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THE MONKEY GLOBUS PALLIDUS: NEURONAL DISCHARGE PROPERTIES IN RELATION TO MOVEMENT

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SUMMARY

1. Recordings were made of the natural discharges of 388 pallidal neurones in awake, free-to-move monkeys in order to describe the discharge properties of such neurones in relation to normal movement performance.

2. Of the 388 neurones, 156 discharged only in association with one direction of movement of the forelimb about a specific joint. If that movement was not taking place the neurone would not discharge.

3. All joints and directions of movement for the upper limb were represented by clusters of cells within the pallidal population.

4. Twenty-nine per cent of neurones co-varied with movement of both the contralateral and ipsilateral limb for the same direction of movement about a given joint; distal movements were represented with similar frequency to proximal movements in this group.

5. Afferent information provided by natural stimulation of peripheral receptors did not directly influence either the discharging or non-discharging pallidal neurones.

6. Movement related neurones were regionally organized and were found in the posterior part of the pallidum.

INTRODUCTION

Aspects of physiological organization of the basal ganglia are still in doubt, despite the vast research effort that has been carried out over the sixty years since the basal nuclei were first implicated in movement abnormalities (Wilson, 1912). Clinico-pathological correlations have repeatedly confirmed Wilson's (1912) original findings (Wilson, 1925; Denny-Brown, 1962; Martin, 1967), but, because of the non-specificity of the pathological processes involved in the genesis of disease states, no more detailed information has been provided.

Similarly, histological, biochemical and pharmacological approaches, although they have added greatly to knowledge of anatomical connections and to the alleviation of symptoms of Parkinson's disease, have been unable to contribute much information regarding cellular function in the basal ganglia. Electrophysiological techniques that require the stimulation of one component nucleus while recording cellular activity in another nucleus are fraught with difficulties which arise in part from the complex anatomical organization that exists within the basal nuclei.

It was considered that a better understanding of function could stem from the use

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of the technique of chronic extracellular recordings from awake free-to-move animals (Porter, Lewis & Horne, 1971). The first step was to obtain a detailed analysis of the discharge properties of basal ganglia neurones in relation to normal movement. Such properties could be used as a baseline for future investigations involving manipulations of basal ganglia function.

There have already been several studies describing the natural discharges of both neostriatal (DeLong, 1972; Kitsikis, Angyan & Buser, 1971; Buser, Pouderoux & Mereaux, 1974) and pallidal neurones (Travis, Hooten & Sparks, 1968; DeLong, 1971; Anderson, 1977) in awake monkeys. However, the results of such studies were of a qualitative nature and failed to reveal much more information regarding function than that suggested by previous clinico-pathological studies, viz. that discharges of cells in the basal ganglia were associated with movement performance. A more detailed description of the natural discharges of basal ganglia neurones is still required. The particular nuclear component chosen for the present study was the globus pallidus as this is the principal efferent nucleus of the basal ganglia (Carpenter, 1976) and also because the histological structure is such that it facilitates unicellular recordings (Fox, Andrade, Luqui & Rafols, 1974). The results of this study concern the description of the natural discharges of pallidal neurones in relation to normal movement performance.

METHODS

Four monkeys (*Macaca fascicularis*) of either sex were trained to perform movements and to participate in the following procedures.

1. *A simple movement task.* This required the animal to pull an electronically controlled horizontal lever through a distance of 1·5 cm, with either the right or the left hand, into a specified target zone restricted to 0·5 cm displacement. A correct pull was signalled to the animal by a 400 Hz auditory cue. The animal then released the lever and collected the food reward from a position alongside the handle which had been released. The force required to displace the lever was linearly related to the lever displacement, and the animal was required to generate 400 g to enter the target zone. A perturbation could be introduced in a pseudo-random fashion during the lever excursion. The perturbation consisted of a 2 kg step increase in force lasting for 8 msec and opposing the direction of lever displacement. The right upper limb, in two animals, was kept relaxed by the animal's side prior to the commencement of each pull–retrieve cycle. Each cycle would commence on an instruction from the experimenter.

In the other two animals the pull–retrieve cycle was purely self paced; the animals pulled the lever and collected the food reward in a continuous and rapid fashion.

2. *Selected active movement of only one joint.* For selected movements of only the wrist and fingers the animal's upper limb was held at the wrist and the whole limb maintained outstretched. Only the animal's fingers, hand, wrist and thumb were fully mobile. A morsel of food was moved in various directions; dorsal, ventral, ulnar-ward or radial-ward, in front of the animal's hand, which the monkey moved to follow the food in all directions. In order to grab the food the animal had to make repeated extension and flexion movements of the fingers and thumb for each of the wrist positions. For selected movements of the shoulder, elbow and forearm the food collect part of the pull–retrieve cycle was varied in a similar manner to that outlined by Lemon, Hanby & Porter (1976).

3. *Passive manipulations of the animal's limbs.* For this task the animals were taught to remain relaxed and to accept passive manipulations of joints and stroking of hairs and skin of both forelimbs and other parts of the body.

The first procedure was used to detect movement-related units and also to obtain a record of cellular discharges associated with lever displacement. The second procedure was utilized to characterize more fully the relationship to particular joint movement and the third procedure was used to determine the passively generated 'sensory' responses of the unit.

Four to six weeks of daily training were required before the animals were proficient at all these tasks. The animals were then anaesthetized with intramuscular ketamine (Ketalar, Parke-Davis) and subjected to surgery with full aseptic conditions. A specially designed headpiece similar to that described by Porter *et al.* (1971) was fixed to the animal's skull so that the turret, which carried the electrode assembly, was positioned over a 16 mm diameter craniotomy which was in turn centred at the stereotaxic co-ordinates A12, L8.

The bared ends of a pair of stainless steel wires were sutured into the bellies of four muscles. The wires were then led subcutaneously to a skin defect in the scalp.

Dental acrylic was used to attach a multipin socket, used for all electrical connections, to the headpiece and also to seal all electrical leads. The animal was allowed to recover for two days following the operation.

