PYRAMIDAL TRACT ACTIVITY ASSOCIATED WITH A CONDITIONED HAND MOVEMENT IN THE MONKEY

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CURRENT UNDERSTANDING OF THE ROLE of the pyramidal tract in the initiation and control of movement stems largely from observations of the responses to electrical stimulation of the pyramidal tract or motor cortex and from clinical or experimental analyses of the effects of lesions of these structures. Studies of the activity of individual pyramidal tract neurons (PTNs) have been highly productive of basic physiological data, but these studies have been largely confined to acute preparations in which it is impossible to observe the relation of PTN discharge to normal movement. With the advances in microelectrode recording techniques worked out by Jasper (6) and by Hubel (4, 5), however, it became possible to record the activity of individual cerebral neurons in moving animals. The present report describes the second in a series of studies which have utilized the technique of single unit recording to study the activity of pyramidal tract neurons in relation to movement. In the first study (3), recordings of the activity of PTNs in the arm area of the precentral motor cortex of the monkey showed that most PTNs in this region undergo marked changes in discharge pattern in association with contralateral arm movements. It was also found that the discharge pattern of PTNs both at rest and during movement is related to axonal conduction velocity: PTNs with the highest axonal conduction velocities tend to be inactive in the absence of movement and to show phasic increases in discharge frequency with movement, whereas PTNs with lower axonal conduction velocities have tonic discharge even in the absence of movement, and show both upward and downward modulation of this discharge frequency with movement. The arm movements referred to here were spontaneous—consisting of scratching, grooming, handling food, etc. Such movements allowed detection of the grossly apparent relations mentioned above, but were entirely too uncontrolled to permit analysis of certain other relations. In particular, observations of PTN discharge under these conditions did not allow determination of the latency between a stimulus which elicited movement and the associated modification in discharge in PTNs. The present study was carried out to obtain information as to the point in the stimulus-response sequence at which discharge of PTNs is modified.

METHODS

Techniques used in training monkeys. Five female monkeys (*Macaca mulatta*) were trained to depress a modified telegraph key (making a contact) until a light came on, and to

laterality of the hand which was to be moved. For most units, response occurred only if the photic stimulus was delivered during contralateral wrist flexion (see section 4 of RESULTS).

3) The occurrence of the PTN response depended on the subsequent occurrence of wrist extension. This could be shown by the process of extinguishing the conditioned response of extension. In the original training, animals were first conditioned to carry out steady flexion; only later were they required to carry out prompt extension at light onset. With repeated failure to receive reward the monkeys would persist in flexing to close the contact, but would not release at light onset. Perhaps the monkeys thought that they were guilty of premature extension. In any event, when they repeatedly failed to receive reward, monkeys would adopt the tactic of maintaining flexion for a much longer period after light onset. With the delivery
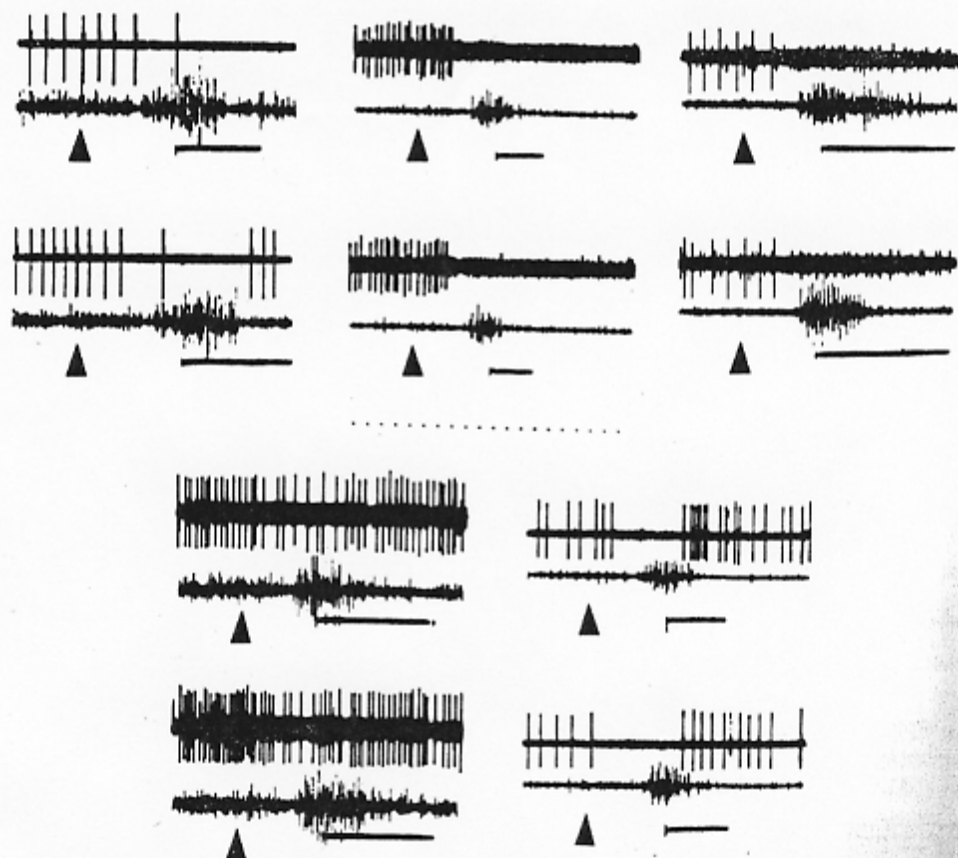

