

Relation of Pyramidal Tract Activity to Force Exerted During Voluntary Movement

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THIS REPORT DESCRIBES the third in a series of studies of the relation of discharge of pyramidal tract neurons (PTNs) to voluntary movement. The first of the previous studies (5) showed that PTN activity both at rest and during movement is related to axonal conduction velocity. PTNs with the highest axonal conduction velocities tend to be silent during motor quiescence and to show phasic activity in association with movement. PTNs with lower axonal conduction velocities are for the most part active even in the absence of movement; with movement they show both upward and downward modulation of their resting discharge frequency. A second study (6) was carried out to obtain information as to the point in the interval between stimulus and response at which PTN discharge takes place in association with a conditioned hand movement. It was found that for many PTNs, responses to the conditioned stimulus (the onset of a light) preceded the first peripheral electromyographic correlates of the conditioned response (wrist extension). The fact that these PTN responses preceded the electromyographic response showed that they were not consequent upon feedback resulting from the movement.

The present study was intended to answer a third question concerning the way in which PTN activity is related to movement: Is the discharge of PTNs related to the force exerted by the moving part, or does PTN activity more nearly parallel the displacement which results from this force?

METHODS

Training the monkeys

Three monkeys (*Macaca mulatta*) were trained to make alternate 30° flexion and extension move-

ments of the wrist for a fruit-juice reward. Juice was delivered only when the duration of the movement fell between certain time limits. These limits were narrowed as the monkey gained proficiency in carrying out the task. It was ultimately required 1) that the movement take more than 400 but less than 700 msec and 2) that each of two successive half cycles of the movement (flexion followed by extension or vice versa) be completed within the specified time limits. Thus, a movement (flexion or extension) taking 400–700 msec was not rewarded unless it followed a previous movement (extension or flexion) which had also taken 400–700 msec.

The apparatus used in the initial phases of training is illustrated in Fig. 1. A panel was attached to the front of the monkey's home cage and on this panel was mounted a tube through which the monkey placed its hand to grasp a vertical rod which could be moved back and forth through an arc of 30°. A string attached to the top of the rod passed over either of two pulleys, and to the end of this string a load was attached. The pattern of muscular activity required of the monkey depended on which of the two pulleys the string traversed. For one of the pulleys the force exerted by the load opposed wrist extension, acting to pull the wrist into the flexed position. In this situation both flexor and extensor displacements of the proper duration required that net force be exerted in the direction of extension. Even during the flexor displacement (when the load was being lowered) the extensors had to exert force to prevent the load from falling too fast, and as a result the predominant activity was in the extensor musculature. When the string passed over the other pulley the situation was reversed: the load now opposed flexor displacements and as a result both flexor and extensor displacements of the correct duration required that net force be in the direction of flexion.

During training both the magnitude of the load and the direction in which it acted were varied, and the monkeys learned to make displacements of the required duration independent of these variations. The apparatus was available to the monkeys constantly for the several months of the training period, and they usually carried out about 3,000

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cycles of the movement daily. The task was one which they took to readily, and when water was made available in a pan in the cage they would usually continue to operate the apparatus in order to receive the fruit-juice reward. Thus, virtually all of the monkey's liquid during a period of several months was earned by performance of the task. Only the right hand was trained and recordings were derived from the contralateral precentral gyrus.

Data acquisition

Unit recording was conducted with the monkey in a primate chair equipped with a manipulandum analogous to that described above. The vertical rod grasped by the monkey during flexion and extension was attached to a force transducer. The axle

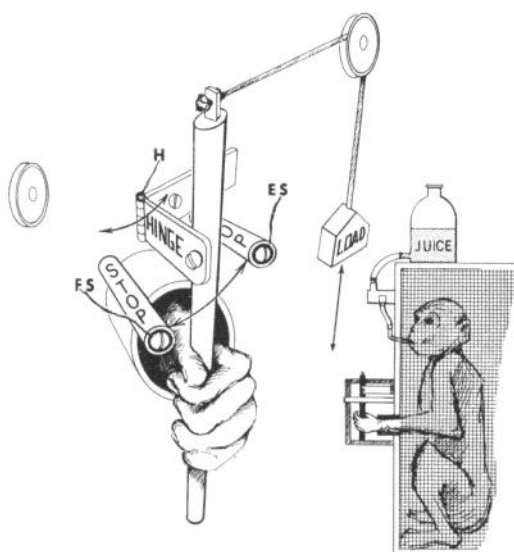


FIG. 1. Initial training was carried out in the monkey's home cage. Here the monkey's left hand is seen to be protruding from a tube in a Lucite panel attached to the front of the cage. In order to receive a fruit-juice reward, the monkey was required to grasp the vertical rod attached to a hinge and to move it back and forth from one stop to the other. The stops are labeled FS (flexor stop) and ES (extensor stop). The monkey was required to contact the flexor stop and then move the handle through the arc between the stops until the extensor stop was reached. If the period between breaking contact with the flexor stop and making contact with the extensor stop was between 400 and 700 msec, and if the previous movement in the other direction also fell within these time limits, the solenoid valve was automatically operated and a reward was delivered. A narrow slit, just large enough to accommodate the monkey's wrist, was placed so as to prevent side-to-side arm movements and require that movements of the handle result from alternate flexion-extension at the wrist.

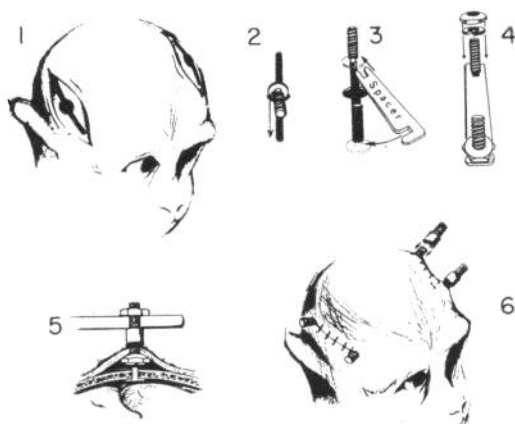


FIG. 2. As a first step in attachment of the head-fixation bolts, two openings were made in the skull, as shown in 1. In 2, the flat head of a bolt is being slipped into the large center orifice, and in 3 the two bolts have been inserted and a spacer is being placed so as to hold the bolts apart and provide a bearing surface for lock washers and nuts, which are shown in 4. Number 5 shows a cross section of the bolt, spacer, lock washer, and nut. Following attachment of bolts, the skin is closed, as shown in 6. For coupling the bolts to the fixation bar, as in 5, an extender is attached to each of the four implanted bolts.

which transmitted the monkey's force to the load was coupled to a position transducer.

The outputs from the force and position transducers were recorded on FM channels of magnetic tape.