Daily recordings from pallidal neurones were then carried out using glass coated tungsten micro-electrodes. The daily recording sessions were continued for a period of 1 month. The records of cellular discharges, an indication of the instantaneous lever position and the electromyographic (e.m.g.) records were simultaneously stored on magnetic tape (Ampex FR1300). On-line analysis of the relationship of cellular discharges to lever displacement was available in the recording laboratory and was performed by a computer (PDP 11/40). The analysis programme could use the lever displacement record or the onset of the perturbation to construct peri-response time histograms in the assessment of neuronal responses associated with active movement and neuronal responses provoked by the perturbation introduced during the movement.

The stereotaxic co-ordinates of all electrode penetrations were recorded and also the depths at which the recorded units were encountered.

At the end of the 4 week period of recording, the animals were deeply anaesthetized and perfused through the heart with formol-saline and the brain was prepared for histology. Marker electrodes were passed through the brain with the head in the stereotaxic frame, and coronal sections, 40 μm thick, were cut with a freezing microtome in the exact plane of the marker tracks and stained with cresyl violet.

The anatomical location of all cells whose activities had been studied was determined by the identification of electrode tracks traversing globus pallidus. This was achieved by matching the stereotaxic co-ordinates of each penetration of the electrode map with the co-ordinates derived from the histological map. Cells were then assigned to the appropriate track and their depths below the cortical surface plotted on enlarged tracings of the relevant histological section. The accuracy of these depths was confirmed by comparing the 'electrical' depths of the functional markers with the anatomical equivalent structure. Pl. 1 illustrates the tissue reaction to the electrode penetrations traversing globus pallidus.

RESULTS

Movement related units

Recordings were made of the discharges of a total of 388 neurones in the left pallidum. All units were recognized by their natural discharges and 156 of the 388 neurones discharged in association with some aspect of the complex movement task. For eighty-one such neurones, recorded from two animals trained to relax the right upper limb, it was found that whenever the animal stopped moving, the discharge of the movement related neurone also ceased. The neurone would only again discharge in association with the onset of the next movement.

This characteristic silence during motor inactivity is illustrated by the relative lack of discharge in the first 1 sec of most peri-response time histograms, before lever displacement (Fig. 1*C*, *D*, *E*, *F*). During that time the animal was not moving but was sitting quietly, arm by the side, awaiting the instruction to move.

The relationship to movement of the discharges of such neurones was found to be very specific. The use of the techniques outlined in the methods, revealed that the

discharges of many neurones were related to only a particular direction of movement about one joint in the right upper limb. If the particular movement was not occurring the neurone would not discharge. The discharges of a total of forty-eight neurones, from both the external segment (GPE) and the internal segment (GPI) were characterized according to their relationship to a particular direction of movement and the specificity of the discharges of these forty-eight neurones is shown in Table 1.

TABLE 1. Specificity of movement relationship. This table sets out the number of cells, with their location in globus pallidus, whose discharges were characterized as being specifically related to a direction of movement about a particular joint.

Movement	GPE	GPI
Finger flexion	9	3
Finger extension	2	1
Wrist flexion	—	1
Wrist extension	—	1
Supination	1	1
Supination/forearm flexion	—	2
Forearm flexion	7	1
Forearm extension	3	2
Arm extension	4	1
Arm flexion	1	—
Shoulder extension	1	—
Shoulder internal rotation	1	1
Shoulder external rotation	1	—
Chewing	—	4
Total	30	18

It is evident that many movements at most joints in the upper limb, distal and proximal, were represented in the discharges of individual neurones. 'Chewing units' in Table 1 refers to pallidal neurones which discharged in temporal association with masticatory movements. It was not possible to determine the exact movement but the periodic discharge bursts occurred in association with either the opening or the closure of the mouth. Further, if the animal stopped chewing the discharge would also cease. Such findings implied that the 'chewing units' had similar properties to the pallidal neurones related to limb movements.

Fig. 1 illustrates some histogram examples of this specificity in association with movement. The trace below each histogram illustrates the time of occurrence and the duration of the lever excursion. The construction of each histogram was triggered at point 0. In the period following lever movement, the animal reached out with the same hand and collected a food reward (about 1 sec after the lever movement).

Histogram *A* i was constructed for a cell whose discharge was related to elbow extension. Two peaks of activity occurred; the first peak of activity was associated with extension of the elbow to grasp the lever. The second peak was associated with antagonist activity at the elbow during lever displacement (see next section of Results) and also with the subsequent extension of the elbow for food collection by the hand. In the construction of the next histogram, the animal was made to collect the food with the limb completely outstretched, thus increasing the amount of elbow extension. Fig. 1 *A* ii is the histogram for such a task; as is apparent the second peak is

greatly pronounced both in height and width, demonstrating a pronounced increase in cellular discharge for the more pronounced elbow extension.