FIG. 4. Patterns of decreased activity in PTNs. The five sets of traces shown here illustrate some of the patterns of decreased activity shown by PTNs in association with contralateral wrist extension. The traces start 200 msec. prior to light onset; light onset is indicated by the black triangle. All of these units were tonically active during the steady flexion which preceded light onset, and then showed a partial or complete cessation of this discharge in relation to wrist extension. Time marks are 50 msec.
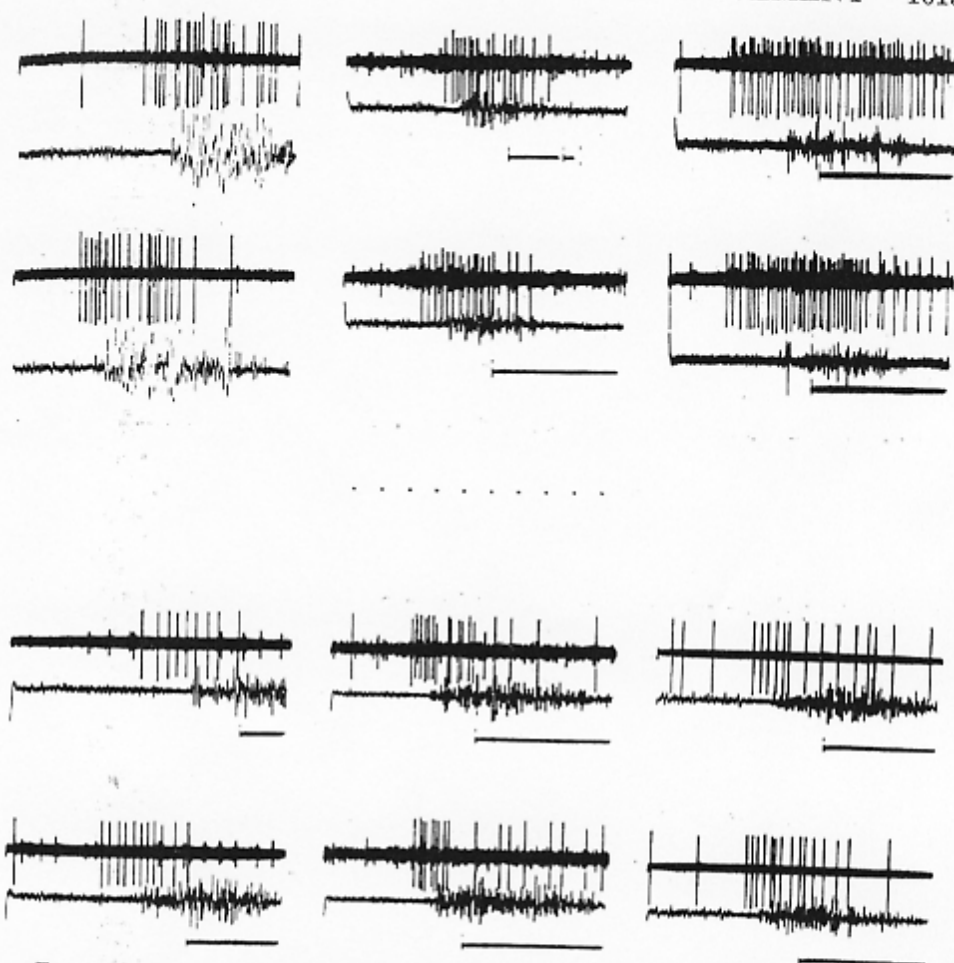
FIG. 3. Patterns of increased activity in PTNs. The six sets of traces shown above illustrate patterns of increased discharge frequency shown by six different PTNs in association with contralateral wrist extension. The minimum PTN response latency here was 100 msec., shown for the unit at top right. The discharge of this unit consistently preceded the EMG response, which had a minimum latency of 200 msec. In some units discharge was of considerably longer latency, discharge actually commencing almost simultaneously with the EMG response. Traces begin at light onset. Time marks are 50 msec.

responses" in PTNs differ from the more classical responses evoked by photic stimuli.

1) The occurrence of the PTN response required that the monkey be prepared to make the conditioned response. Thus, if the photic stimulus were presented with the arm at rest (not depressing the telegraph key), no response occurred.

2) The occurrence of the PTN response depended on which wrist was to be extended. Thus, when a unit was observed during both contralateral and ipsilateral wrist extension, responses to the photic stimulus depended on the

occurred prior to the peripheral electromyographic response. Other PTNs showed pauses commencing after the initiation of the EMG response. A total of 182 PTNs was recorded in association with contralateral wrist extension, and 57 of these showed responses prior to the first change in electromyogram. A statistical definition of response has not been employed in designating units "responsive" or "unresponsive." The reasons for failure to employ such a criterion are discussed under section 3 of RESULTS.

Since the PTN responses described above were evoked by a photic stimulus, it is appropriate to consider certain respects in which these "photic
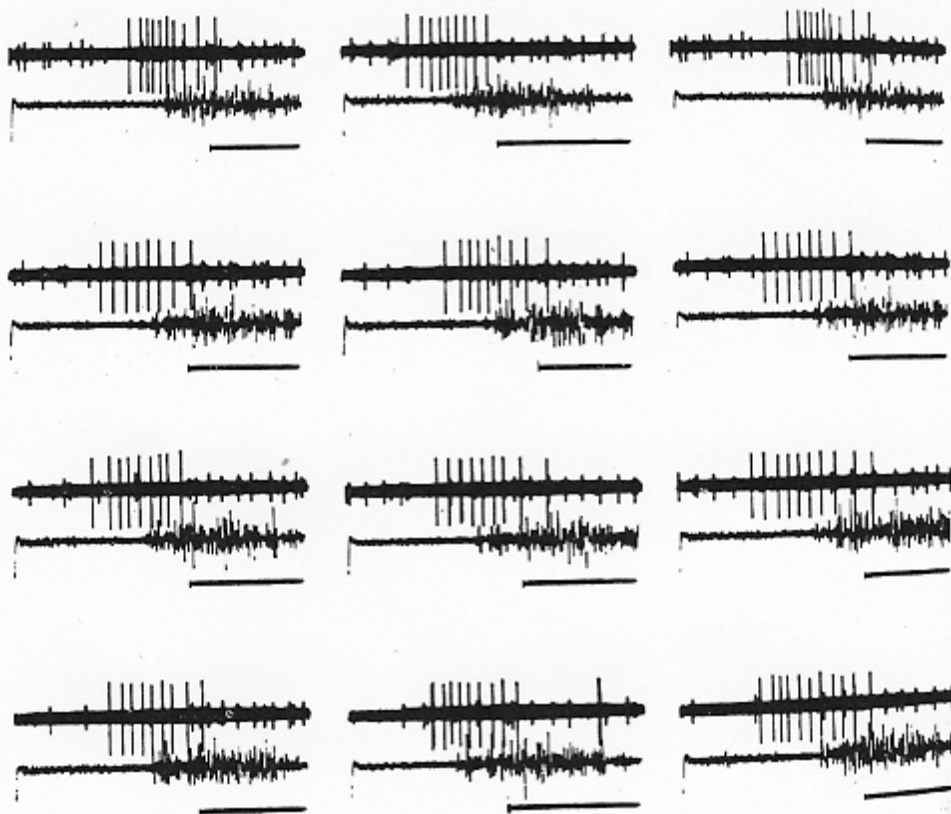

FIG. 2. PTN response, extensor EMG response, and reaction time. This figure illustrates a series of 12 trials for a PTN which was silent during flexion and which consistently discharged prior to extension of the contralateral wrist. All traces start at the onset of the light. The minimum response latency for this PTN was about 120 msec. This latency of PTN response was associated with an EMG latency of 170 msec. and a reaction time of 220 msec. In general, the shortest latency PTN responses were associated with the shortest latency EMG responses. Time marks are 50 msec. apart. The bottom line of each set of traces indicates when the contact opened.

interval between conditioned stimulus (light onset) and conditioned response (wrist extension) does modification of discharge in PTNs occur? 2. Is the occurrence of the wrist movement temporally locked to the PTN response? 3) What is the relation of axonal conduction velocity of a PTN and the response which it shows in association with movement? 4) Is activity of PTNs related only to contralateral movements, or are there some PTNs whose discharge is related to ipsilateral movements as well?

