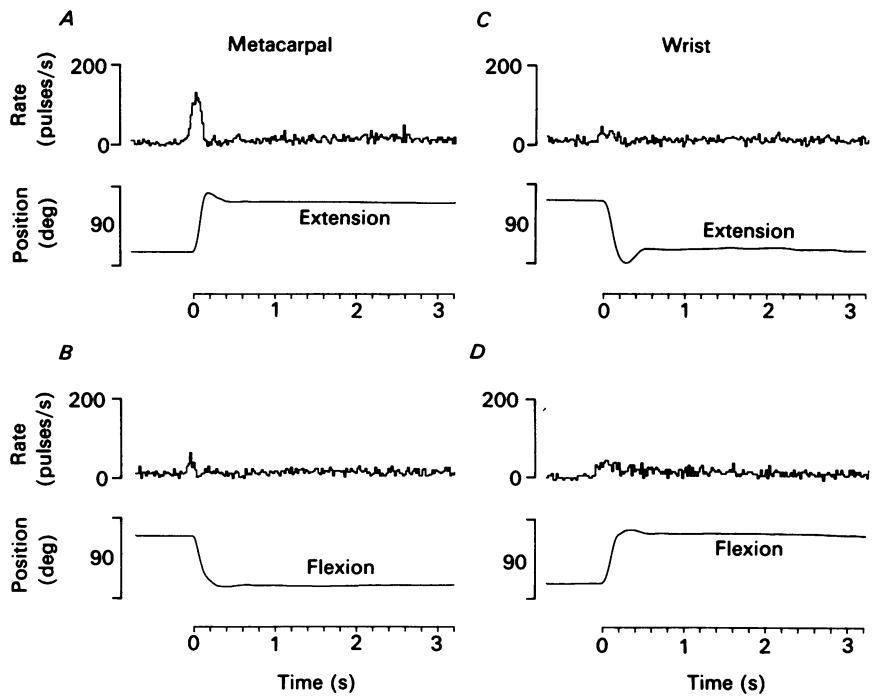

Fig. 11. Comparison of responses of cell H106 during performance on the wrist and metacarpal devices. All panels show averaged responses that were synchronized on movement onset (time zero). This unit was well related to metacarpal extension (*A*) and poorly related to isolated wrist movements. (Number of trials in average *A–D*: 15, 16, 14, 9.)

The metacarpal device elicited relatively pure movements about the metacarpophalangeal joints of the four fingers in combination. Based on a sample of twenty-two cells studied on this device, 27 % had depths of modulation above 50 pulses/s, 23 % showed smaller modulations and 50 % were unresponsive. All but one of the responsive cells showed a directional preference, and for all of these cases, extension was the preferred direction. For six of the latter, performance on the twister was also directionally selective, and in every case the preferred direction was clockwise rotation.

For two other devices that involved flexion and extension of the fingers, the directional preference was opposite to that on the finger and metacarpal devices. Flexion was the preferred direction for both directionally specific cases on the phalangeal device and for the single directionally specific case with the squeezer. The latter cell was also directionally specific on the twister and the preferred direction

was clockwise rotation. It should also be noted that directional preference for the twister was not always in the clockwise direction; from a sample of forty-four directionally specific twister cells, the preferred direction was anticlockwise for 34 %.

Sensory properties and responses to electrical stimulation

After studying a cell during tracking we often attempted to assess its sensory responsiveness and/or test for responses to stimulation at the recording site. The determination of sensory fields required much patience since the monkeys, though trained in tracking, never became well reconciled to sensory exploration. Reactions to touch and joint manipulation were frequent, and modulations related to these reactions could easily be confused with purely sensory responses. Repeated testing was used to habituate motor reactions.