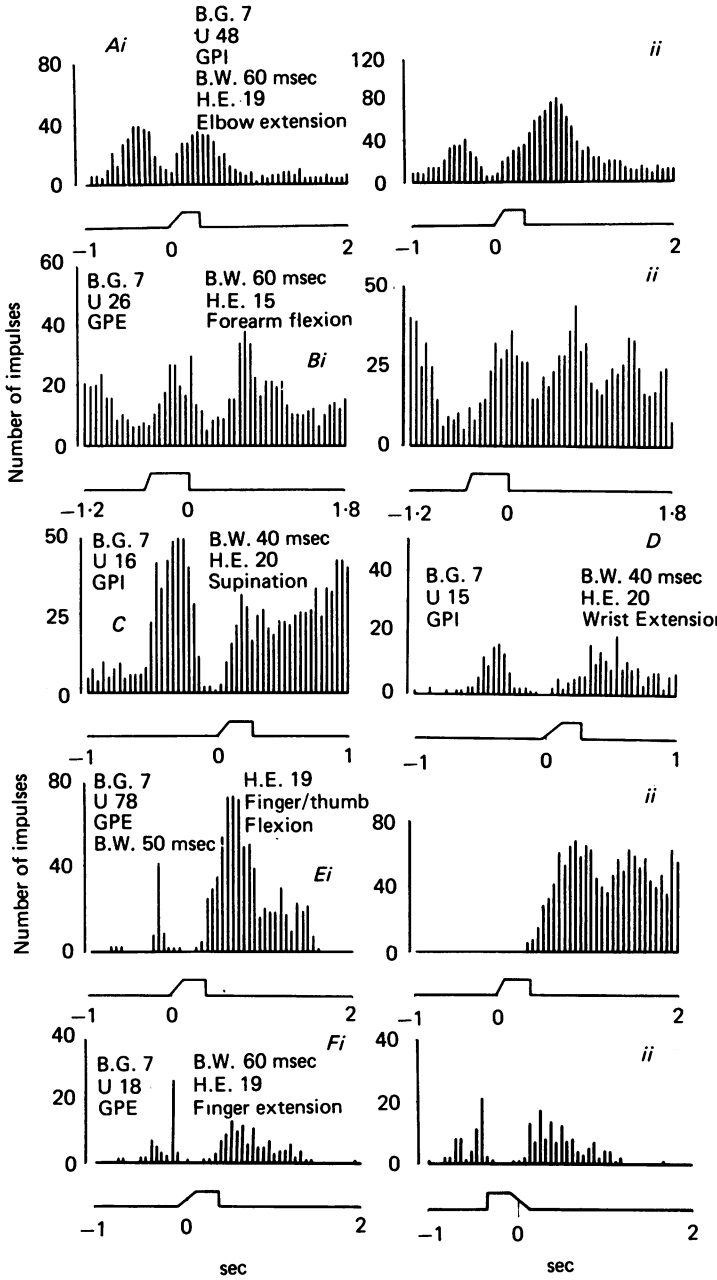

Fig. 1. Examples of histograms of the discharges of individual pallidal neurones in relation to specific movements. In each case the particular movement with which the acceleration of unit discharge was associated is indicated. A full description is given in the text. (B.G. 7, animal identification; U, unit number; GPI, globus pallidus internus; B.W., bin width; H.E., number of repetitions of the task).

The histograms in Fig. 1 *B* were constructed for a cell whose discharge was modulated with forearm flexion. Histogram *B*i shows an early first peak associated with the period when the elbow was in the mid-flexed position; a posture requiring tonic activity in the elbow flexors. The second peak was associated with the elbow flexion required for lever displacement and the third peak was associated with the elbow flexion involved with bringing the food reward to the mouth. The pattern of cellular discharge is different in Fig. 1 *B*ii; this histogram was constructed for pull–retrieve cycles which used banana as a reward. This meant that some banana always stuck to the animal's fingers requiring three or four attempts at licking the fingers clean. The final three peaks of cellular activity in Fig. 1 *B*ii are associated with this repetitive cleaning of the fingers; a motor task requiring alternate small flexions and extension of the elbow as the animal licked the fingers, slightly extended the elbow to look at its fingers and again flexed the elbow to bring the fingers to the mouth for the next lick.

Histogram 1*C* was constructed for a cell whose discharge was modulated with supination of the right forearm. The first peak in cellular discharge occurred just before it grasped the lever as the forearm was supinated from the resting mid-prone position. The second smaller peak was associated with lever displacement and the subsequent sustained cellular discharge was associated with bringing the food reward into the mouth with the supinated forearm.

Fig. 1 *D* is a histogram constructed for a cell whose discharge was modulated with wrist extension. There are two peaks of cellular activity, both associated with slight wrist extension for placing the hand in a 'position of function' for pulling the lever (first peak) and collecting food and bringing it to the mouth (second peak). Histogram 1*E* was constructed for a cell whose discharge was modulated with finger/thumb flexion. The first peak was associated with grasping the lever and the second more pronounced peak was associated with grasping the food and bringing it to the mouth.

Histogram 1*E*ii was constructed for the discharge of the same cell, with a different food collect pattern which required the animal to make repeated grasps at the food with index finger and thumb before the food was released by the experimenter. This led to three peaks in cellular discharge, each associated with the animal's pincer action of the finger. The third of these is seen commencing at the end of the histogram. Histogram 1 *F* was constructed for a cell whose discharge was modulated with finger extension. There are two peaks of activity; one occurred with the extension of the fingers before it grasped the lever and the second occurred on release of the lever. *F*i shows both peaks in activity. *F*ii was constructed using the return of the lever to the zero displacement to trigger each histogram event. The sharp increase in cellular activity forming the second peak has its onset closely related in time with the return of lever displacement to zero.

When responses of external and internal segment cells, firing in association with the same kind of movement, were compared there was no systematic difference between their activity patterns. This similarity extended to movements at each of the several joints examined. A comparison between the discharges of neurones of both segments of the globus pallidus, for four movements of a range of different joints of the right upper limb is shown in Fig. 2.

The discharges of the remaining thirty-three neurones, all of which had demonstrated silence during motor inactivity, could not be attributed to a specific

movement of the upper limb. This was either because the sensitivity of the techniques for determining specificity of movement were not adequate to test all limb movements or that the cellular discharges were involved with movement about other regions of the body such as neck, trunk, pelvis or lower limb. This latter explanation is most likely as it was often noted that cellular discharges appeared to be related to movement of the neck or the leg but this could not be proved successfully with the techniques available because only minor modulations would show up in the histogram.