It might seem that a fifth question, "What is the relation of PTN activity to the initiation of wrist flexion?" should also have been posed. In the present situation, however, reward was not dependent on the time following extension at which flexion was resumed. Moreover, there was no external stimulus which initiated the resumption of flexion. Many units were found to show changes in discharge pattern in relation to the initiation of flexion, but the variability of the flexion movement and the associated modifications of PTN activity precluded consideration of this aspect of the data.

1. At what point in the interval between conditioned stimulus (light onset) and conditioned response (wrist extension) does modification of discharge in PTNs occur?

Figure 2 illustrates the temporal relation between a) the onset of the light to which the monkey responded with wrist extension, b) the occurrence of a PTN response, and c) the initiation of discharge in extensor muscles of the contralateral arm. For the PTN illustrated in Fig. 2, discharge invariably preceded the onset of the increased activity in the extensor EMG of the contralateral arm. The unit was almost totally silent during the periods when the task was being carried out with the ipsilateral arm. The increase in discharge illustrated in Fig. 2 represents but one of many possible patterns of PTN response in relation to wrist extension; Fig. 3 illustrates some of the additional patterns. The unit responses of Fig. 3 began prior to the EMG response, but a number of other PTNs showed increased discharge commencing after the initiation of electromyographic changes. It should be recalled that following the increase of extensor and decrease of flexor activity there is a decrease in extensor and resumption of flexor discharge. Thus, bursts of unit activity beginning shortly after the start of extension are in fact occurring shortly prior to resumption of activity in the flexor musculature. PTN responses starting after the extensor EMG response may thus represent the effects of feedback from the periphery or may equally well be related to resumption of flexion.

Figures 2 and 3 illustrated increases in discharge in relation to transient wrist extension. Figure 4 illustrates an opposite pattern of response, i.e., a decrease of discharge frequency in relation to wrist extension. The neurons of Fig. 4 discharged tonically during the period of maintained wrist flexion prior to light onset, and showed a slowing of discharge in association with the transient wrist extension which occurred following light onset. As in the case of the increases of discharge shown in Fig. 3, the decreases shown in Fig. 4

release the key following light onset; release of the key in less than 350 msec. following light onset resulted in the delivery of a liquid reward (milk, fruit juice, or water, depending on the monkey's preference). Figure 1 shows an electromyographic correlate of the hand movement which the monkey made in this situation. Wrist flexion was necessary for production of contact closure and, as would be expected, the EMG showed a predominance of activity in the wrist flexors during contact closure; contact opening involved a reduction in the activity of wrist flexors and an increase in the activity of wrist extensors. Within a short time (usually less than a second) after the monkey had opened the contact following light onset, she usually closed it again, beginning a new sequence. The period of time for which the monkey was required to flex (maintaining contact closure) prior to light onset was varied from trial to trial over a range of 1–5 sec. so as to prevent the monkey from predicting the time at which the light would appear. A premature release by the monkey (i.e., a release prior to light onset) did not result in reward, and following such a premature release the press had to restart from time zero. Thus, when the monkey released prior to light onset, she reduced the over-all frequency of reward. As a result of these contingencies the monkey maintained steady wrist flexion until light onset, extended her wrist for a fraction of a second following light onset, and then started steady wrist flexion again. During training, two of the five monkeys were required to alternate right and left hands rather frequently—
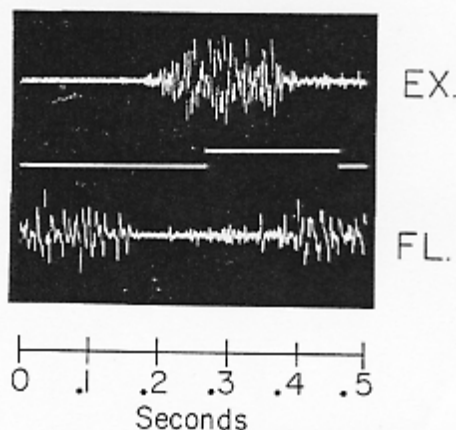

FIG. 1. Flexor and extensor electromyograms. This figure illustrates the reciprocal activity of extensors (top) and flexors (bottom) during the wrist movement which monkeys were trained to perform. Sweeps start at the onset of the light, at a time of wrist flexion. At about 150 msec. following light onset there was a reduction in flexor activity and a reciprocal increase of extensor activity. This EMG response was followed by opening of the contact, as indicated in the center line. The term "reaction time" as it is used in this paper is the interval from light onset to contact opening.

the aim being to have them gain equal proficiency in the use of both hands. The remaining three monkeys were trained on only one hand. In the present experiments it was desirable that performance become highly stable prior to single unit recording and to this end monkeys were given 100,000 trials or more before unit recording was begun.

Data acquisition. The techniques used for picking up and identifying PTNs have been described previously (2, 3). In brief, a hydraulically closed chamber, through which a microelectrode could be lowered into the precentral gyrus, was attached to the bone over the arm area. Macroelectrodes were chronically implanted in the ipsilateral medullary pyramid so that units could be tested for presence of an antidromic response to stimulation of the medullary pyramid.

EMG recordings were obtained from electrodes attached to the skin over the extensor and flexor muscles of the forearm. Two channels of a seven-channel tape recorder were used for recording EMG, and one channel was used for recording unit activity. The remaining four tape recorder channels were used for recording *1)* the condition (open or closed) of the contact operated by the monkey; *2)* a gate which came on 250 msec. prior to light onset, and whose termination was coincident with light onset; *3)* pulses synchronous with stimuli to the medullary pyramid; and *4)* voice.

RESULTS

The presentation of results will be organized according to four questions which have been posed in the current investigation: *1.* At what point in the

of a few rewards, monkeys would resume prompt release at light onset. During extinction of the wrist extension it was thus possible to observe unit responses to the photic stimulus when the wrist was flexed, but when no wrist extension was to follow light onset. In this situation the PTN response disappeared. As soon as the monkey resumed wrist extension in response to the light the PTN response returned.

In general, then, it is clear that the PTN response is evoked by the photic stimulus if and only if the photic stimulus is also to elicit a specific motor response.

2. Is the occurrence of the wrist movement temporally locked to the PTN response?

Given that modification of discharge in PTNs occurs prior to the arm movement, the question arises as to the relation between variations in the latency of PTN response and variations in the latency of motor response. If PTN discharge is an essential link in the chain of neural events that initiates the movement, then fluctuations in the latency of the PTN response should be associated with corresponding fluctuations in the reaction time (the time from light onset to contact opening) of the animal. Such a correspondence was suggested by the results shown in Fig. 2, where longer reaction times were associated with longer PTN response latencies.