The majority of cells showed weak responses or no response to sensory stimulation as contrasted with the strong modulations observed during active movement. A few cells were quite unlike the majority and showed appreciable sensitivity to touch or to joint rotation. Sensory responses were always confined to the limb showing motor relations. However, the fields were frequently large and out of register with the motor fields. For example, cells with distal motor relations often had either a proximal component or a purely proximal sensory field. Combined joint and cutaneous responsiveness was not uncommon.

In some cases, stimulation was delivered as a final test. We waited until the monkey had placed its limb in a relaxed posture, or had allowed us to support it. Movements were observed in 80 out of 151 stimulation attempts with currents in the range 10–120 μA. Since other stimulus parameters were also varied, the level of stimulation was assessed by a measure of charge that took into account variations in pulse width, pulse rate, train duration, and current intensity (see Methods).

The responses observed at or near threshold were localized to one body part in sixty-nine out of eighty cases, the others involving more global limb movements. Among the localized cases fifty-two were extension movements, only one was flexion and sixteen were not easily categorized as pure flexion or extension. Responses were always confined to the limb that had shown motor relations during tracking or free-form tests. In twenty cases movements of digits were produced, and they were all in the extension direction, or extension coupled with abduction. Often hand or finger movements were observed at threshold, and more global movements of the arm were added at higher stimulus levels. The average stimulus strength for eliciting movement was 0·12 μC for digits ($n = 23$), 0·51 μC for wrist ($n = 17$) and 1·28 μC for elbow and shoulder ($n = 17$).

DISCUSSION

Somatotopic organization

Our histological analysis of recording sites indicates that the present results deal exclusively with the magnocellular division of the red nucleus (r.n.m.). Within the r.n.m. we found a clear separation between dorsally located cells that fire during movements of the contralateral upper limb and ventrally located cells that fire during movements of the contralateral lower limb. This finding agrees with previous

descriptions of the somatotopic organization of the r.n.m. which have been based on other techniques. Anatomical studies have shown that the rubrospinal pathway is entirely crossed and that cells projecting to cervical and lumbar levels of the spinal cord are segregated respectively into dorsomedial and ventrolateral groups (Pompeiano & Brodal, 1957; Kuypers *et al.* 1962; Castiglione *et al.* 1978; Kneisley *et al.* 1978). Similarly, microstimulation of the r.n.m. produces discrete contractions limited to the contralateral forelimb at dorsomedial sites and limited to the contralateral hind limb at ventrolateral sites in both cats (Ghez, 1975) and monkeys (Larsen & Yumiya, 1980; Results). Sensory responsiveness, to the extent that it is present, also conforms to this general somatotopy (Ghez, 1975; Larsen & Yumiya, 1980; Results). Both stimulation and recording methods suggest the additional presence of small face and tail regions located respectively at the extreme dorsal and extreme ventral boundaries of the nucleus (Ghez, 1975; Larsen & Yumiya, 1980; Results).

Relation between discharge rate and type of movement

Within the upper-limb and lower-limb zones, different cells were found to be specialized for different components of limb movement with a heavy bias towards the most distal joints. Thus most cells discharged at their highest rates during hand or foot movements, but there were others that showed preferential activity during elbow or shoulder movements. Surprisingly, we did not find any cells that discharged above the 50 pulses/s criterion level during isolated wrist movements, though a larger sample probably would reveal some. The same was true for thumb movements, though in this case a few cells came close to criterion. It seems likely that most components of limb movement are represented in the r.n.m., but that the vast majority of cells are preferentially related to the most distal joints. This conclusion agrees well with the results of lesion studies (Lawrence & Kuypers, 1968*b*; Beck & Chambers, 1970; Schwartzmann, 1978).