The discharges of seventy-five other neurones, which were also related to movement, were not tested for silence during motor inactivity, nor for their specificity to

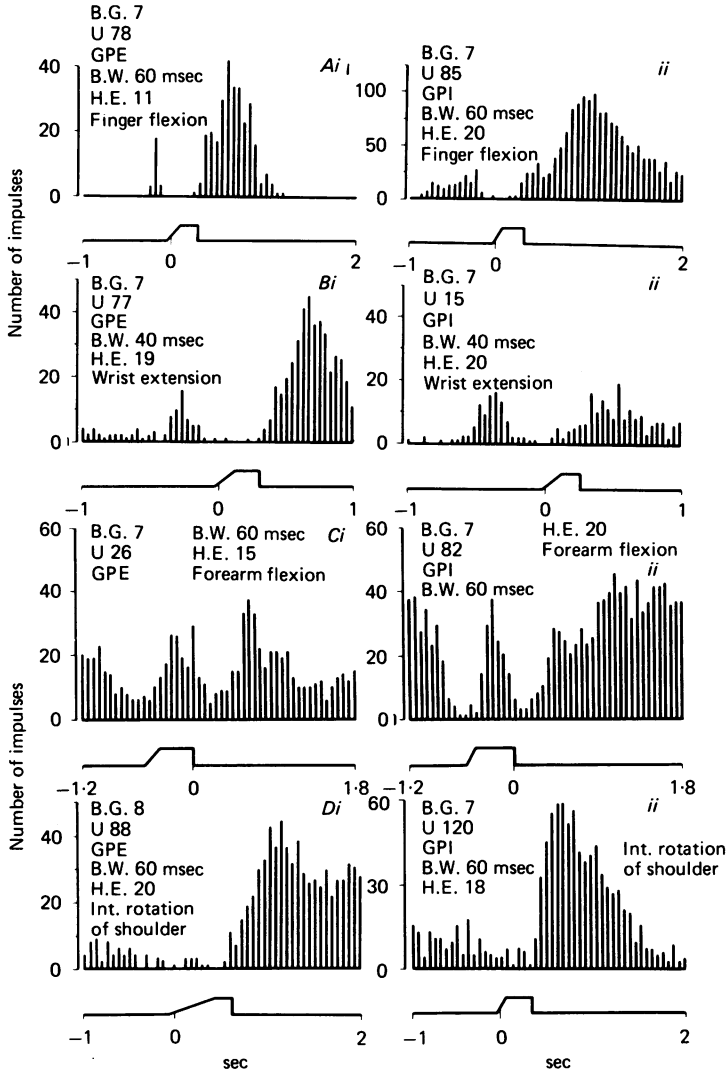

Fig. 2. Examples of histograms illustrating the similarity in discharge patterns between GPE (external segment) and GPI (internal segment) neurones for the same movement at four different joints of the right upper limb. Abbreviations as for Fig. 1.

particular directions of movements about different joints. However many such neurones did show periods of total silence and also histogram patterns not unlike those constructed for neurones whose discharges were definitely characterized. It was thus concluded that discharges of these neurones were probably also related to a direction of movement about a specific joint.

Pallidal discharge and muscle activity

In the analysis of the specificity to movement of pallidal discharge it was noticed that on certain occasions pallidal discharge co-varied with a movement which involved more than one joint, e.g. supination and forearm flexion. This and other observations suggested an association of pallidal discharge with contraction of particular muscles.

Fig. 1*Ai* illustrates a histogram constructed for an elbow extension unit. It is apparent that a burst of discharge occurred during actual lever displacement, at a time when the elbow was actually flexed. This tended to contradict the previous findings in regard to pallidal discharge and direction of joint movement, unless of course, the pallidal neurone discharged in association with the activity of the triceps muscle. This was tested in the following manner. Some of the larger deflections of the e.m.g. record from the right triceps muscle recorded simultaneously with the cell's discharge in left globus pallidus were used to construct a histogram over the same number of lever excursions as those used for the construction of the unit discharge histogram. This allowed a visual comparison of the e.m.g. activity and cellular discharge both referred to the onset of lever displacement. The two histograms are shown in Fig. 3.

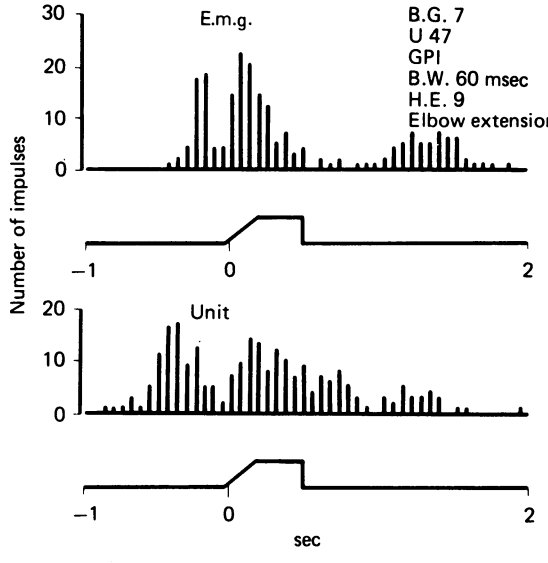

Fig. 3. Comparison of histograms of e.m.g. activity and cellular discharges for a muscle and unit which were both related to elbow extension and which were recorded simultaneously. The histogram of e.m.g. activity was constructed by triggering the computer from some of the larger deflections in the electrical record from the muscle. Abbreviations as in Fig. 1.