Figure 5 shows the activity of a single PTN during 40 consecutive reaction-time trials. In the left-hand section of the figure the trials have been ordered as they actually occurred, but in the right-hand section of the figure trials have been rearranged so that the traces at the top are those for which the monkey's reaction time was shortest, whereas the traces at the bottom are those for which the monkey's reaction time was longest. It may be seen that progressively longer reaction times are associated with progressively longer latencies of unit response. The correlation is far from perfect, however, and it is apparent that the activity of this one PTN is far from explaining the variance in the behavior of the experimental animal.

Additional data on the relation of unit latency and reaction time are shown in Fig. 6. This figure plots reaction time against response latency for one PTN in a series of 80 consecutive trials for a monkey whose reaction times reached a minimum of 180 msec., a reaction time which corresponds to that of a proficient human subject in a comparable situation. Figure 6 shows that for reaction times of about 200 msec. the latency to unit response is about 100 msec. Longer unit latencies are associated with longer reaction times, though the reverse is not invariably true. Thus, short latency of unit discharge was a necessary but not a sufficient condition for the occurrence of short reaction time.

3. What is the relation of axonal conduction velocity of a PTN and the response which it shows in association with movement?

Figures 7 and 8 illustrate the responses of 24 PTNs in relation to extension of the contralateral wrist. The 24 PTNs were selected from 75 PTNs re-

than the response of the unit at the upper left of Fig. 7. Even in the case of the relatively "weak" response of the unit at lower left, however, the response is highly significant from the statistical standpoint. For the less responsive unit, the numbers of impulses during the 20 consecutive 200-msec. periods prior to light onset are: 6, 6, 7, 6, 7, 7, 9, 6, 7, 7, 9, 8, 6, 8, 9, 6, 8, 9, 9, and 8. For the period between 200 and 400 msec. following light onset the corresponding numbers of impulses are 4, 4, 3, 2, 5, 4, 6, 5, 4, 5, 4, 5, 4, 5, 5, 4, 5,


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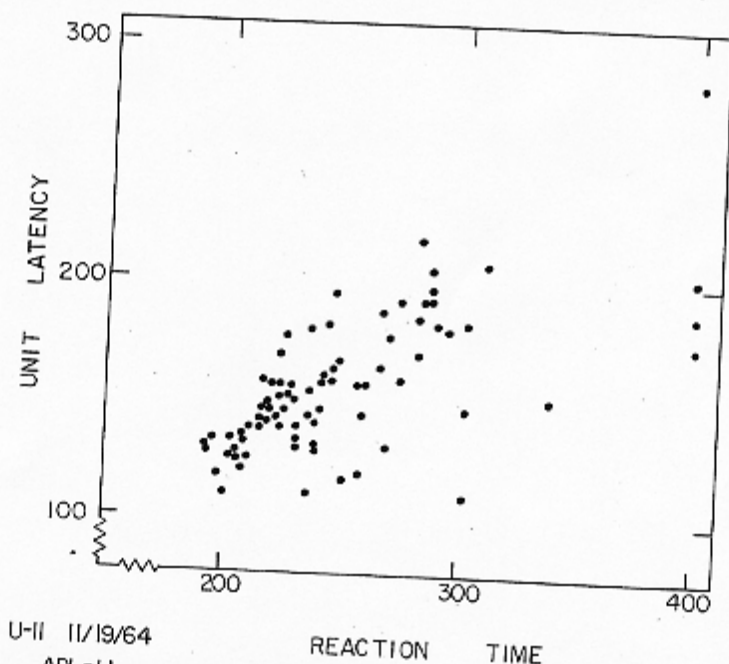
ADL=1.1

REACTION   TIME

Fig. 6. PTN latency and reaction time. Reaction times for 80 trials are plotted on the abscissa and corresponding PTN latencies are plotted on the ordinate. It may be seen that in association with reaction times of about 200 msec. this particular PTN had response latencies of about 110 msec. All of the short reaction times were associated with short PTN response latencies, but the converse was not true: there were a number of short-latency PTN responses which were not followed by rapid reaction times.

5, 6, and 4. The probability that these two distributions might have been drawn from the same population is negligibly small. Thus, the "less responsive" unit is actually highly responsive in a statistical sense. Among units which have been called "unresponsive," there are actually a considerable number which were responsive in the statistical sense. At this stage, however, it does not seem useful to deal with responses weaker than the weakest of the responses shown in Figs. 7 and 8.

The PTNs whose discharge patterns are illustrated in Figs. 7 and 8 had antidromic latencies (ADLs) ranging from 0.9 to 6.2 msec. Assuming a conduction distance of 70 mm., these ADLs would correspond to conduction
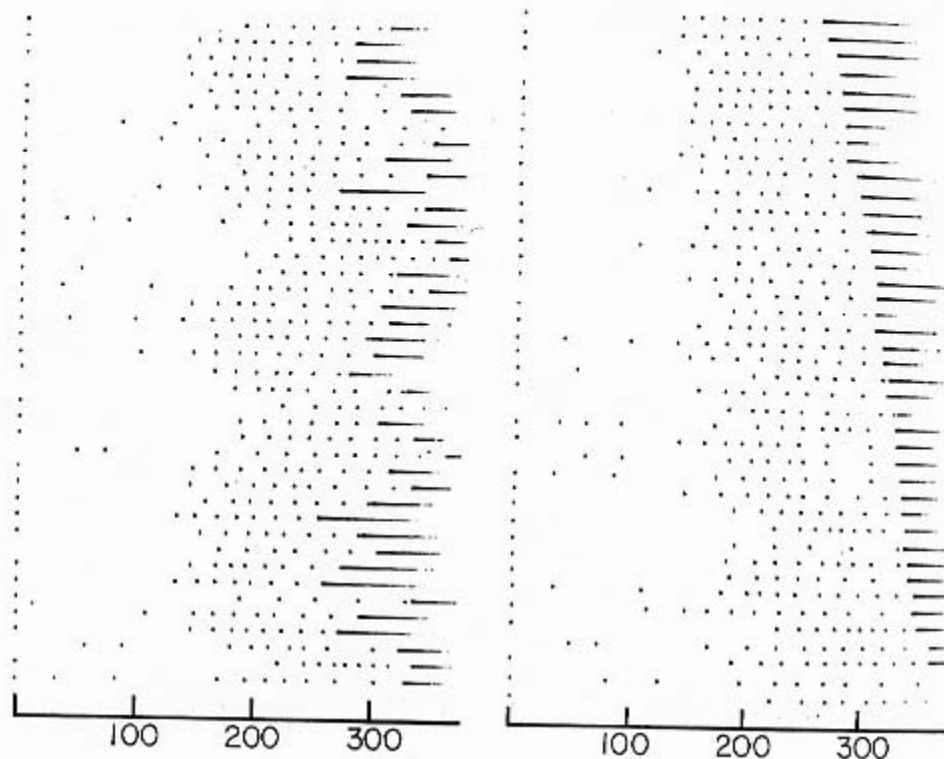
U-33   3/10/65   ADL= 1.0