The twister was the best device for evoking large modulations in r.n.m. discharge, and its efficacy appeared to result from an involvement of the fingers in this task. The potential involvement of elbow and shoulder muscles was excluded by e.m.g. recordings. While wrist motion was an important component of twister operation, cells active on the twister did not fire well during isolated wrist movements. In contrast, a large percentage (67 % from Table 3) of cells active on the twister fired well during performance on finger devices. This certainly points towards a finger involvement, but one must also account for the other third of the cells. One possibility is that these cells were related to types of finger movement that occurred during twisting but were not elicited by the particular finger device used. In support of such specialization, a small percentage of cells active on a finger device did not fire on the twister. However, another idea that warrants consideration is that cells in the r.n.m. may be specialized for the control of co-ordinated movements about several joints. This could come about if descending fibres of single r.n.m. neurones branch to activate many motoneurone pools and thus control co-ordinated movements involving several muscles.

The actual branching patterns of individual r.n.m. fibres have not been studied in the primate, though they have in the cat (Shinoda, Ghez & Arnold, 1977; cf.

Jankowska, 1978). Antidromic stimulation of local axon branches within the cervical grey matter suggested that branching to more than a single motor pool is frequent. Injections of neuroanatomical tracer confined to the forelimb region of r.n.m. do not reveal single fibre branching patterns, but they do show a widespread pattern of input to interneurones at all levels of the cervical cord (Robinson, Houk & Gibson, 1982). Interneurone axons in turn branch extensively (Czarkowska, Jankowska & Sybirska, 1976). This apparent evidence for anatomical divergence in the rubrospinal pathway in cats needs to be reconciled with the report that microstimulation in the same species evokes discrete contractions of individual muscles (Ghez, 1975).

Microstimulation in the monkey also evokes discrete contractions at threshold (Larsen & Yumiya, 1980; Results), and in our study threshold contractions frequently involved the fingers. However, there was a spread of activity to proximal muscles when either intensity or duration of stimulation was increased. This result coupled with the evidence for anatomical divergence might reflect a pattern in which strong input is focused upon a localized group of muscles and a weaker input diverges to neighbouring groups.

Directionality of responses

Cells in our sample showed predominantly unidirectional or bidirectional firing patterns. The prominence of bidirectional patterns may indicate that the muscles which are activated by these cells serve to stabilize a joint rather than functioning as a prime mover. This interpretation is based on the patterns of extensor carpi radialis activity observed by Hoffman & Strick (1980) during different directions of wrist movement. When the movement was in the plane of the muscle's action, the first agonist burst displayed a reciprocal pattern of activity. However, when the direction of movement was orthogonal to the direction of muscle action, the muscle was activated in a bidirectional pattern, thus serving to stabilize the joint. The occurrences of bidirectional and reciprocal patterns of motor cortical discharge in association with two-dimensional shoulder movements appear to be well explained by this mechanism (Georgopoulos, Caminiti, Kalaska & Massey, 1983).

The former discussion suggests that cases in which r.n.m. discharge is directional (either unidirectional or reciprocal) may be easier to interpret than bidirectional cases. Directional activity should correlate with the movement as recorded, whereas bidirectional activity might not be associated with any observable movement. Bidirectional patterns might also arise as a consequence of co-contraction of muscles that alternately promote or oppose the prime movement.

All cells that showed directional responses during metacarpo-phalangeal movements and during co-ordinated finger movements had preferences for extension. This may correspond to our finding that a large percentage of the responses to stimulation were finger extension (25%) whereas finger flexion was never seen. In contrast, the directional cells studied on a device requiring use of the phalanges fired preferentially during flexion. E.m.g. studies in human subjects have shown that the extensor digitorum is the active extensor muscle of the metacarpo-phalangeal joint, and that this muscle is also activated during flexion of the phalanges so as to prevent simultaneous flexion of the metacarpo-phalangeal joint (Long & Brown, 1964). This muscle may be an important target for input from a subset of r.n.m. neurones.

The directional preferences for cells studied on the twister are more difficult to interpret. The majority of the directional cells (66 %) showed preferences for clockwise rotation, and this group included cells that were also preferentially active during metacarpo-phalangeal extension. One might think that clockwise twister motion would be promoted by metacarpo-phalangeal flexion and not extension, but this may not be the case.