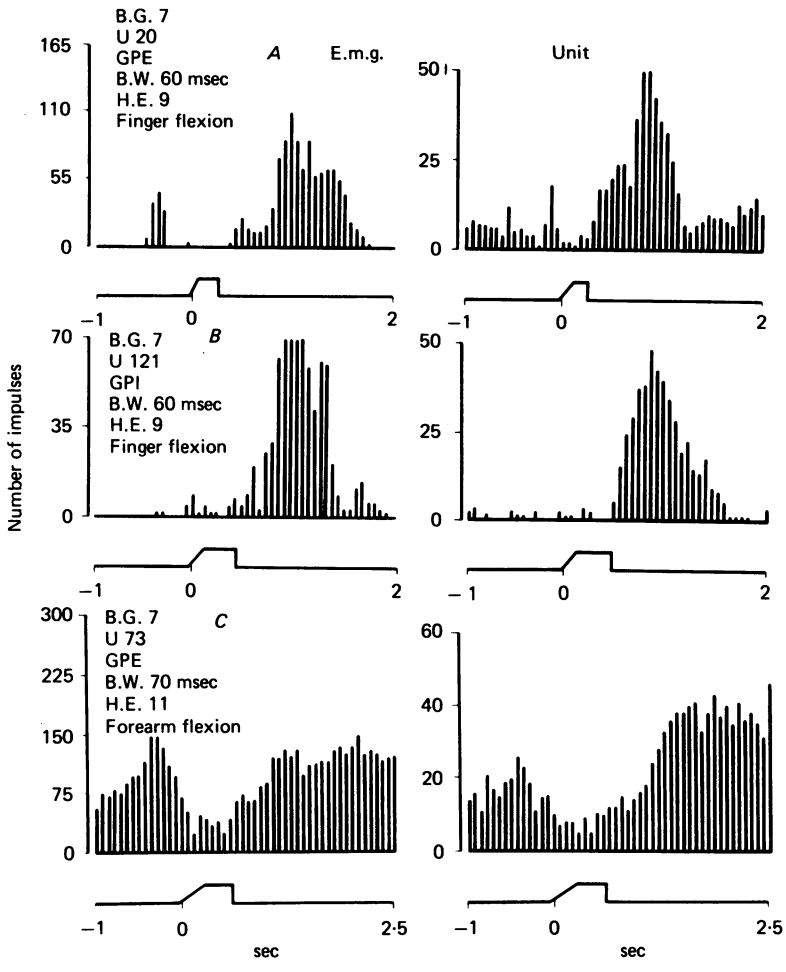

Fig. 4. Comparisons of histograms of e.m.g. activity and cellular discharges recorded simultaneously. Abbreviations as in Fig. 1.

It is apparent that a similarity existed between the timing and duration of the waves of e.m.g. activity for these large deflections in the muscle record and of the unit discharges. More important, the unit discharges during lever displacement coincided with 'antagonistic' e.m.g. activity during the same period. This finding seemed to confirm the suggestion that pallidal discharge covaried with muscle activity. The relative timing of the waves of e.m.g. activity and of cellular discharge deserves comment, however, because, even for the one cell and muscle pair, increases in cellular discharge would sometimes lead and at other times follow increases in e.m.g. activity. In other instances the cellular and muscle activities appeared to coincide. Whereas the first peak of unit discharge occurs before the first peak of e.m.g. activity in Fig. 3, the same is not true of the second peak. This serves to emphasize the looseness of the association between neuronal and muscular activity and does not support a tight coupling between pallidal activity and muscle contraction. Cross-correlation analysis

for individual performances of natural movements also revealed these differences in relative timing.

It was possible to compare the discharges of another twelve units with an appropriate one of the four simultaneously recorded e.m.g.s in the same way as was done for Fig. 3. All twelve examples showed this form of general covariation between the unit discharge and muscle activity and three such comparisons are shown in Fig. 4.

Responses of pallidal neurones to bilateral movements

From a total of 104 movement related units, thirty were found, from two animals, which discharged in association with movement of both the contralateral and the

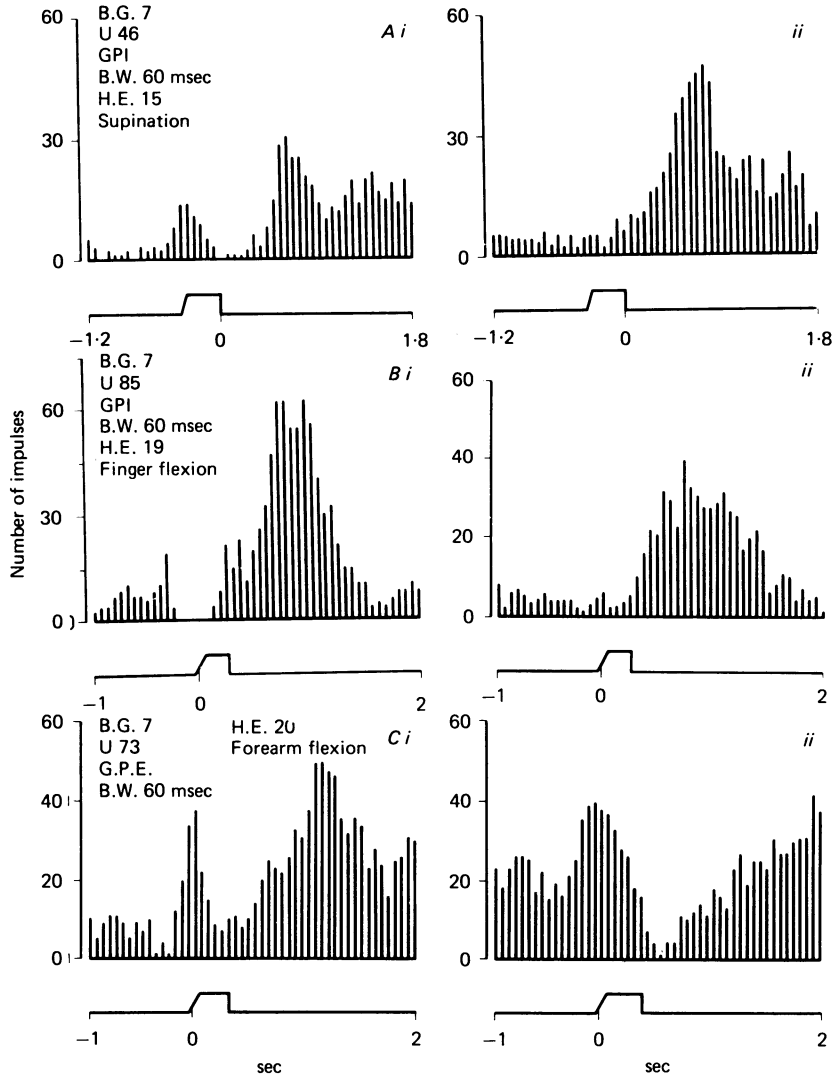

Fig. 5. Examples of histograms of neurones in the left pallidum whose discharges were related to the same movement of the ipsilateral and contralateral limbs. RH, right hand limb used; LH, left hand limb used. Other abbreviations as in Fig. 1.

ipsilateral limb. Units with a bilateral relation to movement were found in equal numbers in both segments of the pallidum. In one animal in which fourteen units were clearly characterised according to their relationship to a specific movement, it was found that the relationship to movement of each unit was to the same direction about the same joint for both limbs.

