LOCALIZATION IN HUMAN THALAMUS OF UNITS TRIGGERED DURING ‘VERBAL COMMANDS,’ VOLUNTARY MOVEMENTS AND TREMOR

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(Accepted for publication: June 25, 1985)

Summary Microelectrode recordings in the rostral (n. reticularis) and lateral (ventralis lateralis) human thalamus were carried out in locally anaesthetized diskinetic patients during stereotaxic operations. Their responses to voluntary motor tasks prompted by imperative verbal stimuli were tested. Spontaneous and evoked unit activities were studied using computer processing techniques. In the n. reticularis thalami and immediately adjacent thalamic zones, not only units reacting during the initiation of voluntary movements (100–200 msec before the movement), but also units responding to the verbal command itself (‘triggered verbal command’ units) were found. They proved to be concerned directly with the semantic meaning of the command. In the VL anterior area (Voa-Vop in German nomenclature) the majority of the units responded during the phases of initiation and/or realization of the voluntary motor act (‘voluntary movement’ units of Jasper and Bertrand 1966); when these units were not spontaneously rhythmic they were transiently transformed into rhythmic (5 ± 1 Hz) ones. This transformation appeared during the preparation and realization of movement but also in some cells as a rebound phenomenon. In patients without tremor (akinetic and rigid forms of parkinsonism, torticollis), the transient rhythmogenic transformation was frequently provoked by the repetition of motor tasks.

In the posterior part of VL (Vim), cells were driven by proprioceptive inflow coming from a specific peripheral region. They react also during the voluntary movement of the same region. The majority of these units were rhythmic at 5 ± 1 Hz, and they presented a close correlation in phase and frequency with the tremor. The anatomical locations of the three main pools of neurons were determined. ‘Triggered verbal command’ units were placed more anteriorly and laterally. ‘Voluntary movements’ and ‘rhythmic 5 ± 1 Hz units’ had identical spatial localizations. This fact supports the contributions of these two last types to the central mechanisms of both tremor and voluntary movement.

Keywords: human thalamus – unit – verbal command – voluntary movement – tremor

Neurophysiological methods employing micro- or semi-microelectrode techniques make it possible to record activity of single units in the human brain during stereotaxic surgery (Albe-Fessard et al. 1962, 1966, 1967; Gaze et al. 1964; Li and John 1964; Li et al. 1965; Umbach and Ehrhardt 1965; Jasper and Bertrand 1966; Bertrand et al. 1967, 1969; Crowell et al. 1968; Bates 1969, 1973; Ohye and Narabayashi 1972; Ohye et al. 1972; Raeva 1972, 1977a; Hongell et al. 1973; Albe-Fessard 1974; Bechtereva 1974, 1980; Raeva and Livannov 1975; Ohye and Albe-Fessard 1978; Hardy et al. 1979; Martin-Rodriguez et al. 1982; Ohye 1982). The authors mentioned used these methods mainly as a control during the operation to determine the precise localization of some deep structures to be surgically destroyed, thus enabling the surgeon to perform the individual corrections directly during the course of stereotaxic surgery, and greatly improving the effectiveness of the surgical treatment.

Additionally, these techniques provide an opportunity to study subcortical neuronal mechanisms related to the preparation and realization of voluntary movements in man, or to the involuntary peripheral rhythmicity in parkinsonian patients. Some interesting correlations of the rhythmic 5 ± 1 Hz neuronal activity of the ventrolateral nucleus (VL) of the human thalamus with parkinsonian tremor have been described by different authors (see Discussion for references). In the VL, units concerned with the performance of voluntary movement (‘voluntary movement units’ of Jasper and Bertrand 1966) have also been studied (Umbach and Ehrhardt 1965; Crowell et
al. 1968; Raeva 1972, 1977a,b; Hongell et al. 1973). Units in the rostral thalamus, the head of the caudate nucleus (Cd) and the lateral part of the globus pallidus (Pl) which respond selectively to the onset of a verbal command have been described in our previous studies (Raeva 1972, 1977a,b; Raeva and Livanov 1975). The unit responses usually preceded the performance of voluntary motor or mental activity.

The aim of the present study was to analyse the unit activity in the anterior and ventro-lateral parts of the thalamus in non-anaesthetized man during voluntary and involuntary movements and, more precisely, to characterize the neuronal processes which take place during the preparation and performance of voluntary acts provoked through the brain speech understanding system. The data obtained should provide guidelines for further functional delineation of the thalamic nuclei, giving additional possibilities for individual corrections of anatomical coordinates during surgical treatment.