Timing of discharge

Our study is the first to report that r.n.m. activity consistently leads movement onset in the monkey (97 % of 132 cases). Previous investigators reported that discharge usually lags movement onset (Otero, 1976; Fromm *et al.* 1981) or that it lags in half of the cases (Cheney, 1980). One previous study in the cat reported consistent leads (Ghez & Kubota, 1977), whereas two others reported a majority of lags (Padel & Steinberg, 1978; Otero & Lamas, 1982). In two of the monkey studies (Otero, 1976; Fromm *et al.* 1981) no distinction was made between magnocellular and parvocellular regions of the red nucleus, so it might be postulated that recordings from parvocellular neurones account for the lags.

The reports of lag instead may have represented cases in which the monitored movements were different from the movements actually controlled by the sampled neurone. For example, Otero (1976) compared the timing of discharge with the onset of e.m.g. activity in a shoulder muscle for a task that required the monkey to extend its arm before using its hand and fingers to push a button. Though discharge usually lagged shoulder movement, it may have led hand and finger movements had these been monitored. In the pronation–supination task studied by Fromm *et al.* (1981), the delayed activity may have been related to an alteration of the grip on the handle as the monkey approached the precision target zone that they employed. The placing movement studied by Padel & Steinberg (1978) required the cat to flex its limb before setting its foot on a platform. Though discharge lagged limb flexion, it may have preceded contractions in digit muscles preparatory to placing of the foot.

We wish to emphasize that the above interpretations of prior data are tentative and meant only to represent possibilities that warrant further consideration.

Comparison of motor and sensory relations

Our free-form tests provided a good setting for comparing movement-related discharge with responses to natural somatosensory stimulation. There was a striking contrast between the high frequency discharge that accompanied movement and the weak responses or absence of response to touch or joint rotation that characterized the vast majority of cells. This finding of strong motor and weak sensory relations agrees with observations reported for the red nucleus in the cat (Ghez, 1975) and for the cerebellar interpositus nucleus in the monkey (Harvey, Porter & Rawson, 1979). The latter observations are quite relevant to the present results since the interpositus nucleus is the main source of input to the primate r.n.m. (Humphrey & Reitz, 1976; Humphrey, Gold & Reed, 1984). The report by Larsen & Yumiya (1980) stresses sensory responses of red nucleus cells, but these authors did not make comparisons with movement related activity.

In conclusion, the results presented here suggest that neural activity of the

primate r.n.m. is preferentially related to movements of the hand and fingers in the upper extremity and to the foot and toes in the lower extremity. Since the bursting patterns of discharge consistently begin before these movements and since discharge is relatively insensitive to somatosensory input, the r.n.m. seems more likely to transmit motor commands than feed-back-produced adjustments. Further evidence in support of this hypothesis is presented in the following paper.

We thank Dannie Hansma for preparing the illustrations and for other technical assistance, John Chelgren and Hank Jakiela for writing the data collection program and Philip Kennedy for assisting with electromyographic recordings. This work was supported mainly by grant R01-NS-14703 to Dr Houk; core support was provided by P01-NS-17489 to Dr Houk. Pilot studies were done in the Department of Physiology, The John Hopkins University Medical School, and were supported by NIH grant P01-NS-06828 to Dr Vernon B. Mountcastle.