FIG. 5. Relation of PTN latency and reaction time. In this figure the first dot at the left indicates light onset and subsequent dots indicate the occurrence of PTN discharge; each row of dots represents one flexion-extension sequence. At the moment of contact opening the dots representing PTN discharge are replaced by a continuous horizontal line. Thus, the reaction time on each trial is the interval from the leftmost dot to the commencement of the continuous line. The left-hand section of this figure shows 40 consecutive trials; in the right-hand section of the figure these same 40 trials have been rearranged with the shortest reaction times at the top and the longest reaction times at the bottom. It may be seen that there is a tendency for the shorter reaction times to be associated with shorter latencies of PTN discharge, and for longer reaction times to be associated with longer latencies of PTN response. The method of Wall (7) was employed in making this and subsequent rasters.

corded from the precentral hand area of a single monkey, most of whose reaction times were between 275 and 400 msec. The remaining 51 PTNs (not illustrated in Figs. 7 and 8) showed little or no response in relation to the contralateral wrist extension, though practically all of the 75 PTNs showed striking modifications of discharge pattern during spontaneous arm movements. A statistical criterion of response has not been adopted in this study and, as a result, designation of units as "responsive" and "unresponsive" is somewhat arbitrary. Thus, in Fig. 7 the unit whose activity is shown at the lower left was called responsive, but its response is certainly less obvious
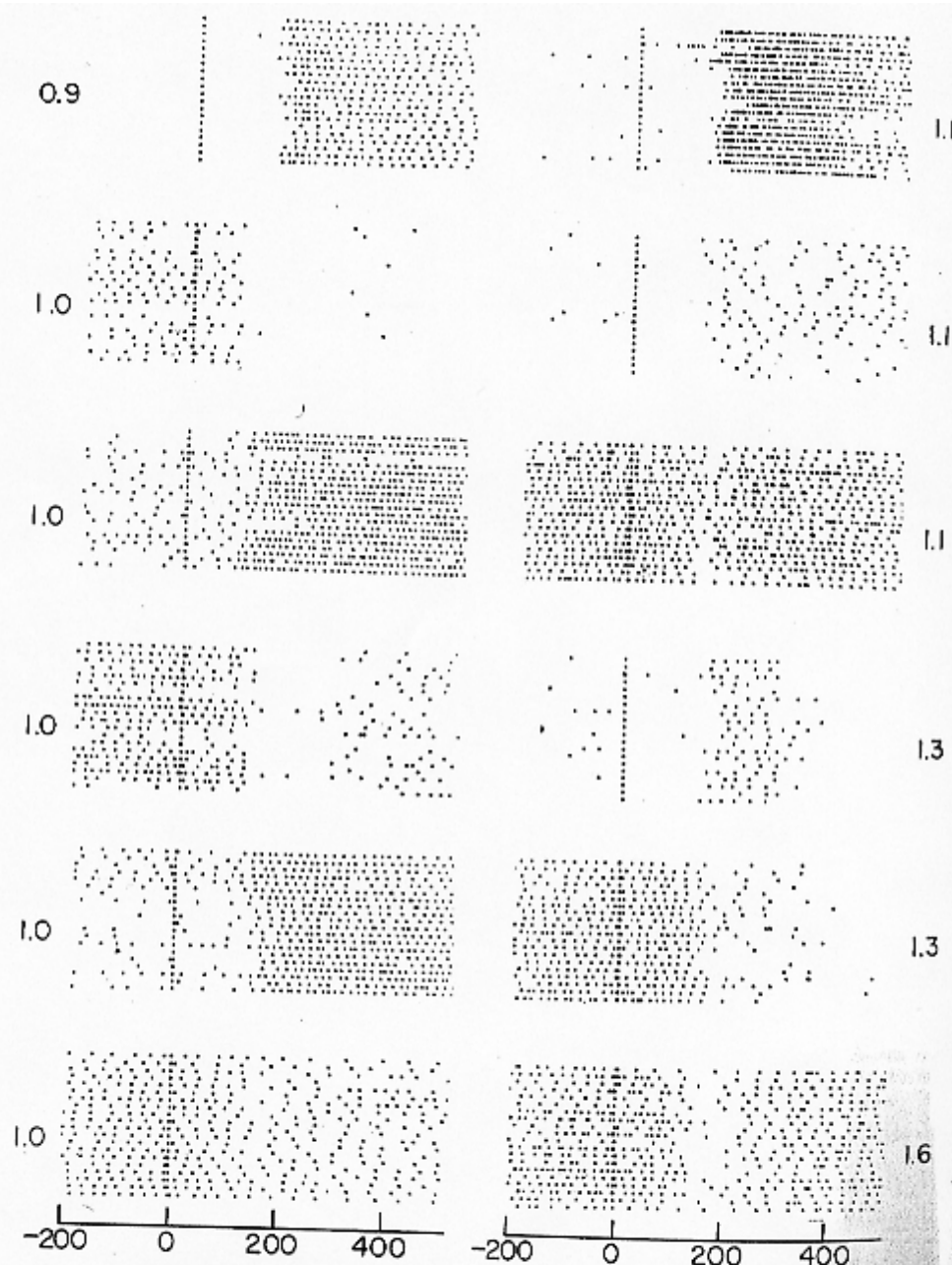
FIG. 7. Relation of discharge pattern and antidromic response latency. Each group of 20 rows of dots depicts the discharge of 1 PTN in relation to 20 successive flexion-extension sequences. Light onset is indicated by the vertical column of dots above "time zero." Thus, the discharge during the 200 msec. prior to light onset is indicated by the dots to the left of this column, from −200 msec. to 0 msec. The number beside each group of dots is the antidromic latency of the PTN whose activity is depicted by the dots. Several of the units represented here were inactive during the period of maintained flexion which preceded light onset (from −200 msec. to 0 msec.) and then became quite active in relation to transient extension.
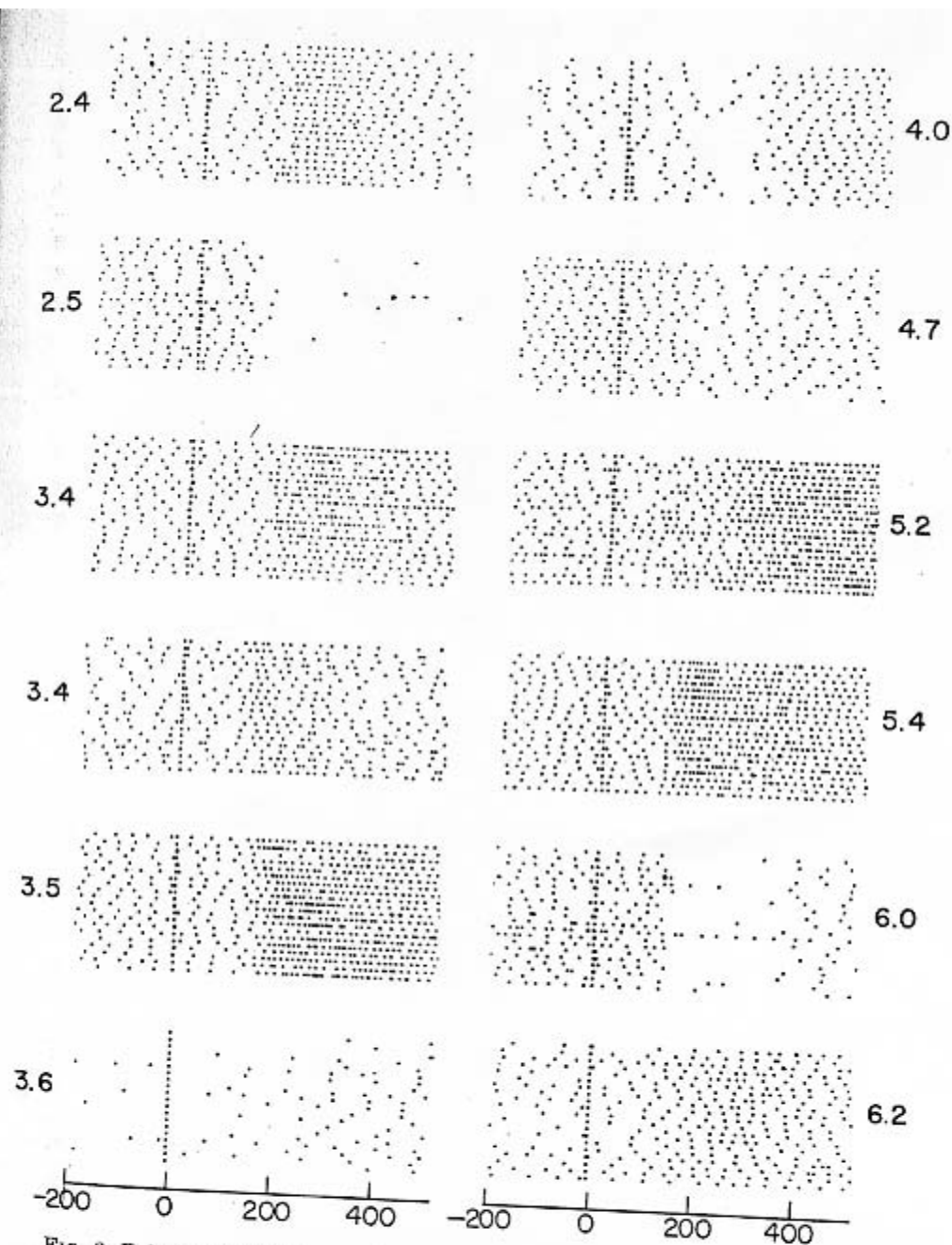
FIG. 8. Relation of discharge pattern and antidromic response latency. The general explanation of this figure is the same as that for Fig. 7. The 12 units represented here were recorded from the same monkey as the units of Fig. 7. The units of this figure had relatively long ADLs. Some of these units had increased activity in relation to extension, but these increases were superimposed on a background of maintained discharge. Increases in discharge frequency with extension following previous silence during flexion occurred only in the group of PTNs with shorter ADLs.