Table 2 sets out the specificity of neuronal discharge for ipsilateral movements at the various joints of the upper limb. Fig. 5 illustrates some histogram comparisons of cells, whose discharges were modulated in relation to ipsilateral and also to contralateral movements.

TABLE 2. Specificity of movement relationship to ipsilateral limb. This table sets out the characterization of cellular discharges in relation to specific directions of joint movement for those cells in the left globus pallidus shown to change their discharges for both ipsilateral and contralateral limb movements

Finger flexion	4
Finger extension	1
Wrist flexion	1
Supination	1
Supination/forearm flexion	2
Forearm flexion	3
Elbow extension	1
Internal rotation of shoulder	1
Unknown	4
Total	18

Location of movement related units

The only cells used for localization were those whose discharges were characterized as being related to specific directions of movement or those cells whose discharges, although not definitely characterized, were nevertheless phasically modulated with movement. This latter criterion was considered to be justified as all neurones whose discharges were characterized demonstrated phasic modulations in association with the pull-retrieve cycle.

A common feature in all animals was that the great majority of cells whose discharges were related to arm movement were located in the posterior half of globus pallidus well posterior to its maximum expansion. In establishing the regions of globus pallidus, the measured antero-posterior stereotaxic co-ordinates were less useful than the location of the maximum mediolateral width of the structure in each of the animals. Using this to compare results obtained in different animals, almost all cells with movement related cellular discharges were found in the posterior part of the globus pallidus. This applied to both the internal and external segments. The most clear cut example of this finding was in one animal in which multiple penetrations, all in a regular manner, were made over the anterior half of globus pallidus without finding more than one or two cells whose discharge was movement related. However, on reaching a region well posterior in globus pallidus, a group of cells whose discharges were associated with movement was found. These cells were all in the upper half of the external segment of the globus pallidus and all within half a millimeter of each other in nearby penetrations. There was a tendency for cells, whose discharges were

movement related, to occur in clusters separated by areas containing cells whose discharges were not movement related.

Another finding was that all cells in the external segment with discharges related to arm movements were located in the upper half of the external segment. The lower half of the segment was always explored by the same electrodes but cells with movement-related cellular discharges were not encountered. Cells in the internal segment, whose discharges were movement related, had no such organization. These findings are illustrated in Fig. 6 for the histological observations made in one of the animals.

It was observed that the groupings of cells whose discharges were modulated with chewing movements were always in close proximity to cells whose discharges were

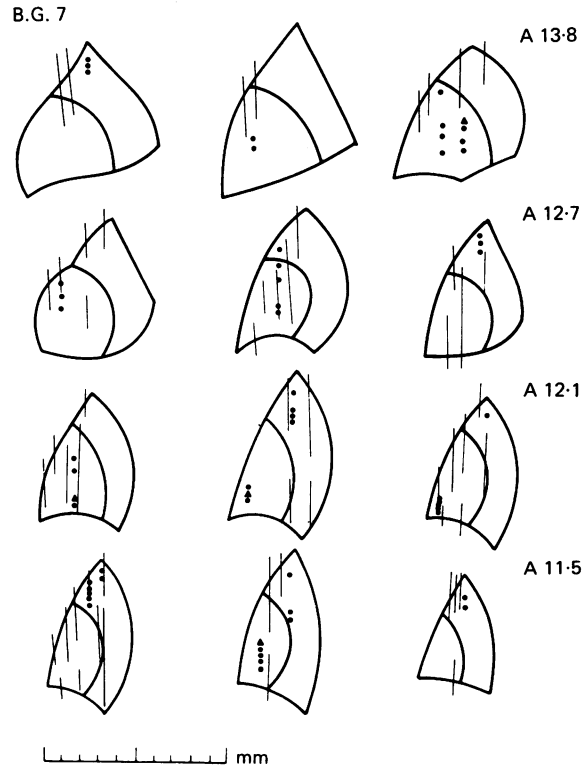

Fig. 6. Illustration, for one animal, of the regional organization of pallidal neurones whose discharges were characterized as related to specific movements of the upper limb (filled circles) or to chewing movements (filled triangles). The tracings were taken from coronal sections of the whole electrode field on the left side. The antero-posterior order of these sections begins at the top left and is to be read from left to right in successive lines. The stereotaxic co-ordinates indicated are those actually pertaining to the sections of the brain of this animal for the right hand column. No attempt has been made to match the actual histology to diagrams from a standard atlas because of the inherent inaccuracies and approximations involved. The fine vertical lines indicate the segments of other identified electrode tracks visualized in these same sections. Although recordings of neuronal activity were made in these other tracks, none of the discharges were clearly associated with arm movements.

modulated with movements of the upper limb. Fig. 6 shows this feature. Records were made of only four 'chewing' cells but there were numerous other such cells in the close vicinity of the ones studied in detail in this animal.

Response of pallidal neurones to sensory inputs

A total of 112 pallidal neurones was examined from two relaxed animals for a possible response to peripherally generated sensory stimuli. The aim was to examine as many cells as possible whose discharges were movement related, and also to assess some other local cells unrelated to movement in case a sensory response existed in spite of their lack of modulation with movement. Seventy of the 112 cells which were tested had discharges that were movement related. No cell was found to have consistent responses to any sort of non-noxious peripheral sensory input which could be tested.

Similarly, 257 pallidal neurones were analysed for possible responses to imposed perturbations during the actual movement performance. The discharges of 105 of these neurones were modulated with some aspect of the movement task. None of the neurones showed any consistent response to the imposed perturbation.