**Method**

Unit activities were recorded extracellularly with tungsten microelectrodes (1 μm at the tip, resistance from 1 to 5 MΩ), inserted by means of a specially developed device into the brains of patients during stereotaxic operations. The trephine hole was positioned 2–3 cm lateral to the midline and 1–1.5 cm anterior to the coronal suture. Stereotaxic determination of the VL coordinates was based on the planes of the atlas of Schaltenbrand and Bailey (1959) which contains the trajectory towards the target point chosen by the surgeon. The microelectrode trajectories — from the premotor cortex toward the VL — were monitored by X rays (Fig. 1). On average, from 40 to 70 levels in various subcortical structures were explored in each patient. Operations were performed under local anaesthesia.

A protective cannula, fixed to the patient's skull with a modified Fairman stereotaxic device, was used to guide the microelectrode along a certain distance to the target point. A microdriver, providing micron graduated extrusion of the tip (up to 20 mm) from the cannula, was used afterwards. Monopolar records of unit activity were provided using the cannula as a grounded shield and a stainless steel clip attached to the scalp incision as a reference electrode. The spike discharges were amplified with an AC amplifier (input impedance 10 MΩ, frequency bandwidth 0.2–5 kHz, amplification factor up to 10⁶) and simultaneously recorded on film and magnetic tape.

A battery of functional tests was used, including various forms of voluntary motor acts such as clenching the fingers to make a fist and opening them, lifting and lowering the extremities, shuttering and opening the eyes, etc. All tests were directed by verbal commands, such as; 'Be ready!,' 'Clench your hand!,' 'Unclench!,' 'Raise your hand!,' 'Lower your hand!,' etc. Passive movements and tactile stimuli were applied as well. For each thalamic unit recorded the same combination of tests was used: the surface EEG and the EMG from the flexors and extensors of the fingers contralateral and ipsilateral to the explored thalamus were recorded in parallel with the thalamic spike activity. The data obtained before, during and after the performance of the tests were analysed.

Along the microelectrode trajectories the localizations of neuronal populations responding to test stimuli were determined. These zones were placed in a stereotaxic triangular system, determined by X ray methods. The line joining the anterior (CA) and the posterior (CP) commissures formed the
antero-posterior X axis, the line perpendicular to the middle of CA-CP and parallel to the median plane of the brain was the Y axis, lateral positions were measured on the Z axis. Functional trajectory 'maps' were constructed for each patient, using the results of microelectrode observations, checked also by the effects of monopolar electrostimulations using rectangular pulses (amplitude from 1 to 4 V, duration 1 msec, frequency 50/sec). All surgical and experimental procedures were explained carefully to the patients and their consent was obtained.

Spontaneous and evoked spike activity and the EMG data were analysed using a computer data processing system. The following statistical functions were estimated: firing rate/time histograms of neuronal and EMG activities, interspike and interburst interval histograms, auto- and cross-correlation histograms between activities of the same or different units and/or pathological tremor, Fourier transforms of these processes and appropriate auto- and cross-spectral distributions and others. Each of these traditional statistical functions was determined in the course of functional tests; their alterations characterized the pattern of the evoked activity and temporal relations between different units, on the one hand, and units and tremor on the other. In the latter case the cross-correlation between unit and EMG activities was estimated by averaging the firing rate of the unit synchronized with tremor wave forms as a reference.

The present work is based on the data obtained during 113 stereotaxic operations on dyskinetic patients (mainly on patients with parkinsonism, stage III-IV). In total 1075 neurones were recorded, of which 492 are presented in this paper; 205 units were located in the nucleus reticularis thalami (Rt), 287 units in the VL-200 in the antero-lateral part of the VL (nuclei ventralis oralis anterior (Voa) and posterior (Vop)) and 87 in the posterior part of the VL (nucleus ventralis intermedius (Vim)). The results are illustrated on maps of the atlas of Schaltenbrand and Bailey (1959). We should note here that, according to the nomenclature used by these authors, the VL of Walker's nomenclature (1938) is divided into 3 nuclei: Voa, Vop and Vim. We shall use both systems of nomenclature and designate VL as the area consisting of Voa, Vop and Vim.