About 1 month prior to unit recording, four bolts were attached to the monkey's skull as illustrated in Fig. 2. During unit recording head movements were prevented by attaching these bolts to the frame of the primate chair via ball-joint couplings. This method of eliminating head movements was painless to the monkeys, who performed their task and drank their reward quite readily under these circumstances. Monkeys were given about 10 days of experience carrying out the hand movement under conditions of head fixation prior to unit recording. During this period of adaptation they were placed in the primate chair each morning and returned to their home cage with a collar and leash attached at night. The monkeys learned to be quite cooperative in reentering the chair in the morning, since entrance into the chair was rewarded by the fruit juice of their choice (grape, apple, or orange).

Upon completion of training and adaptation the monkey was anesthetized and a 12-mm-diameter circular opening was made in the skull; the center of this hole was at Horsley-Clarke coordinates A12, L17. These coordinates were selected so as to place the opening over the precentral wrist area as identified by Woolsey (13). The dura was left in-

tact beneath this opening. A stainless steel cylinder of 10-mm internal diameter was attached to the bone at the margins of the circular opening. The method used to implant this cylinder is shown in Fig. 3. Electrodes to be used in eliciting antidromic responses for identification of PTNs were permanently implanted in the ipsilateral medullary pyramid as part of the same operative procedure. The method of Sheatz (11) was employed for this implantation.

During unit recording the stainless steel cylinder served as a support for a hydraulic microdrive. The microdrive was coupled to the steel cylinder by means of a circular adapter whose center was 2 mm eccentric to the center of the steel cylinder. This adapter accepted the circular base of the microdrive, whose microelectrode was in turn 2 mm eccentric to this circular base. These two 2-mm eccentricities (1: center of circular adapter with respect to center of steel cylinder; and 2: center of microdrive base with respect to microelectrode) could be made to add or subtract such that the microelectrode could be made to enter the stainless steel cylinder at any eccentricity from zero to 4 mm. Markings on adapter and microdrive base allowed the desired eccentricity to be selected. The adapter could be rotated on the steel cylinder, allowing a penetration of a given eccentricity to be made at any point on a circle of radius equal to the eccentricity selected as described above. Markings on the adapter and steel cylinder allowed selection of the circumferential point of penetration. By means of this system it was possible to insert the microelectrode at any point in an 8-mm-diameter circle of cortex. This double-eccentric system has been described in another report (7).

Recordings were begun 3 days following implantation of stainless steel cylinder and electrodes for stimulating the medullary pyramid, and were carried out daily for about 5 days. The number of days over which penetrations could be made was sometimes limited by toughening of the dura, with a resultant increase in the probability of damage to the glass-insulated platinum-iridium microelectrodes (11) as they passed through the dura.

RESULTS

Outline of data presentation

The experimental results will be presented in three sections: I, arm muscle activity under different load conditions; II, parameters of movement to which PTN discharge is related; III, additional results.

SECTION I will present data on the electromyographic correlates of the wrist movement which monkeys were trained to carry out, and is intended to clarify relations between 1) load, 2) pattern of contraction in flexor and

extensor musculature, 3) force exerted by monkey's hand on the manipulandum, and 4) wrist displacements. Information on these points was presented in METHODS, but since interpretation of the experimental results is so much dependent upon dissociation of force from displacement it seemed that it would be useful to present additional details on this part of the experiment.

SECTION II will introduce the two aspects of movement to which PTN activity was found to be most clearly related. More specifically, unit discharge will be shown to be related to 1) magnitude of force (F) and 2) rate of change of force (dF/dt).

SECTION III will present quantitative analyses of the relation of discharge frequency to load, and will also give results on certain

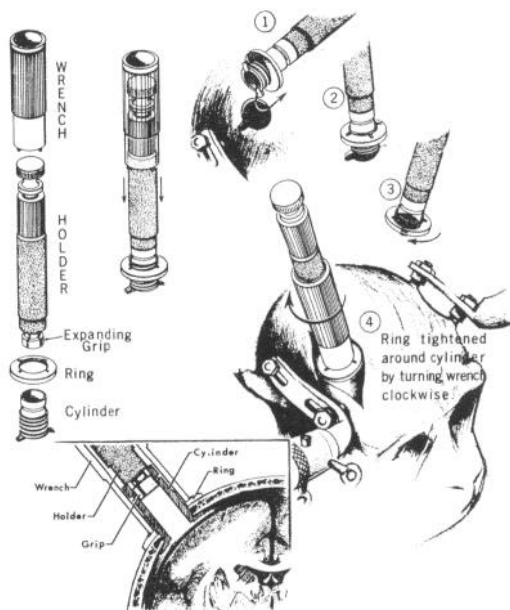


FIG. 3. Method for implantation of stainless steel cylinder. First, a hole with a small extension was made in the skull. Next, one of the small base projections of the cylinder was slipped beneath the bone opposite the extension, 1, and the other base projection was dropped through the extension, 2. The cylinder was then rotated 90°, 3, and the retaining ring was tightened firmly, 4. The inset at lower left shows a cross section of the cylinder following tightening of the ring, with the wrench still in place. The wrench and holder were removed by loosening the expanding grip on the wrench, and dental cement was applied at the junction of the ring and bone so as to provide a hydraulic seal at the lower end of the cylinder. Following this, the skin was closed and a cap was attached to the top of the cylinder. The monkey was then returned to its home cage for 2 days prior to unit recording.

other aspects of the relation of PTN discharge to movement.

SECTION I: ARM MUSCLE ACTIVITY UNDER DIFFERENT LOAD CONDITIONS. Figure 4 illustrates EMG recordings picked up from electrodes