DISCUSSION

The results reported here not only agree with those of DeLong (1971) but also extend his findings. In addition, they provide baseline observations for future manipulative experiments. A new finding was the presence of neuronal silence during motor inactivity for neurones whose discharges were related to a particular movement. Certainly neither DeLong (1971) nor Travis *et al.* (1968) described such a property in pallidal neurones. In DeLong's (1971) experiments this phenomenon would not be detected during the movement task as this was rapid and continuously repeated with the animal's hand always grasping the lever; the animal never relaxed its limb during the motor task. Hence, during the rest phase, while posture was held, DeLong described the discharge patterns of the movement related units as being either of high frequency (HFD) or low frequency with superimposed bursts (LFD-B). The only possible explanation for the discrepancy between the findings of this report and those of DeLong is that his animals were at no time fully relaxed. Similarly, Travis *et al.* (1968) were interested in gross complex movements associated with behavioural situations and they failed to describe detailed properties of their three movement-related pallidal neurones.

The movement-related cellular discharges demonstrated forms of relationship to movement not previously described for pallidal neurones. Each neurone displayed modulation of discharge specific for a particular direction of movement at a particular joint of the right upper limb. Modulation of the discharge of individual neurones to various directions of movement was found for most joints of the upper limb involved in the movement task, i.e. neurones related to movements at proximal or distal joints were equally represented in the pallidum. Further, this property was equally present for both external and internal segment neurones related to either proximal or to distal joint movements. This phasic relationship to specific directions of movement about certain joints has been shown to also occur in motor-sensory cortex neurones by other

workers in this laboratory (Lemon *et al.* 1976; Brinkman, Bush & Porter, 1978) and more importantly, this relationship has also been demonstrated for primate substantia nigra neurones (R. Iansek & M. K. Horne, personal observations); suggesting that this is a common feature for basal ganglia nuclei.

Another observation concerned the co-variation between the activity of a pallidal neurone and the e.m.g. activity of a muscle when both were related to the same direction of movement about one given joint. This co-variation, in addition to the similarity of pallidal neuronal discharge to e.m.g. activity when movement occurred at many joints or even when muscle activity was involved in an antagonistic role, implied that the pallidal neurones may have been loosely coupled to the activity of specific muscles, and perhaps it was this coupling which was manifested as a relationship to the direction of movement about a joint.

Definitive proof for such a concept and the examination of the nature of the loose coupling would require simultaneous recordings of e.m.g. from all muscles involved in all possible movements at any one joint. A comparison would have to be made of the pallidal neuronal discharge for all movements with all e.m.g.s involved in those movements. Such a difficult experiment is required for proof of the relationship of cellular responses to muscle contraction.

The finding within the pallidum of many neurones, whose discharges, although unrelated to movement, were nevertheless tonic, requires some further elaboration. DeLong (1971) described this tonic activity in great detail and used differences in its features to differentiate between internal and external segment neurones. However, on the basis of the findings of this report, it may be that one of the reasons for the continuous nature of this discharge of unrelated units was that such neurones were coupled to postural muscles acting to support the trunk, neck and head or involved with the upper and lower limb girdles. These muscles were obviously involved with stabilizations and movements about vertebral and proximal joints. Even in a seated, relaxed animal there was continual changing activity of such musculature, not to mention continuous small movements of the arms, trunk and legs. If the animals were not relaxed then the possibilities for muscle activity were greatly increased and cellular discharges accompanied this.

The location of arm-movement related units within the pallidum and indeed the possible clustered organization of such units are in agreement with the known anatomical organization within the basal nuclei. Both Kunzle (1975, 1977) and Jones, Coulter, Burton & Porter (1977) implied that the arm and leg zones of the sensory motor cortex were represented in the upper half of the rostro-caudal extent of the putamen. The termination of the cortico-striatal projection to this region was arranged in multiple patches, each patch separated from the other by 0·5–2·0 mm. Further, the strio-pallidal projection has been shown to be organized in such a way that the upper half of the putamen projects to the upper part of both segments of the globus pallidus (Szabo, 1962, 1967, 1968; Cowan & Powell, 1966; Kim, Nakano, Jayaraman & Carpenter, 1976). These anatomical data are consistent with the findings in this report of the presence of arm movement related units in the upper half of the external globus pallidus and of the clustered arrangement of such units.

In addition, Kunzle (1975, 1977) and Jones *et al.* (1977) found that the face zone of the sensory-motor cortex projected to the putamen in close proximity to the arm

zone, again providing a basis for the close association in the pallidum of units related to upper limb movement with those units related to chewing movements.

Another indication of the likely location of movement related neurones in the posterior part of globus pallidus came from the finding of Kuo & Carpenter (1973) on the pallido-thalamic projection in the monkey. They claimed that the caudal portions of the medial pallidal segment established synaptic connections predominantly with neurones of the ventro-lateral nucleus of the thalamus, pars oralis (VL_o), a region known to project to the precentral gyrus. By comparison more rostral parts of the internal pallidal segment were found by Kuo & Carpenter to project to the parvocellular component of the ventro-anterior nucleus of the thalamus, a region related anatomically with the premotor cortex (Kievit & Kuypers, 1977).

A substantial proportion (29 %) of movement related neurones was found to be related to both ipsilateral and contralateral movement. This was in agreement with DeLong's (1971) finding, although he reported a proportionally smaller number (15 %) of bilaterally modulated neurones. The higher proportion of such neurones found in the present study can be explained partly by the more complex movement task and partly by the more complete analysis of movement carried out at most joints of the upper limb.

The bilateral relationship to movement of pallidal neurones was again in accord with anatomical data as both sides of the motor cortex have been shown to project to the putamen (Kunzle, 1975; Jones *et al.* 1977) implying that in relation to movement of one limb both the ipsilateral and the contralateral motor cortex have access to the ipsilateral putamen and as a consequence could influence the ipsilateral pallidum.

A final point relates to the functional significance of the demonstrated bilateral relationship to movement of pallidal neurones and to their organization. Many workers (Ranson & Berry, 1941; Kennard, 1944; Laursen, 1955; Carpenter, Whittier & Mettler, 1950; Denny-Brown, 1962) had noticed in the past that small experimental lesions placed in the putamen, the caudate or the pallidum resulted in no observable effect on motor performance. It was only when larger lesions were produced (Mettler, 1945; Carpenter *et al.* 1950; Denny-Brown, 1962) that motor abnormalities became manifest.