Abbreviations in the text and figures are as follows:

- Cd = caudatum
- Ce = n. centralis thalami
- Cp = capsula interna
- D = n. dorsalis thalami
- Do = n. dorso-oralis
- GM = corpus geniculatum mediale
- MD = n. medio-dorsalis thalami
- Ni = substantia nigra
- Pf = pallidum laterale
- Pm = pallidum mediale
- Pu = pulvinar thalami
- Stb = corpus subthalamicum
- Th = thalamus opticus
- Vci = n. ventro-caudalis internus (thalami)
- Vim = n. ventro-intermedius (thalami)
- VL = n. ventralis lateralis thalami
- Voa = n. ventro-oralis anterior
- Vop = n. ventro-oralis posterior
- Z = n. centro-lateralis thalami
- Zi = zona incerta
- Zo = n. centro-lateralis oralis (thalami)

Results

The data presented here concern the changes in thalamic activity during periods of preparation, initiation and realization of voluntary movements performed in response to verbal commands. The behaviour of these units during parkinsonian tremor is also described. The units were located mainly in the Rt and VL of the thalamus. The spontaneous and evoked neuronal activity obtained in some other regions of the human brain during the performance of intellectual tasks (calculating, solving arithmetical problems, Binet's test of short-term memory) have been described elsewhere (Raeva 1972, 1977a,b).

Activity of nucleus reticularis neurones

In the anterior part of the thalamus, mainly in the n. reticularis (n. Rt) and immediately adjacent nuclei (Voa, Zo, Do, Zi) units were found (83 out of 205; 40%) which responded with phasic activation (32) or inhibition (51) just after a verbal command, to provoke a voluntary movement, was given. The activation began 700 msec to 1 sec
before the performance of the voluntary act. The phasic responses had a duration of 100–200 msec and were observed during the periods of preparation for the movement. Examples of such responses are shown in Figs. 2, 3 (neurone a) and 8A. Fig. 2 presents the changes in activity of Rt neurones and EMG of finger flexors recorded simultaneously. A marked phasic activation appeared just after the verbal command ‘clench your fist’ was received. It was followed by the muscular contraction. The activation occurred about 700 msec before the beginning of the EMG change (i.e., before the start of the movement).

When the unit response to verbal command was an inhibition, this appeared also just after the verbal command but it had a longer duration (about 1 sec). An example of such a response is presented in Fig. 3 (neurone c). As can also be seen in this figure, two adjacent neurones of Rt had clearly reciprocal responses to verbal command (compare neurones a and c in Fig. 3).

Another group of Rt neurones (25 out of 205; 12%) showed an activation 100–200 msec before or just at the moment when an EMG change signalled the beginning of the performance of the motor act (Fig. 3, neurone b).

When a succession of orders was given, the early responses did not habituate (Fig. 3). Therefore, the neurones driven by the verbal command cannot be of the ‘detectors of novelty’ type observed by Jasper (1964). Moreover, they did not respond to verbal stimuli that did not require the

Fig. 2. Phasic response of an RT unit to the verbal command ‘clench your fist’ (same unit as in Fig. 8A). At left: schema of deep human structures on the lateral 16 sagittal plane of the atlas of Schaltenbrand and Bailey (1959). In this and following figures the zone studied is signalled by a black dot. At right: time histogram of unit firing rate (line 1) and of EMG of the contralateral finger flexors (line 2). The solid line under the lower image delimits the time interval during which lower traces were taken. Below: 1 = unit activity, 2 = EMG of the contralateral finger flexors. The arrows indicate the beginning of verbal commands ‘clench your fist’ (downward arrow) and ‘unclench’ (upward arrow). Note that the units respond to the verbal command by a phasic activation which appears 700 msec before the performance of the movement signalled by the EMG activity.
execution of motor acts, or to meaningless sensory, auditory, tactile and proprioceptive stimuli. We have described previously the functional characteristics of these neurones, which we have called 'triggered verbal command units' (Raeva 1972, 1977a,b; Raeva and Livanov 1975). Responses of these cells were obtained only when verbal stimuli were presented, which may differ in their acoustic spectrum, but are similar in their semantic meaning, serving as a 'trigger' signal, causing a subject to perform purposeful activity. These units were found mainly in the Rt. However, some were also present in non-specific and associative nuclei of the human thalamus (Voa, Zo, Do, Pf, Ce, MD, Zi) and in the striatum (Cd, Pl). They responded similarly during the preparation for different kinds of voluntary acts (movements of the upper or lower, right or left limbs, intellectual tasks). In our previous studies a connection was established between the activation of triggered verbal command neurones and selective attention (or intentional effort) in man. It was found that these responses were present only when a person concentrated his attention in order to perform a voluntary act.