EMG response associated with extension, showing that these PTN responses were not consequent upon the feedback associated with the movement.

3. There was a strong positive correlation between latency of modification of PTN discharge and latency of occurrence of the movement.

4. Responses taking the form of increased activity prior to extension following quiescence during the flexion were restricted to the group of PTNs with relatively short antidromic response latencies (ADLs). When PTNs with long ADLs responded with increased discharge frequency prior to extension this increase was superimposed on a background of tonic discharge which had persisted throughout flexion. Many PTNs showed abrupt cessation of discharge prior to extension; the abruptness of this cessation was not related to ADL.

5. Most of the PTNs showing transient responses prior to extension were related to movement of the contralateral but not the ipsilateral wrist, though a few units were found which were related to movement of the ipsilateral but not the contralateral wrist.

6. The minimum latency of PTN response following light onset was 100 msec., a latency which is 70 msec. greater than the 30-msec. latency of PTN responses to retinal illumination in animals under chloralose anesthesia.

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Relation of response pattern to axonal conduction velocity

Observations of PTN discharge during spontaneous arm movements in a previous study (3) showed that PTNs with the shortest ADLs tend to be inactive with the arms at rest and to show phasic increases in discharge frequency with certain aspects of movement. PTNs with longer ADLs tended to be tonically active in the absence of movement and to show modulation of discharge with movement. There was a somewhat analogous relation between ADL and response pattern in the present study. Thus, units which were quiescent during flexion and showed bursts of discharge prior to extension had short ADLs. Units with long ADLs often had bursts of discharge prior to extension, but these bursts were superimposed on a background of discharge which had been maintained during flexion. A number of units with short ADLs were inactive during periods with both arms at rest, became active during maintained flexion, and then showed transient responses prior to extension. For some of these units the transient response took the form of a pause, while for other units the response consisted of a further increase in discharge.

Latency of response

It has been found that even in cases of minimum (180 msec.) reaction times by the monkey, the latency of the antecedent modification of PT discharge does not fall below 100 msec. This 100-msec. latency stands in sharp contrast to the 30-msec. latency with which PTNs in the motor cortex discharge in response to a photic stimulus in animals anesthetized with chloralose (1, 8). It is clear, then, that for this conditioned movement the latency of response in PTNs is delayed at least 70 msec. beyond the minimum latency demanded by the anatomical connections between the retina and motor cortex. What sequence of neuronal events takes place during this 70-msec. delay? An answer to this question would provide useful clues as to mechanisms of sensorimotor integration.

SUMMARY

1. This study was carried out to obtain information concerning the temporal relations between modification of discharge pattern in pyramidal tract neurons and the occurrence of a conditioned hand movement. Each of five monkeys was trained to carry out wrist flexion (depressing a modified telegraph key) until a light came on, and to extend the wrist promptly following light onset: light onset thus gave rise to the conditioned response of wrist extension. The activity of 182 pyramidal tract neurons (PTNs) was recorded from the hand area of the precentral motor cortex in association with this movement. Analysis of the results was focused on the modifications of PTN discharge which intervened between light onset and the first peripheral electromyographic correlates of wrist extension.