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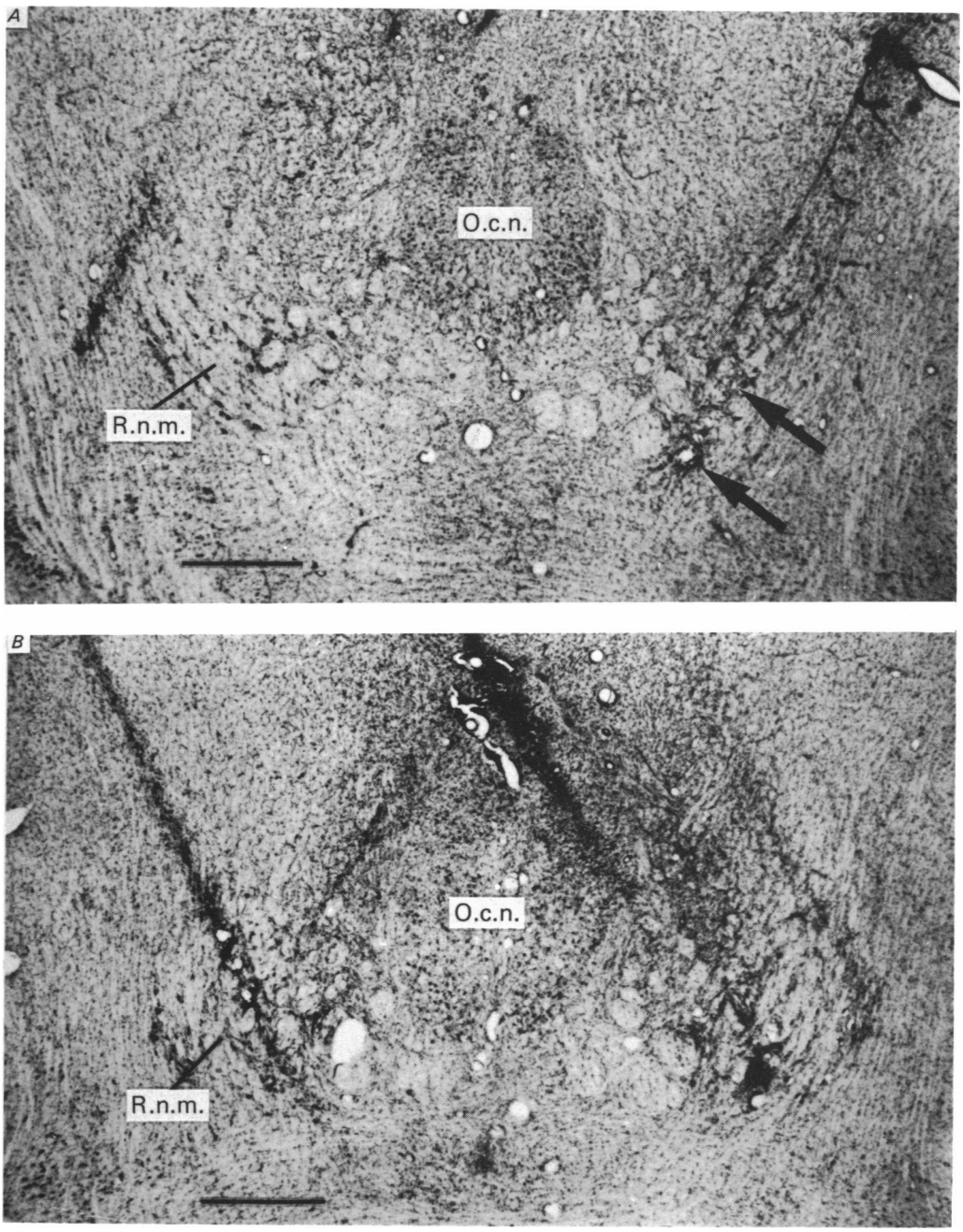
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EXPLANATION OF PLATE

Histological verification of recording sites. *A*, low-power photomicrograph of a 40 μm thick coronal section through a rhesus (H) monkey brain. Electrode track gliosis and marking lesions are seen in the hand (upper arrow) and foot (lower arrow) area of the right r.n.m. One chamber was used in this animal. *B*, photomicrograph of a 40 μm coronal section through monkey M's brain. Two chambers were implanted in this animal, and electrode tracks are seen approaching from both sites. O.c.n., oculomotor nucleus; r.n.m., magnocellular red nucleus. Scale bars indicate 1 mm.