In n. Rt, units (105 out of 205; 51%) fired in burst patterns and had unstable frequencies (2–5 bursts/sec). These rhythmic units never revealed any valid cross-correlations with peripheral parkinsonian tremor. This indicates the absence of any relationship between burst and tremor and shows that n. Rt neurones differ on this point from VL ones (see next paragraph).

It should be noted, however, that Rt neurones just adjacent to VL, and which do not present spontaneous rhythmicity, were able to present a rhythmic pattern at 5 ± 1 c/sec during the performance of a motor task (see neurone a in Fig. 3). This transformation of a non-rhythmic into a rhythmic unit could also occur as an aftereffect of a motor act (see next section).

**Activity of ventralis lateralis neurones**

Our present data show the complexity and diversity of cellular organization of the VL. Sharp boundaries between Voa, Vop and Vim nuclei and adjacent structures (Rt, Zi, Sth) are difficult to ascertain. We can say, however, that an essential feature of VL neurones, which clearly distinguishes their functions from those of the Rt, is the absence of triggered verbal command units. Changes in VL neurone activity were closely connected with the performance of various motor tasks, but also some of the cells responded to passive movement of the limbs and compression and stretching of muscles, thus suggesting that the most effective stimuli for them were provided by somatosensory afferents.

**Units in Voa and Vop.** We have studied 200 neurones of these subnuclei in detail and grouped them into 5 categories (a–e) according to their
activity before and during voluntary movements prompted by verbal commands. We must note that there is some overlapping between the different categories.

(a) Fig. 4 illustrates one of the typical responses observed in 132 neurones out of 200 (66%). During the performance of a voluntary movement prompted by the command ‘clench your fist,’ a tonic activation began during the early stages of the movement when an initial EMG modification can be seen (about 200 msec before the start of the movement). This activation continues throughout the entire period of muscle contraction. Passive movements provoking unitary responses were not always easy to find for these units.

(b) Another type of Vao-Vop neurone is illustrated in Fig. 8C. We observed 23 such neurones among the 200 (12%) studied. Their activity was altered only during the performance of the movement when the muscular contraction was maximal. These tonic changes could be ‘activation’ or ‘inhibition.’ These responses were produced by a wide range of different voluntary movements of the upper and lower limbs contra- and ipsilateral. However, the response intensity was maximal when the provoking movement was contralateral. These units were never excited by a passive movement of the same limb. Certainly, these cells and a part of the first group are the ‘voluntary movement’ cells described by others (see Discussion for references).

(c) Among these two types of cells a group of non-rhythmic cells sometimes presented rhythmic activity for a short time. Computer analysis of the data revealed this transformation of non-rhythmic into rhythmic activities (5 ± 1 Hz) for 64 cells; 32% of all the cells studied). This transient rhythmic activity occurred at both the moments of initiation and realization of voluntary movements (Figs. 4

Fig. 4. Responses of a non-rhythmic unit in the antero-lateral part of the VL (Voa-Vop) in a rigid parkinsonian patient during the performance of a voluntary movement elicited by the verbal command ‘clench your fist.’ At left: schema of deep human structures on a sagittal plane (SL 13.5). At right: A, histogram of unit firing rate and EMG of the contralateral finger flexors; B, variation with time of the frequency spectra obtained during the realization of the motor task. The coordinates of the triangular system correspond to time (X), frequency (Y), number of intervals (Z). Calibration: 1 sec for X, 1 Hz for Y, and 5 counts for Z. Frequency resolution 0.8. Note that the initiation and realization of the voluntary movement are accompanied by a tonic activation with a transient short-term appearance of grouped discharges at a frequency similar to that of the parkinsonian tremor.
and 5). It could also be an aftereffect of motor action (Fig. 5).

Figs. 4 and 5 present the analysis which demonstrates this transient rhythmic phenomenon. In Fig. 5, we see that this quasi-rhythmic phenomenon is more prominent just after termination of the motor task. This transient rhythmicity, appearing after repetition of a motor task, occurred in 42 of the non-rhythmic ‘voluntary movement’ cells studied.

In patients without tremor (akinetic and rigid forms of parkinsonism, torticollis) repetitive motor acts also provoked rhythmic 5 ± 1 Hz patterns of discharge in VL neurones. However, this rhythmic pattern was present for only a short time (a few seconds) at the onset and termination of the movement.