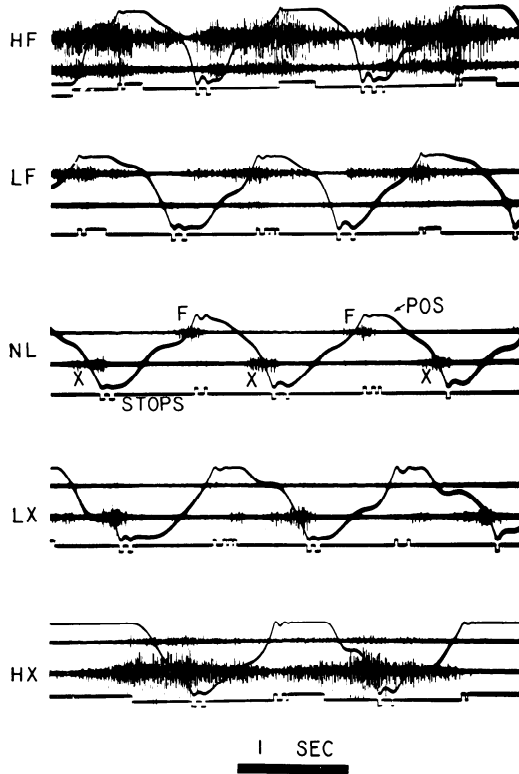


FIG. 4. This figure shows electromyographic tracings and records of displacement for five of the different loads which were used in this experiment. In the middle set of traces (marked NL) the line marked POS is the potentiometer output indicating wrist position. The potentiometer output is up for wrist flexion and down for wrist extension. The line marked STOPS can assume one of three positions: down for the wrist maximally extended, intermediate for the wrist in an intermediate position (the handle not contacting either of the stops), and up for the wrist maximally flexed. The EMG from the extensor musculature is marked X and from the flexor musculature is marked F. When a heavy load (400 g) opposed flexion (HF), the flexor muscles had predominant activity. When the heavy weight opposed extension (HX), the predominant activity was in the extensor musculature. When no load (NL) opposed the movement, there was alternate activity of flexor and extensor musculature. With the heavy flexor (HF) load there was predominant activity in flexor musculature, but also considerable activity in extensor musculature. The sets of traces marked LF (100 g opposing flexion) and LX (100 g opposing extension) show electromyographic patterns at intermediate loads.

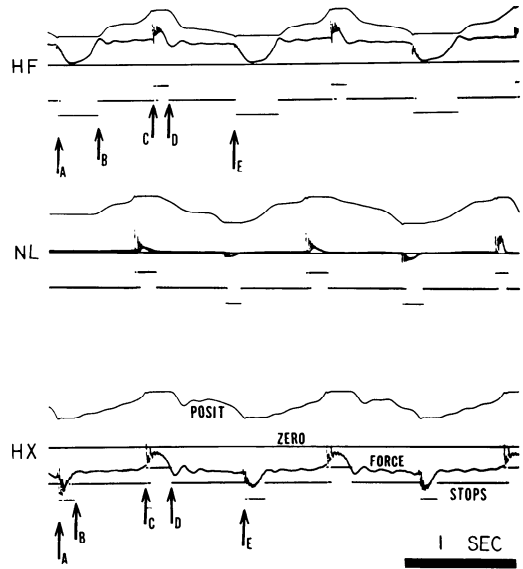


FIG. 5. This figure shows the relation of displacement and force at three different loads. When the record of force is above or below the zero reference (ZERO), force is exerted in the direction of flexion or extension, respectively. When the heavy load opposed flexion (HF), force was above the zero reference (i.e., net flexor force) during both flexor and extensor displacements. With no load (NL) opposing movement the actual amount of force was small during both flexor and extensor displacements. When the heavy load opposed extension (HX), force was in the direction of extension during both flexor and extensor displacements.

pasted to the skin over forearm flexors and extensors under five of the seven load conditions employed in these experiments. It may be seen that when the heaviest load (400 g) opposed extension, there was 1) maximum EMG activity in extensor musculature, 2) extensor muscle discharge during both flexion and extension displacements, and 3) relatively little activity in flexor musculature during either flexor or extensor displacements. The situation was reversed when the 400-g load was shifted so as to oppose flexion. When no load was employed (flexion and extension being alternately opposed only by the friction and inertia of the apparatus), the flexor and extensor EMGs showed approximately equal and alternate activity.

Figure 5 illustrates the relation between force and displacement for three of the seven load conditions. When the load opposed extension, force was exerted in the direction of extension during both flexion and extension displacements of the wrist, and there was

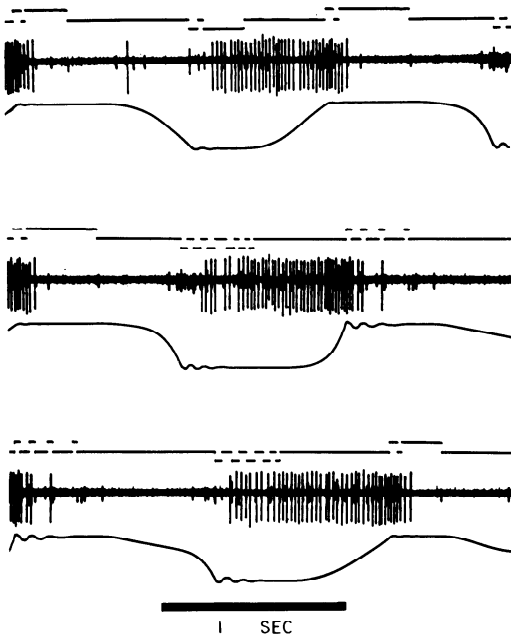


FIG. 6. This figure illustrates records of wrist displacement and unit activity on three successive cycles of the flexion-extension movement carried out with no load at all opposing the movement. The bottom line of each set of traces is the potentiometer output. When the potentiometer output is at its lowest position, the wrist is maximally extended and when the potentiometer is at its highest position, the wrist is maximally flexed. It may be seen that this unit was active during the flexion displacement and silent during the extension displacement.

little difference in the magnitude of the force in relation to the direction of wrist displacement. Likewise, when the load opposed flexion, force was exerted in the direction of flexion for both flexor and extensor displacements.

This dissociation of force and displacement should not be surprising. If one considers periods when the mass (M) attached to the string is being raised or lowered at constant velocity and therefore zero acceleration, it is clear that the net force (F) acting on the mass is zero, since the acceleration (A) of the mass is zero and since $F=MA$. At certain phases of the wrist movement acceleration was near zero, and thus the force exerted by the monkey's hand on the handle had to be approximately equal in magnitude (but opposite in direction) to the weight attached to the string (neglecting friction). Even during constant velocity, of course, there is a difference between the force

exerted by the monkey when raising the weight as compared to lowering it, this difference resulting from the apparatus friction.¹ Thus, when raising the weight the monkey was required to exert force equal to the weight plus frictional forces, but when lowering the weight the monkey's force output equaled the weight minus frictional forces. Of course, upward acceleration of the mass involved additional force increments and downward acceleration involved force decrements.

SECTION II: PARAMETERS OF MOVEMENT. 1.

Magnitude of force. Figure 6 illustrates the discharge pattern of a PTN in association with flexion-extension of the wrist under the "no-load" condition (no load at all opposing the movement). It is clear from inspection of this figure that the unit was active during flexion and inactive during extension, and that this behavior was quite consistent over consecutive cycles of the movement. The unit was almost totally silent when the contralateral wrist was at rest and had an antidromic response latency of 0.9 msec, indicating a conduction velocity of about 80 m/sec. On the basis of the results shown in Fig. 6 it cannot be decided whether this PTN is related to the flexion displacement per se or to the slight flexor force associated with this displacement. Examination of changes in the behavior of the PTN when the movement was carried out under several load conditions, however, shows that the magnitude of flexor force is, indeed, an important factor. Figure 7 illustrates modifications of discharge pattern which this unit showed as a function of load. Let us first consider what happened when the movement was carried out with a load which opposed flexion and which therefore required contraction of the flexor musculature during both the flexor and the extensor phases of the displacement. Figure 7 shows that under this circumstance the unit ceased to be silent during the extensor displacement, becoming approximately as active during the extensor displacement as

¹ In addition to apparatus friction there is the internal friction of the muscles and joints. Also, a controlled movement of the type studied here involves cocontraction of agonists and antagonists. The force output picked up by the force transducer is thus a resultant of forces generated by several cocontracting muscle groups, and modified by internal frictional effects within the muscles and joints.

it had been during the flexor displacement when no weight at all opposed the movement. The occurrence of discharge during the extensor displacement was not the sole consequence of requiring greater activity of the flexor musculature; Fig. 7 shows that discharge frequency was also enhanced during the flexor displacement. When the weight was shifted so as to oppose extension (Fig. 7), an opposite effect occurred; under this load condition the unit became virtually silent during both the flexor and the extensor displacements.