Carpenter *et al.* (1950) examined this problem more closely when they investigated the experimental production of hemiballismus in the monkey. They found that the destructive lesion in the subthalamic nucleus had to be at least 20 % by volume. Further, they found that a lesion in globus pallidus or its efferent path could relieve the movement abnormality following the subthalamic lesion but only if the internal segment lesion was greater than 17 % by volume. The unilateral pallidal lesion did not produce any motor abnormalities *per se*; by contrast, bilateral pallidal lesions in animals with bilateral hemiballismus resulted not only in the abolition of the abnormal movement but also in marked akinesia.

The relationship between paucity of movement and bilateral destruction of the pallidum in the monkey had been previously described by Mettler (1945) and Richter (1945) and confirmed by Denny-Brown (1962). Martin (1967) found a similar relationship for man. The underlying physiological mechanisms for these findings have never been explained.

The findings of this report provide a possible answer to this problem. It has been suggested that movements of the arm are 'represented' in the discharges of neurones arranged in separate clusters distinct from one another. This finding may explain the requirement in the Carpenter *et al.* (1950) investigation for a lesion of a certain size, as all the clusters of relevant neurones would have to be destroyed before relieving the previously produced movement abnormality. However, when all the clusters of neurones relevant for a movement of a particular body part were destroyed unilaterally, there still existed a basis for normal motor control through the utilization of similar clusters in the contralateral pallidum. This could explain the other findings of Carpenter *et al.* (1950) that a unilateral pallidal lesion was capable of alleviating hemiballismus but produced no motor abnormalities. It should be mentioned that in the Carpenter *et al.* (1950) case, the contralateral pallidum could not have been driven in an abnormal manner by the disordered subthalamic nucleus output as that subthalamic nucleus had no access to the contralateral pallidum. When both pallida were destroyed there was no more neuronal reserve and the motor abnormality characteristic of absent pallidal function (akinesia) became manifest.

The 29 % of bilaterally movement related neurones could form a minimum substrate for the potential bilateral contribution of a single pallidum to movement and this percentage may increase dramatically if consideration is given to the plastic capabilities of the central nervous system, should destruction of pallidal cells occur.

In conclusion, this report demonstrates that the function of pallidal neurones is intimately concerned with movement performance, as very discrete movements were represented by the discharges of individual neurones. The basis of this relationship to movement may have been due to a co-variation between pallidal discharge and the activity of an individual muscle; however such a concept requires further proof, and it is clear that the association is probably a loose one. The relationship of pallidal discharge to the same movement performance bilaterally, in addition to the clustered arrangement of such neurones within the pallidum, both provides an explanation for, and emphasizes, the great functional reserve of the pallida for movement performance.

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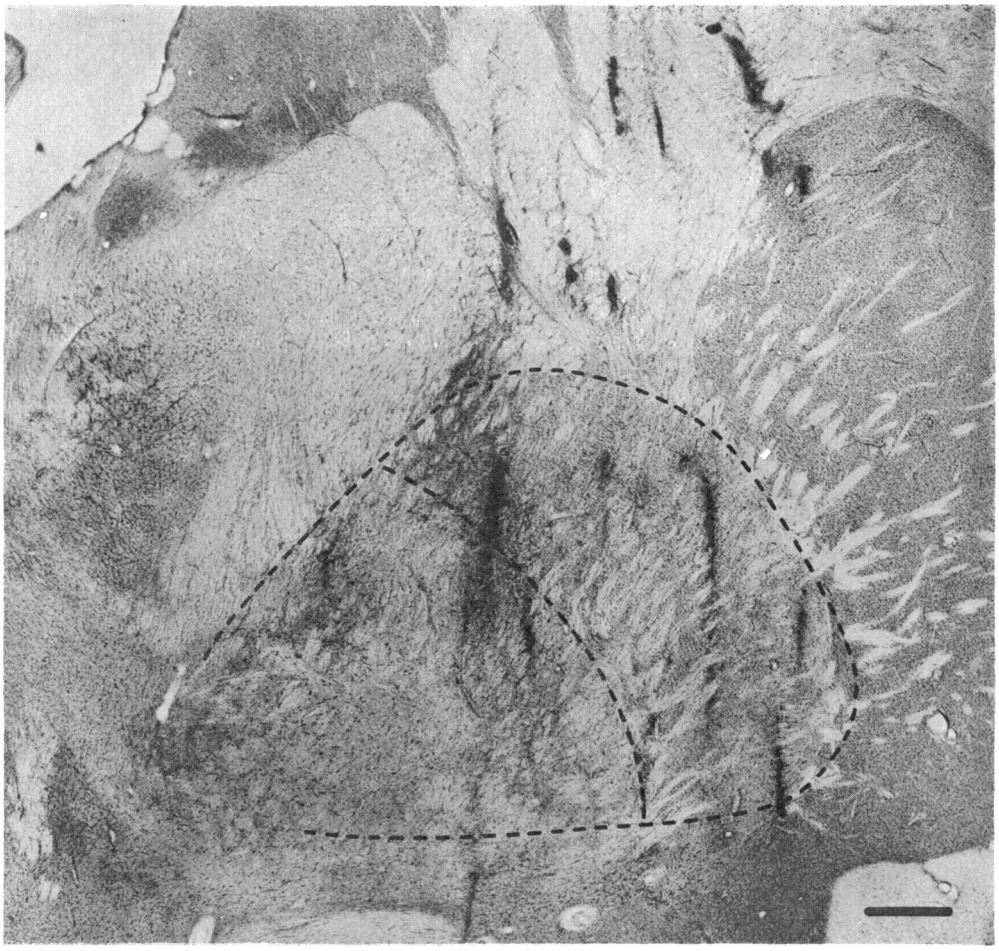

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EXPLANATION OF PLATE

Photomicrograph of a coronal section illustrating the tissue reaction to electrode penetrations which traversed globus pallidus (scale = 1 mm). The globus pallidus is approximately outlined. The putamen is clearly evident to the right of this.