Fig. 6 illustrates this transformation of a non-rhythmic pattern into a rhythmic one, after the repetition of voluntary motor acts in a rigid parkinsonian patient. The interspike interval histogram before the motor task was characterized by a dispersed distribution without definite mode, indicating a random firing pattern (Fig. 6A₂). A grouping of discharges according to the autocorrelation interburst histogram (Fig. 6A₃) does not exist in this case. Cross-correlation between the unit activity and the peripheral EMG tremor does not exist either (Fig. 6A₄). After the performance the firing rate of discharges is highly increased.
HUMAN THALAMIC UNITS AND VERBALLY PROVOKED MOVEMENTS

Fig. 6. Difference in firing patterns of a non-rhythmic unit of the VL (Voa-Vop) before (A) and after (B) the performance of repetitive motor acts in a rigid parkinsonian patient. 1, unit activity (L-Thal) and EMG of contralateral finger flexors (R-F); 2, interspike interval histogram; 3, autocorrelation histogram; 4, cross-correlation histogram between unit and EMG activities; 5, autocorrelation histogram of the EMG activity. Calibrations: 20 counts for A2 and B2, time up to 200 msec for A2 and B2 and 1 sec for A3 and B3, bin 2 msec for A3 and B3 and 20 msec for A3 and B3. Note that after the repetition of the motor acts this non-rhythmic unit presents a rhythmic 5 ± 1 Hz activity closely cross-correlated with the rhythm of the peripheral tremor.

(Fig. 6B1). The interval histogram shows a narrow distribution with the appearance of a clear central peak, indicating an increase in regularity of firing (Fig. 6B3). The interburst autocorrelogram clearly demonstrates a marked tendency to fire in rhythmic bursts at a frequency of 5 ± 1 Hz (Fig. 6B3). Both spike and EMG bursts, according to the cross-correlation histogram and autocorrelogram of the EMG tremor (Fig. 6B4,B5), tend to appear synchronously at the same frequency.

It is logical to conclude that the ‘voluntary movement’ neurones encountered in Voa and Vop, even if they are not spontaneously rhythmic, reveal a ‘latent’ rhythmogenic 5 ± 1 Hz tendency, which is accentuated by a somatic afferent inflow during movement performance. Consequently, this inflow must exist, even if we were not always able to demonstrate it by passive movements. It is also evident that the neurones of this type are linked not only to the motor control system processes but also to the rhythmogenic 5 ± 1 Hz thalamic mechanisms.

(d) Spontaneous rhythmic discharges at 5 ± 1 Hz were found in 75 units out of 200 (38%). The frequency of the bursts was closely correlated with the tremor frequency but their phase was not.

Using our motor testing procedure we have shown that in these units motor performance was accompanied by suppression of the rhythmic activity and a decrease in impulse firing. The activity returned to a rhythmic pattern just after the movement was accomplished (Fig. 7). A rebound effect was even observed, consisting in an increase of the discharge frequency and a corresponding reduction of the interburst intervals.

(e) A few Voa units (7 out of 200) had a response pattern very similar to that found in n. Rt; they were all encountered at the boundary between Voa and Rt.

Units in Vim. At this level the majority of the neurones reacted to passive proprioceptive stimuli as well as to the motor performance (59 units out of 87; 68%). These responses, phasic or tonic in nature, were specific for a given cell for the stimulation of an appropriate part of the body or limb. Rhythmic bursts discharges were observed in the majority of Vim cells (56 units out of 87; 64%). Unlike those of Voa-Vop the rhythm of Vim cells was correlated with the tremor EMG not only in frequency but also in phase and revealed a certain topical organization absent in the former.

Location of different pools of neurones

The great individual variability of deep brain structures makes the identification of different thalamic nuclei of great importance for the effectiveness of stereotaxic surgery. We have tried to see if the characteristics of units in each individual case can help in making accurate the spatial delineation of subcortical structures chosen as surgical targets.

Fig. 8A, B and C represent 3 examples of the main patterns of unit activity recorded during the performance of the same motor task in rostral and lateral thalamic areas along the trajectories used by our surgeons (see Fig. 1). The neurones having different functional properties were located along the trajectory, not randomly, but in a definite
Fig. 7. Response of a rhythmic 5±1 unit recorded in the VL (limit of Vop-Vim) during the performance of a voluntary movement. Legend as for Fig. 2. Note that the preparation and realization of the motor act are accompanied by the suppression of the central rhythmic activity and some decrease in firing rate which is followed by a gradual return to the initial pattern.