The results pictured in Fig. 7 show that this unit was not related simply to the wrist displacements that the monkey was making but that, on the contrary, it was very strongly related to the forces which gave rise to these displacements. When flexor or extensor displacements were associated with extensor force of sufficient magnitude, the unit was virtually silent regardless of the direction of displacement, whereas both of these displacements were associated with intense unit

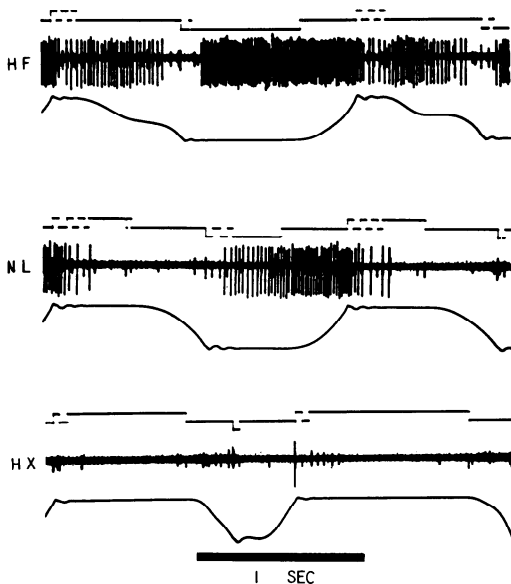


FIG. 7. This figure illustrates the activity of the same unit shown in Fig. 9, but in this case the activity of the unit is shown at each of three load conditions. The three loads employed are 400 g opposing flexion (top), 400 g opposing extension (bottom), and no load opposing the movement (middle). It may be seen that the unit became much more active with a load which opposed flexion, and which therefore required increased flexor force. Conversely, the unit was almost totally silent during periods when the movement was carried out with a heavy load opposing extension.

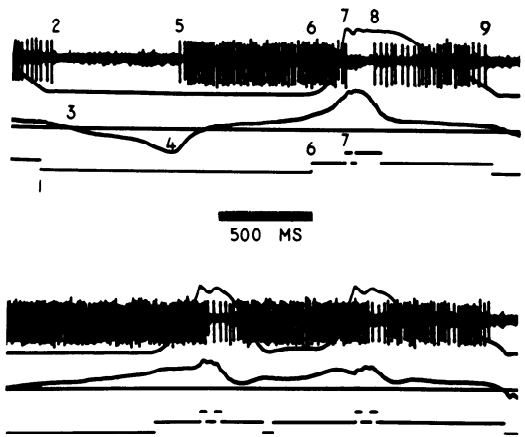


FIG. 8. This figure shows records of unit discharge, displacement and force for the same unit shown in the previous two figures. For this figure, the 400-g load was opposing flexion. See text for explanation of the upper section of this figure. The lower section of this figure shows additional records of force and displacement. It may be noted here that the monkey carried out these two cycles of the displacement without dropping into net extensor force (except at the very end of the figure). It can also be seen that with this maintained flexor force the unit remained active. It was only at the end of the trace that the unit paused, following which net extensor force developed.

activity when there was sufficiently great flexor force.

2. *Rate of change of force.* In the previous paragraphs, variation of applied force during displacement was not considered. However, inspection of Fig. 5 shows that, particularly with the heavier loads, the magnitude of the force varied considerably. These variations of force allowed determination of the extent to which the discharge frequency of this PTN was related to the magnitude as compared to increases or decreases of flexor force. Figure 8 illustrates records of force, displacement and unit activity under the load condition of 400 g opposing flexion. The figure begins during the course of an extensor displacement with net force exerted in the direction of flexion since the load was opposing flexion. At 1 the extensor displacement was completed, following which the unit paused (2) and the force crossed the zero force line (3) into net extensor force in association with the "follow-through" of the wrist extension. At 4 the magnitude of extensor force began to fall. The unit began to discharge at 5, and shortly after this flexor force began to be exerted. Force then continued to rise over a period of about 1 sec before it reached a value sufficient

to lift the weight and initiate the flexor displacement (6). At 7 the flexor displacement was completed, and the unit discharge stopped, following which there was a sharp fall in force. At 8 the unit began discharging again and force fell less rapidly. At 9 the unit paused and shortly thereafter force began dropping more rapidly, passing over into net extensor force.

If the discharge frequency of this neuron had been related simply to the magnitude of force the unit should have been more active between 7 and 8 (when magnitude of force was high but falling) than between 5 and 6 (when force was low but rising). This was not the case, however, and it is apparent that a low but rising force is associated with a higher discharge frequency than a high but falling force. If one assigns a positive sign to force exerted in the flexor direction and a negative sign to force exerted in the extensor direction, then dF/dt will be positive for increases in flexor force or decreases in extensor force, and dF/dt will be negative for decreases in flexor force and increases in extensor force. The unit under consideration was in general more active for positive dF/dt than for negative dF/dt , but positive dF/dt was not itself a sufficient condition for prior discharge of the neuron. Thus, at 4 of Fig. 8, dF/dt became positive but F was at its most negative. No discharge occurred until F approached the zero line on its way up to the zone of positive (flexor) force. Thus, this unit was related to dF/dt when F was positive or slightly negative, but not when F was markedly negative. For sufficiently negative F , the unit was silent regardless of dF/dt . It is thus clear that the discharge of the neuron was related both to F and to dF/dt . Figure 9 shows additional examples of the relation of discharge frequency to dF/dt . In this figure the record of force has been differentiated so as to display dF/dt directly. It is apparent that under conditions of positive F , sharp rises in dF/dt are preceded by marked increases in discharge frequency.