2. Many PTNs were found to show responses prior to the peripheral

to the contralateral movement, then it would seem unlikely that the response which seems related to ipsilateral movement is actually related to some change in the status of the contralateral arm. Figure 9 shows a unit which had a burst of discharge prior to ipsilateral wrist extension, but which was almost totally quiescent during all aspects of the flexion-extension sequence for the contralateral arm. Figure 10 shows a different unit, in which there was increased discharge prior to extension of either contralateral or ipsilateral wrist, but in which the discharge was more intense and of somewhat shorter latency for ipsilateral than for contralateral extension. For some trials the unit of Fig. 10 actually failed to show any increase at all prior to contralateral extension, whereas the increase always occurred prior to ipsilateral extension. Of the 40 PTNs recorded during both ipsilateral and contralateral hand movements, 3 showed stronger relation to ipsilateral than to contralateral movements. Thirteen of the 40 had transient responses which were more strongly related to contralateral than to ipsilateral wrist extension. A number of these 13 units, though more strongly related to contralateral than to ipsilateral extension, showed some degree of transient modification in relation to ipsilateral extension. The number of units observed was too small to allow any estimate of the over-all incidence of precentral motor cortex PTNs related to contralateral versus ipsilateral movement, but the data at least indicate the existence of PTN discharges related to ipsilateral movement and point to the need for a more thorough quantitative analysis of this problem.

DISCUSSION

The present results make it clear that arm movements are preceded by responses (either increases or decreases of discharge frequency) in PTNs and that the latency of the PTN response is related to the latency of the movement. It has also been found that the occurrence of the PTN response is dependent on whether movement involves the ipsilateral or contralateral arm. Most PTNs are related primarily to movement of the contralateral arm, but a few PTNs show a strong relation to ipsilateral arm movement.

The movement here considered involved an increase of discharge in wrist extensors and a reciprocal decrease of activity in wrist flexors, followed by an increase in the activity of flexors and a reciprocal decrease in the activity of extensors. Since the activity of these two muscle groups was reciprocally linked, it is impossible to say whether a given PTN response corresponds to an increase in the activity of extensor motoneurons, to a decrease in the activity of flexor motoneurons, or to some combination of the two. Moreover, the observations reported here fail to cast light on the way in which variations in the velocity and force of movement are related to the response pattern in PTNs. Investigation of these points is now being carried out in monkeys trained to perform a task in which the force and speed of movement are recorded, and in which the monkey is required to carry out alternate flexion-extension movements of the wrist under a wide range of load conditions.
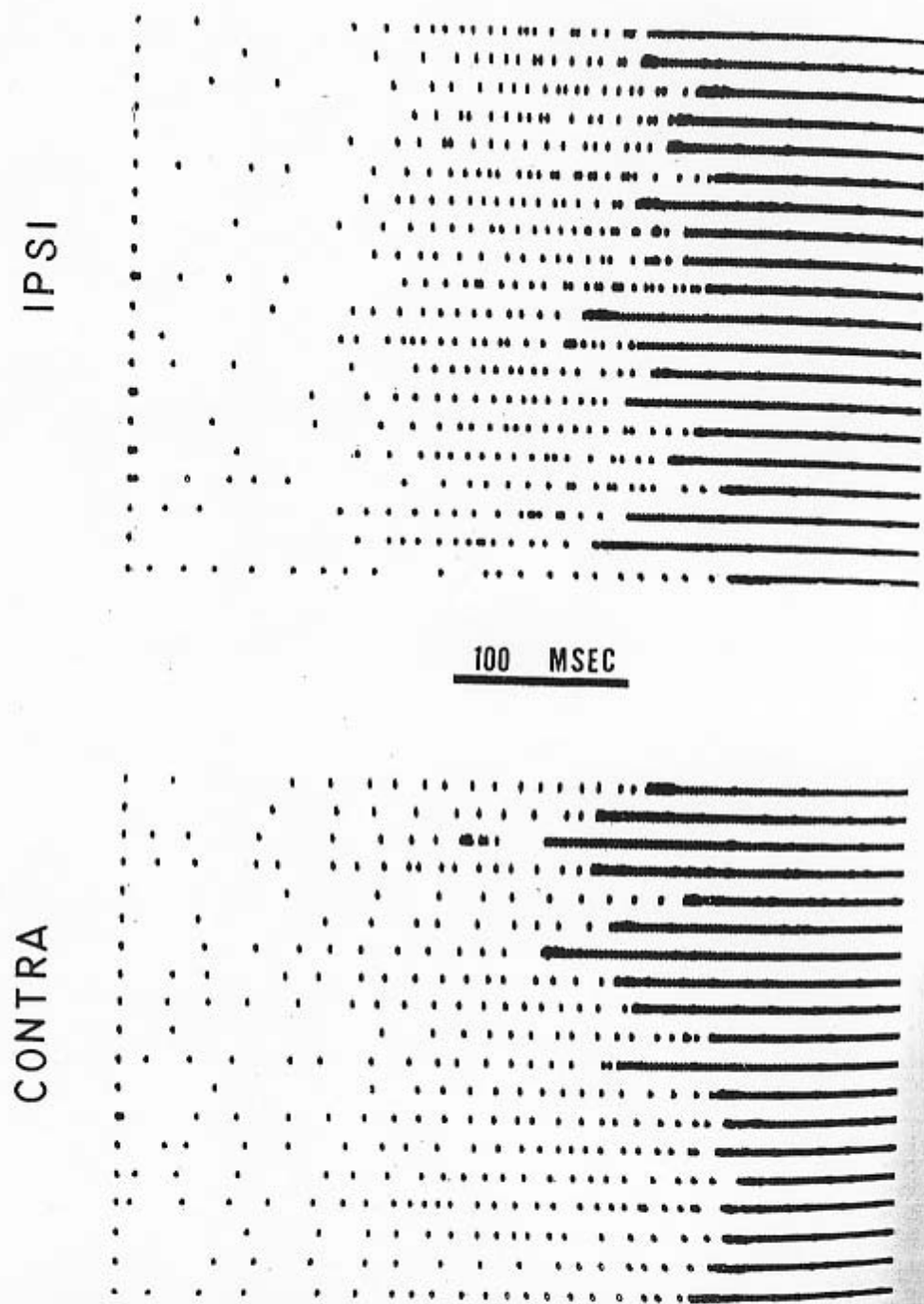
IPSI