SECTION III: ADDITIONAL RESULTS. 1. *Quantitative analyses.* More than 100 PTNs were recorded from the precentral gyrus during the conditioned wrist movement, but only 31 of these had sufficiently clear and consistent relation to performance of the task to warrant quantitative analysis of their activity. Those

PTNs unrelated or weakly related to wrist movement were often strongly related to finger, elbow, or shoulder movements. If the first PTN picked up in a penetration was related to movement at a particular joint, it was common for deeper PTNs to be related to movement at the same joint. Units related to shoulder movements, for example, would show striking modifications of activity when the arm was put into or taken out of the tube leading to the manipulandum, but during the conditioned wrist movement these units showed relatively weak or no relation to the changing loads or to the phases of the wrist displacement. Other units were found to be related to opening or closing the fingers but unrelated to wrist flexion and extension. A number of units were related to both wrist and finger movements. When the region containing PTNs related primarily to wrist movements was found within the 8-mm-diameter circle available for penetration, suc-

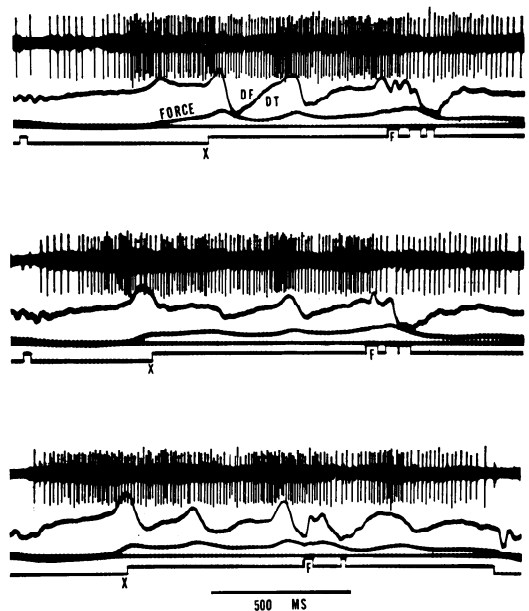


FIG. 9. This figure illustrates records of force (F) and derivative of force with respect to time (dF/dt). The uppermost line in each group of traces is the unit. Below this is the differentiated record of force output (dF/dt). Below dF/dt is a record of magnitude of force; the straight line below this is the zero reference line for force. When the record of force is above this zero reference line, net force output is in the direction of flexion. When the record of force output is below this zero reference, net force output is in the direction of extension. The figure shows that bursts of unit discharge precede rises in dF/dt .

cessive penetrations were made in steps of 1 mm within this region.

There was no sharp delineation between units which were or were not involved in the performance of the task. This fact is not surprising, since (as will be pointed out in greater detail in DISCUSSION) the conditioned wrist movement involved flexors and extensors of the wrist as prime movers, but the numerous other muscles of the upper extremity were also involved in their secondary roles of maintaining the over-all postural set of the arm. Since this postural set changed somewhat for different loads and different directions of displacement, it was not surprising to find that certain units which were very strongly involved in shoulder or elbow movements were also involved, but less strongly, in the alternate flexion-extension of the wrist.

Quantitative description of the group of units related to wrist movement required that certain numerical indices of activity be derived for each unit. The indices selected were: *a*) number of impulses occurring in the course of each displacement, and *b*) the duration of this displacement. Thus, each cycle of the movement gave rise to two pairs of figures: 1) number of impulses during flexion and the duration of flexion, and 2) number of impulses during extension and duration of extension. Figure 10 illustrates the method employed in extracting these numerical indices from data which had been recorded on magnetic tape. The indices were determined for many cycles of the movement at each of the seven load conditions (no load, and 100, 200, and 400 g opposing flexion and extension, respectively). As a result of these analyses, information became available on *a*) the average discharge frequency of the neuron during the flexor displacement at each of seven load conditions, and *b*) the average discharge frequency during the extensor displacement at each of seven load conditions. It was pointed out in METHODS that monkeys were rewarded only for displacements whose duration fell between 400 and 700 msec. The actual duration of the displacements often fell outside these limits, but discharge frequencies which serve as a basis for the analyses to be summarized below were based on displacements of durations falling between 500 and 600 msec.

Figure 11 shows the results of this quantita-

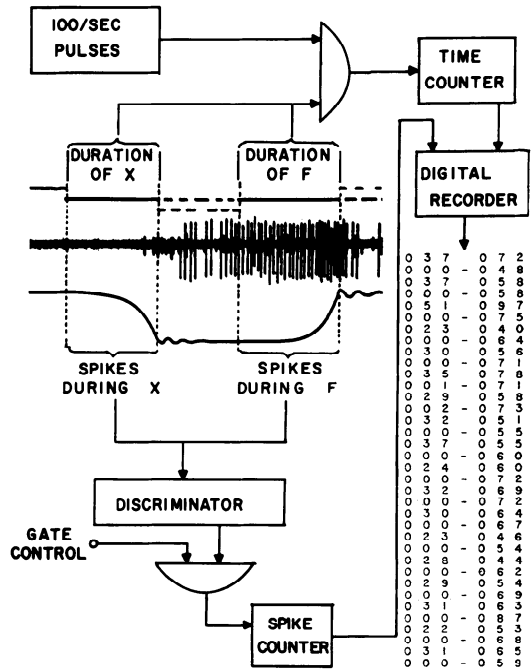


FIG. 10. This figure shows how records of unit activity were processed so as to provide data on the number of spikes and duration of displacement for successive wrist movements. The gates for spike frequency and time were open when neither stop was contacted, and otherwise closed. Counters were reset to zero each time contact with either stop was broken, so as to eliminate counts accumulated during bounces off of the stops. When the flexor stop was contacted for the first time following a previous contact with the extensor stop, the digital recorder "read" the counters, held the count in memory, and then printed the number of spikes and time that the counters had accumulated between last leaving one stop and first contacting another stop. In the printout shown at the right, the left column gives number of spikes and the right column shows duration of displacement in 10-msec units. Alternate rows of numbers contain dashes to identify the extensor displacement. For this PTN, rows in the left column of numbers are alternately high and low, indicating that the unit is alternately active in flexion and inactive in extension.

tive analysis for the unit whose activity was described in SECTION II, a unit which was more active when the load opposed flexion than when the load opposed extension. The curve of discharge frequency during the flexion displacement in Fig. 11 shows that frequency increased with flexor loading, having minimum value (3/sec) with the heaviest load opposing extension and maximum value (93/sec) with the heaviest load opposing flexion. In comparing data for extensor and flexor displacements one should recall that for flexor loads

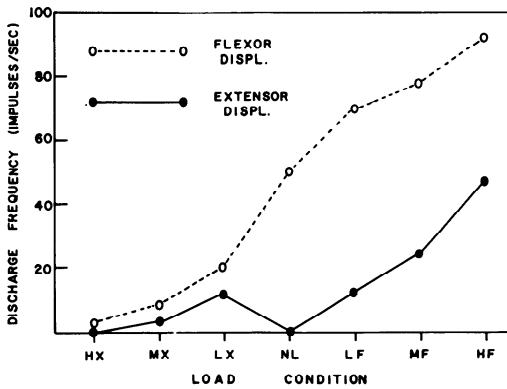


FIG. 11. Discharge frequency in impulses/sec (ordinate) is plotted for flexor displacements and extensor displacements at each of seven load conditions. HX, MX, and LX are loads of 400, 200, and 100 g opposing extension, respectively. LF, MF, and HF are loads of 100, 200, and 400 g opposing flexion, respectively. NL is no load. See text for further explanation of this figure.

force tended to rise during the period when the weight was being raised and to fall when the weight was being lowered, and that the flexor displacement was therefore associated with both high magnitude of flexor force and positive dF/dt , whereas the extensor displacement involved high flexor force but negative dF/dt . Thus, Fig. 11 shows a discharge frequency of 50/sec during the flexor displacement with no load (when force was low but rising) and a discharge of 47/sec during the extensor displacement with 400 g opposing flexion (when the force was high but falling).

The data on the 31 PTNs which were analyzed as indicated above may be summarized² as follows: 1) 26 of 31 units showed changes of 50% or more in discharge frequency with changing load. 2) Of these 26 units, 7 were more active with load opposing flexion than with load opposing extension; 16 showed an opposite relation to load, being more active with loads opposing extension than with loads opposing flexion; 2 were more active with flexor loads during extensor displacements but more active with extensor loads during flexor displacements; 1 was most active with no load—becoming less active with either extensor or flexor loads. 3) Several of the units showed a nonmonotonic relation between discharge frequency and load, hav-

ing peak discharge frequency at some load intermediate between the heaviest load opposing extension and the heaviest load opposing flexion.

The method of analysis employed to obtain these results was adequate for demonstration of the most obvious effects of changing loads, but it failed to detect certain of the more subtle effects—effects which could often be seen rather easily on examination of the raw data. In particular, this method of analysis failed to provide a measure of unit activity occurring during periods of force buildup prior to the occurrence of the displacement. The method also lost information concerning differences in discharge frequency in relation to different phases of the movement. Certain units which were clearly related to load had higher discharge frequencies during the earlier phases of the displacement than during the later phases. Other units discharged more briskly during the later phases. An effect of load on phase relations between PTN discharge and movement is shown in Fig. 12, where with a 200-g load opposing flexion the unit discharged throughout the entire flexor displacement, whereas with a 100-g load opposing extension the unit discharged only at the end of the flexor displacement.

It has been pointed out that 26 of the 31 PTNs clearly related to the wrist movement were related to load. But what of the 5 exceptions? Figure 13 illustrates the discharge pattern of a PTN which was active during flexor displacements and silent during extensor displacements regardless of load. Actually, this unit was not more active during flexion than it had been during immobility; it was suppressed during the extensor displacements rather than being activated during the flexor displacements, and was suppressed during extensor displacements regardless of the pattern of forces associated with these displacements. Though this unit was silent with extension and active with flexion, its discharge frequency did not vary with the position of the wrist or with the speed of flexor displacement. Thus, though the activity of this unit did not seem to represent force, neither did it represent the quantitative aspects of the displacement. The remaining units which failed to reflect force were essentially similar in their behavior, being related to direction of movement but failing to reflect either the position

² Tables in the APPENDIX present the results for the 31 individual PTNs.

of the wrist or the speed of the wrist movement.

2. *A nonmonotonic relation to force.* As mentioned above, some units showed peak discharge at an intermediate load, such that a unit which discharged briskly when no load opposed the movement might be considerably less active when the 400-g load opposed either flexion or extension. Several units failing to reveal such a nonmonotonic relation for the 500- to 600-msec displacements showed nonmonotonic relations if one examined not merely the displacements lasting 500–600 msec, but looked also at the more rapid displacements involving faster elevation of the load and therefore requiring the greatest values of F and dF/dt . As a matter of fact, the unit considered in SECTION II showed

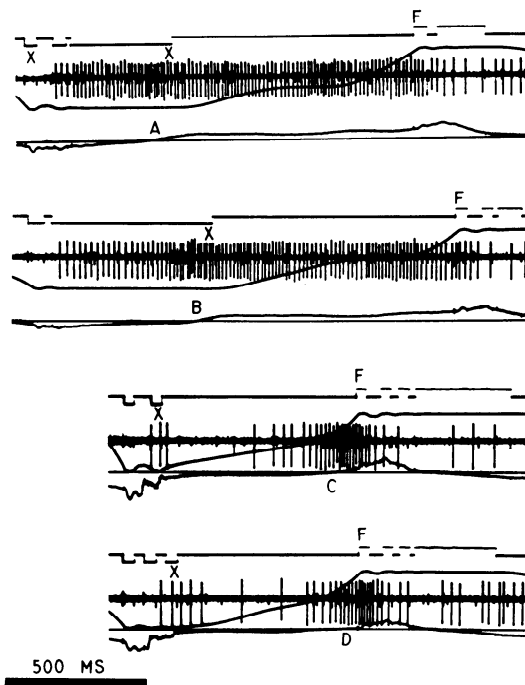


FIG. 12. Changing loads may lead to shifts in the phase relation between unit activity and movement, as illustrated in this figure of unit activity at two different loads. In the top half of the figure are shown two flexor displacements with 200 g opposing flexion. Here the unit was active throughout the displacement, but especially active at points A and B, where the force trace is seen to cross the zero reference from net extensor into net flexor force. In the lower half of the figure the load has been changed to 100 g opposing extension. Now the unit is inactive for the early part of the displacement, but becomes quite active at C and D, where the force record crosses zero from net flexor into net extensor force.

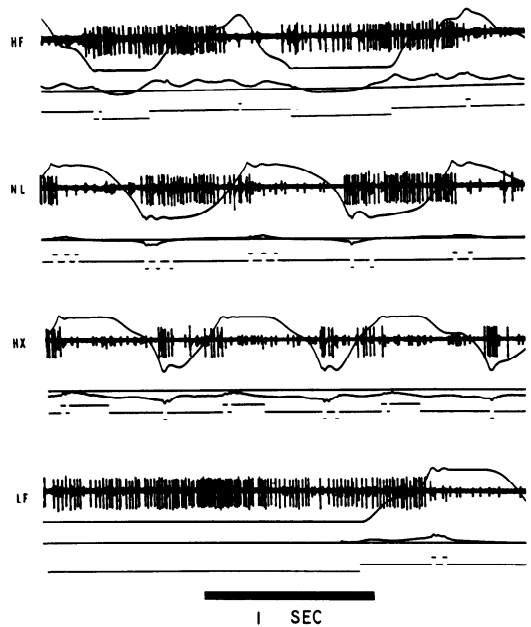


FIG. 13. This unit was active during flexor displacement and inactive during extensor displacement regardless of the force associated with the displacement. The loads for which activity is shown are 400 g opposing flexion (HF), no load (NL), 400 g opposing extension (HX), and 100 g opposing flexion (LF). The unit became active shortly prior to completion of extension, and paused shortly prior to completion of flexion. Though unrelated to force, discharge frequency was also independent of the details of the displacement. At the bottom of the figure (LF) is shown activity for a period during which the monkey paused with the wrist in the extended position. During this pause discharge was brisk, and there was no striking change prior to or during the wrist flexion which occurred near the end of the trace. The unit paused shortly prior to completion of flexion.

a drop in discharge frequency with the fastest displacements at the greatest flexor loads. This effect is shown in Fig. 14, where it is seen that for the most rapid movements the discharge frequency of the unit fell to about 55/sec. Table 1 shows the discharge frequency of this unit during flexor displacements of durations varying from 0.13 to 0.57 sec at the load condition of 400 g opposing flexion. It may be seen that discharge frequency fell from 92/sec for displacements taking 0.50–0.59 sec to 55/sec for displacements taking less than 0.20 sec.