100 MSEC

CONTRA

FIG. 10. PTN discharge in relation to both ipsilateral and contralateral movement. This figure depicts the discharge pattern of a PTN in relation to contralateral and ipsilateral wrist extension. This unit showed transient modifications of discharge in relation to both ipsilateral and contralateral wrist extension, but the increase of discharge was more marked for the ipsilateral than for the contralateral movement. Rows of dots start with light onset, the first dot being triggered with light onset. Subsequent dots represent PTN discharge. The continuous line at the right of each row begins at the instant of contact opening resulting from wrist extension.

cations of contralateral arm posture cannot be ruled out. This alternative possibility arises because the status (position and postural tone) of the contralateral arm with both arms at rest is likely to be different from its status during use of the ipsilateral arm.

b) Transient extension. The problem of interpretation which arises for changes in maintained unit activity during ipsilateral flexion is somewhat less severe for the case of transient unit responses in association with ipsilateral wrist extension. If a unit shows a transient response prior to ipsilateral extension, and if this response is time-locked to the ipsilateral but not
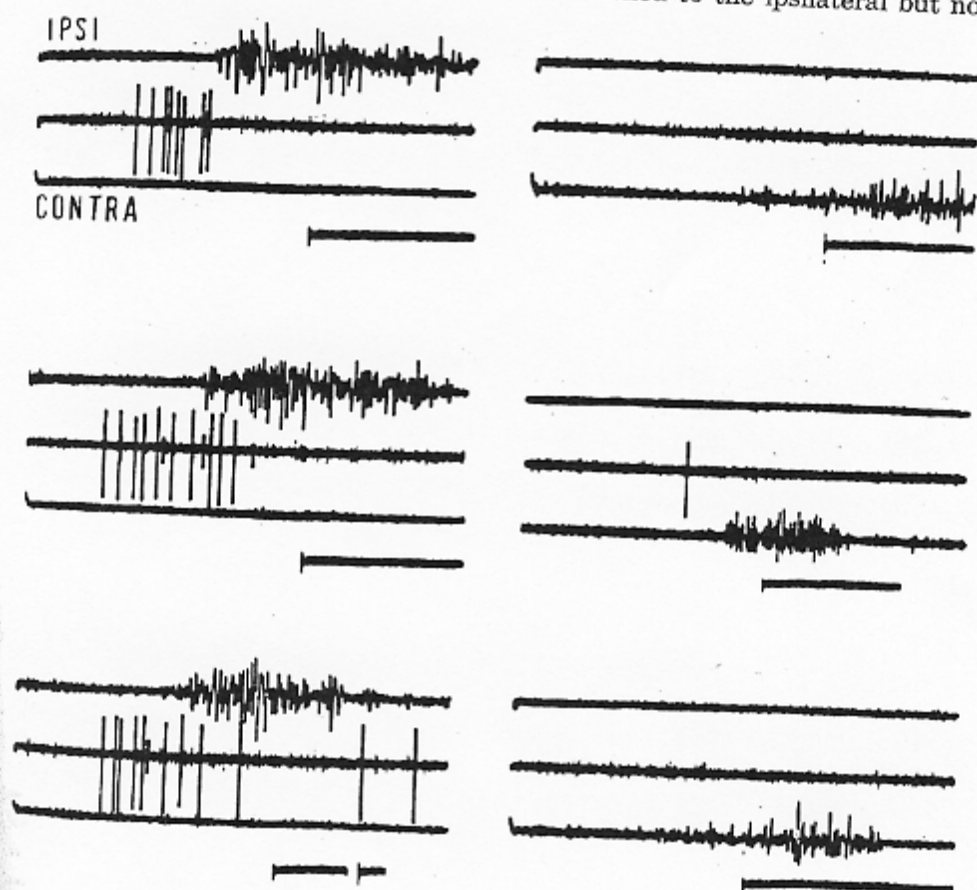

FIG. 9. PTN discharge in relation to ipsilateral movement. This PTN was studied in relation to both ipsilateral and contralateral wrist movement. It showed a consistent burst of discharge prior to initiation of discharge in ipsilateral extensors (*left*) but was almost totally inactive during both flexion and extension of the contralateral wrist (*right*). The four traces in each group are, from above down, ipsilateral extensor EMG, unit, contralateral extensor EMG, and contact condition.

velocities ranging from 78 to 11 m/sec. Latencies of modification in discharge pattern in relation to movement did not differ appreciably as a function of ADL. Thus, the increases or decreases of discharge frequency in units with short ADLs had latencies which were approximately the same as the latencies for increases or decreases of discharge frequency in units with long ADLs. Neither did direction of change in discharge frequency (increase or decrease) distinguish between units whith short and long ADL. The major difference between responses of units with long versus short ADLs is typified in the contrast between the responses of the unit with ADL = 0.9 in Fig. 7 and the unit with ADL = 5.4 in Fig. 8. For the unit with short ADL there was complete quiescence prior to the burst of discharge which preceded extension, whereas the increased discharge of the unit with the longer ADL was superimposed on steady tonic activity which had persisted throughout flexion. For the entire sample of 182 PTNs recorded from all 5 monkeys, phasic increases of discharge frequency in the absence of prior tonic activity were confined to units with ADLs of less than 1.5 msec. The converse was not true. Thus, a number of units with short ADLs were quiescent with both arms at rest, but became tonically active during flexion and then showed further increases (or decreases) prior to extension.

The abruptness of reduction in discharge in those units responding with decreases of discharge frequency did not distinguish between units with long and short ADLs. Thus, the unit with ADL of 6.0 in Fig. 8 paused just as abruptly as the units with ADLs of 1.0 in Fig. 7.

4. Is activity of PTNs related only to contralateral movements or are there some PTNs whose discharge is related to ipsilateral movements as well?

Two of the five monkeys used in these studies were trained to use either hand. In these two monkeys the activity of 40 PTNs was compared for ipsilateral versus contralateral wrist movement. Two aspects of the activity of these 40 PTNs will be considered: *a*) discharge frequency during maintained wrist flexion versus discharge frequency during periods when both arms were at rest, and *b*) changes in discharge frequency in relation to transient extension of the ipsilateral wrist.

a) *Maintained flexion.* Thus far in this report there has been no consideration of changes in discharge frequency of PTNs between a condition with arms at rest versus a condition of steady flexion preceding transient extension. Many PTNs showed a striking change (either increase or decrease) of activity during steady flexion of the contralateral wrist as compared to a period with the arms at rest. Many units also showed differences in discharge frequency between rest and steady ipsilateral flexion. Ten of the 40 PTNs showed a twofold or greater change in discharge frequency during ipsilateral flexion as compared to rest. Of these 10 units, 6 showed reduced activity and 4 showed increased activity. These changes during ipsilateral flexion probably indicate relations of PTN discharge to ipsilateral movement, but the alternative possibility that they are actually associated with modifi-