DISCUSSION

The present study was undertaken to test two alternative views of the way in which

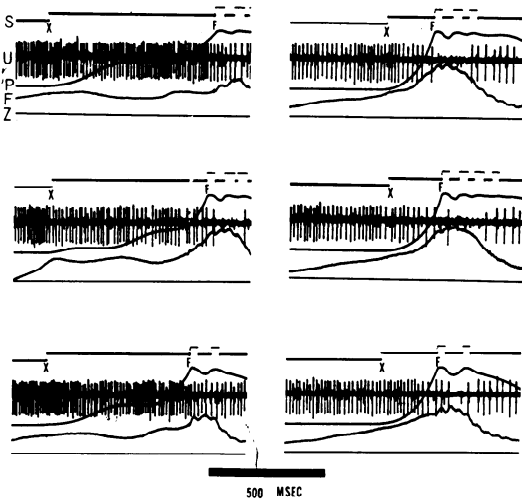


FIG. 14. Some units showed a paradoxical effect, becoming increasingly active with increasing force up to a point and then becoming less active as force rose above this point. For the unit shown here the most rapid displacements with highest forces (right three sets of traces) were associated with less activity than the three sets of traces at the left, where force rose less abruptly and where displacements were slower. The traces are identified at upper left as follows: S, stop contacts; U, unit discharge; P, potentiometer output indicating wrist position; F, force output; Z, zero reference for force output.

PTN output might be related to movement. The first view conceives of PTNs as displacement controllers, whose outgoing signals call for changes in the position of the moving part without specifying the forces required to achieve these changes. According to this model, other parts of the sensorimotor system would sense the resistances experienced by the moving part and elicit appropriate patterns and magnitudes of muscular contraction. An alternative model of PTN function holds that PTNs specify forces directly, and that force rather than displacement is the primary output variable. The view of force as the primary output quantity has been favored by Bates (2), according to whose notions it should be more complex to generate a given displacement or velocity than to generate a given force.

The displacement model might involve the following sequence: 1) a command for a displacement descends over PTN axons; 2) this command is translated into appropriate patterns of muscular contraction; 3) a displacement results; 4) information concerning this change in position feeds back to the cortex as a result of activation of joint receptors or

TABLE 1. *Nonmonotonic relation to force*

	Duration of Displacement*				
	<20	20-29	30-39	40-49	50-59
	14/19	20/25	33/37	46/45	45/50
	10/18	11/27	27/33	23/42	51/53
	7/18	14/21	25/30	41/46	45/56
	5/15	28/29	30/31	35/40	46/52
	9/17	22/24	31/35	32/41	46/57
	10/19	23/28	33/28	43/47	52/50
	6/18	14/24	33/38	40/46	53/55
	8/16	23/28	18/31	41/45	47/51
	19/19	16/25	32/33	36/42	54/52
	6/13	15/25	26/34	47/49	50/56
Totals	94/172	186/256	288/330	384/443	489/532
Freq	55	73	87	87	92

In the first column are data for 10 displacements taking less than .20 sec. The second column tabulates results for 10 displacements taking between .20 and .29 sec, etc. It may be seen that more rapid displacements were associated with fewer spikes. The values for mean discharge frequency (Freq) at the bottom of the table show that not only was the total number of spikes reduced for the most rapid displacements, but that the frequency of discharge was reduced as well. The data shown were obtained for flexor displacements under the condition of 400 g opposing flexion. * The five columns show numbers of impulses/duration of displacement in hundredths of a second.

cutaneous touch or pressure receptors; 5) a new command is initiated; and so forth. If the type of training that a subject has received (force control versus displacement control) were to modify the primary output variables of the control system then the fact that monkeys employed in this study were trained to control displacement independent of force would seem to have favored the operation of the displacement model rather than the force model. Prior to the experiment it was actually this author's prejudice that the displacement model was the more correct of the two and the problem on which monkeys were trained was chosen in the belief that it would provide a good situation in which to demonstrate the operation of this model. In fact, the experimental results showed that variations of force were very strongly represented in PTN output: a PTN which discharges at 100/sec during a flexor displacement associated with strong contraction of flexor musculature may be almost totally quiescent during a similar flexor displacement associated with strong contraction of the extensor musculature.

It was found that for many PTNs discharge frequency reflected dF/dt quite strongly. If the observed PTN discharges had occurred as sensory responses to muscle stretch one might have referred to them as "rapidly adapting," but in this case the changes in discharge frequency of PTNs preceded the muscular events. Nevertheless, this relation of PTN activity to the dynamic aspects of muscular contraction brings to mind the dynamic responses of the Ia afferents of the "nuclear bag" fibers in the muscle spindle. Interestingly enough, group I muscle afferents have now been shown to project to the motor cortex of both monkey (1) and cat (9). The existence of this projection of muscle afferents is in harmony with findings on PTN activity during voluntary movement, for the fact that activity of precentral PTNs is strongly related to the dynamic aspects of muscular contraction would seem to imply need for a feedback whereby information on these aspects of the status of muscle might reach the cortex. It should be emphasized that presence of the Ia input to motor cortex does not imply that this particular pathway plays a predominant role in the feedback control of movement. Information reaches the motor cortex from cutaneous and joint receptors (cf. 4, 10) as

well as from the cerebellum (cf. 3) and extrapyramidal structures (cf. 8), and it seems likely that performance of the skilled movement of the present experiment depended upon all of these inputs.

Even a seemingly simple movement involves the activity of many muscles and a slow, controlled movement of the type which has been investigated in the present study involves cocontraction of agonist and antagonist muscle groups (as illustrated in the electromyographic records of Fig. 4). In addition, wrist movement depends not only on the forearm musculature but also on the maintenance of arm posture by the musculature of the entire upper extremity. Thus, when a unit is found to be related to the wrist movement, it cannot be inferred that this unit is specifically related to one of the prime movers of the wrist. Ideally, the monkeys employed in this study should have been trained to carry out a wide repertoire of movements which involved differential activity of each of the numerous muscles of the upper extremity and the trunk, but the difficulty of achieving this degree of training seemed so great that it was not attempted. A study of motor function which investigates only one movement is analogous to a study of sensory function which investigates the effects of a stimulus applied to only one part of the body, regardless of the location of the receptive field of the unit under investigation. In such a study certain units would be strongly affected by the stimulus and others would be weakly affected or unaffected. Actually, the interpretation of the results of the present study is beset by difficulties even more severe than those involved in the hypothetical study of sensation in which the locus of stimulation cannot be varied. In such a study the investigator could at least specify locus of stimulation with precision, whereas it is impossible to state the precise extent to which various muscle groups are involved in the task which the monkeys were trained to carry out in the present study. It is known that a load opposing flexion demands greater activity of flexors than of extensors, and vice versa, but it is difficult to say much more than this with any certainty. Thus, when a PTN shows variations of discharge frequency in relation to the wrist movement but is independent of load, it is possible that this unit is related to the

activity of a muscle which sets the posture of the hand or arm or shoulder, but which is not called upon to vary its force output in relation to increased force output by the hand.

It was mentioned earlier that 16 units were more active with extensor loads than with flexor loads, and that only 7 units were more active with flexor loads than extensor loads.

TABLE 2. *Relation of load to discharge frequency*

Unit No.	Displ	HX	MX	LX	NL	LF	MF	HF	Unit No.	Displ	HX	MX	LX	NL	LF	MF	HF
1	F X	32 147	23 119	31 95	38 64	42 47	42 34	44 33	17	F X	19 26	13 15	11 6	9 5	6 0	4 0	4 0
2	F X	17 2	28 6	38 4	49 9	63 11	66 17	85 22	18	F X	33 50	25 42	21 34	24 34	16 18	8 9	2 11
3	F X		15 30	18 36	12 31	6 33	6 29		19	F X	2 8	2 14	2 14	3 13	2 11	2 13	2 4
4	F X		22 3	43 4	54 8	72 16	78 18		20	F X	11 41	16 47	24 40	13 36	22 36	23 31	
5	F X	22 74	22 70	22 49	20 45	22 34	17 33	20 23	21	F X	58 16	36 29	37 34	30 32	28 34	31 36	15 58
6	F X	2 9	3 18	4 20	0 15	4 24	11 28	20 81	22	F X	54 98	47 78	34 53	44 56	51 60	63 46	67 57
7	F X	16 60	6 45	4 44	14 27	6 14	6 6		23	F X	77 71	50 71	46 40	31 18	29 12	31 18	18 26
8	F X		15 16	17 13	33 25	44 25	44 49		24	F X	53 44	67 42	44 19	24 11	18 6	18 1	11 2
9	F X	35 93	15 84	13 72	23 42	29 27	32 42		25	F X	7 9	7 6	12 4	24 5	27 12	34 27	45 42
10	F X	3 1	9 3	19 9	50 0	70 12	78 24	93 47	26	F X	18 26	13 36	7 38	4 38	0 15	0 12	0 12
11	F X	6 8		10 17	6 19	6 22		4 9	27	F X	14 14			13 36			2 58
12	F X	39 37	42 38		23 35		31 30	23 30	28	F X	0 40	2 38	0 35	0 15	0 1	0 0	0 1
13	F X	42 38	31 31		26 16		25 16	23 17	29	F X	0 50	0 49	0 31	0 10	2 2	1 3	4 4
14	F X	21 24			6 17			3 3	30	F X	26 80	26 46	28 33	13 29	16 22	47 24	40 24
15	F X	16 2	20 2	21 3	3 26	2 24	2 16	3 10	31	F X	28 47	21 34	29 34	33 31	24 34	27 24	28 24
16	F X	27 2	27 4	29 2	34 2	29 2	27 4	33 0									

This table shows discharge frequencies (impulses/sec) for flexor displacements (F) and extensor displacements (X) at each of 7 loads. The abbreviations HX, MX, LX stand for loads of 400, 200, and 100 g opposing extension. HF, MF, and LF stand for loads of 400, 200, and 100 g opposing flexion. NL stands for no load at all. For most of the 31 PTNs, 14 values for discharge frequency are listed, corresponding to the two directions of displacement (F and X) at each of 7 load conditions (HX, MX, LX, NL, LF, MF, and HF). Missing values in table result from failure to collect the data. The columns giving data for the heavy loads have the greatest number of omissions. This results from the fact that as the monkey became relatively satiated with fruit juice it would fail to operate the apparatus when the heavy loads were attached, but would work for intermediate or light loads.

This result seems surprising until one realizes that when the load opposed extension the vertical rod had to be grasped by the fingers or thumb, and that increased loads opposing extension required increased activity of thumb and finger flexors as well as increased activity of wrist extensors.

Given these complexities, it is obvious that interpretation of the present results must be quite limited. It seems clear that activity of PTNs is related to variations of force output, but a great deal more refinement of this experimental approach will be necessary before the details of this relationship can be even tentatively proposed.

SUMMARY

Monkeys were trained to carry out alternate flexion-extension movements of the wrist for a fruit-juice reward. Reward was delivered only when the durations of two successive displacements (flexion followed by extension, or vice versa) fell between 400 and 700 msec. At certain times a load opposed flexion, and as a result both the flexor and the extensor displacements of the required duration involved activity of the flexor musculature and exertion of flexor force. At other times the load opposed extension, requiring that both flexor and extensor displacements be associated with extensor force. Force was thus dissociated from direction of displacement,

and it was possible to determine whether PTN discharges recorded from the precentral motor cortex in association with this movement were related to direction of force or to direction of displacement.

For the majority of PTNs discharge frequency was related primarily to the force (F) and dF/dt and was only secondarily related to the direction of displacement.

Some PTNs which were unrelated to force were related to the direction of displacement, but not to the fine details of the displacement in the way that numerous other PTNs were related to the fine details of applied force.

APPENDIX

This appendix consists of data on the quantitative relations between load and PTN discharge for displacements lasting 500–600 msec. The results listed pertain to 31 PTNs which showed a phasic relation to the alternate flexion-extension of the wrist. Discharge frequencies for these 31 PTNs are listed in Table 2.

Several features of the data in this table may be singled out for attention: 1) Discharge frequencies rarely exceed 100/sec. Only one of the 31 PTNs ($U1$) showed a frequency in excess of 100/sec. 2) Peak discharge frequencies may occur at some load intermediate between HF and HX, as is seen in units 11, 15, and 19. 3) Units 12, 16, 19, 20, and 31 showed no consistent variations in discharge frequency in relation to load (unit 16 is the unit pictured in Fig. 13 of this report).

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