Fig. 8. Differences in patterns of activity in two rostral (A, B) and one more posterior (C) thalamic units located along a trajectory from the premotor cortex toward the VL during performance of the same motor task. In each case a comparison was made between unit activity (1) and EMG of contralateral finger flexors (2). At left: schematic representation of the anatomical position of the units A, B, C. At right: histogram of unit firing rate (line 1) and of the EMG (line 2). The arrows mark the beginning of the verbal commands 'clench' (downward) and 'unclench' (upward).
Fig. 9. Spatial localization of units triggered by ‘verbal command’ (A) and ‘voluntary movement’ (B), compared to that of ‘rhythmic units 5 ± 1 Hz’ (C). These were recorded in 33 parkinsonian patients along the electrode tracks currently used in this study. The coordinates were determined on ventricular X rays. In the sagittal plane (at right) they are plotted on the intercommissural line CA-CP, the zero being the middle of the CA-CP distance. In the frontal plane (at left) the lateralities are the distances to the medial plane of the brain. Note that the distribution of units having different functional properties is not at random but in a definite order, the units being spatially grouped into functionally organized pools. The ‘triggered verbal command’ cells (A) are located the most anteriorly and laterally; the ‘voluntary movement’ cells (B) and the ‘spontaneously rhythmic 5 ± 1 Hz’ cells (C) have similar localizations.

Fig. 10. Schema summarizing the localization in the rostral and lateral thalamus of 33 parkinsonian patients, of the 3 main pools of units having functional organizations. A and B units were triggered respectively by ‘verbal command’ and ‘voluntary movement;’ C corresponds to the pool of spontaneously rhythmic units (5 ± 1 Hz). At left: schema of the anatomical positions in a sagittal plane of the different functional types (A, B, C). At right: different nuclei in which the different types of response were found are given in proportional distribution. Note that the zone where ‘triggered verbal command’ units were found corresponds to the rostral part of the thalamus, and RT in particular; the zone with rhythmic and ‘voluntary movement’ units corresponds to the VL nucleus.

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Discussion

(1) Our data demonstrate the existence in the rostral thalamus (mainly in the anterior part of nucleus reticularis) of units whose activities are linked to the verbal command which provokes a voluntary movement, as well as to the voluntary movement itself. We called them ‘triggered verbal command units’ to differentiate them from the ‘motor units’ first described by Jasper and Bertrand (1966) and which are activated shortly...
before (200–300 msec) or only during the execution of the voluntary movement. In our present and previous papers (Raeva 1972, 1977a,b; Raeva and Livanov 1975) we have described the functional characteristics of the triggered verbal command neurones: close correlation of their activity with the imperative ‘psychic’ stimuli given verbally and with focussing of selective attention; the ‘triggered’ anticipatory nature of the time course of unit preceding the performance of voluntary activity; the universal polyvalent non-specific form of their manifestations connected with the realization of various kinds of voluntary motor (or mental) acts. According to our previous studies, cells of this type were found essentially in the n. Rt but also in some other non-specific and associative nuclei of the human thalamus (Voa, Zo, Do, Pf, Ce, MD, Zi) and in the striatum (Cd, P1). So these ‘triggered’ processes proved to be acting simultaneously in a range of subcortical structures related to the functioning of the non-specific activation system.

Moreover, the analysis of specific features of triggered neuronal effects suggests that an important role is played by the cortex in respect of their organization. An anticipatory spike activity correlated with voluntary motor activity or selective attention was observed in the motor and prefrontal cortex as well as in the Cd and some nuclei of the thalamus in many animal experiments (Kitsikis et al. 1971; Kubota and Niki 1971; Alexander et al. 1973; Buser et al. 1974; Brinkman and Porter 1979; Seal et al. 1983). It is possible that these types of neuronal activity change may be grouped in general categories of physiological phenomena such as ‘setting,’ ‘readjustment’ and ‘warning’ which are active during the preparation of corrections in the voluntary act’s program. From this point of view the Rt of the human thalamus concerned with the performance of voluntary movements of a limb but not activated by passive movements of the same extremity, ‘voluntary movement’ units, have been described by several authors (Umbach and Ehrhardt 1965; Jasper and Bertrand 1966; Bates 1969, 1973; Bertrand et al. 1969; Albe-Fessard 1974; Ohye and Albe-Fessard 1978; Ohye 1982). The problem of rhythmicity in the central nervous system of man was also examined by us and we have discussed its relation to the tremorogenic mechanism in parkinsonian patients (Raeva 1972, 1977a).

Neurones in the VL of the human thalamus concerned with the performance of voluntary movements of a limb but not activated by passive movements of the same extremity, ‘voluntary movement’ units, have been described by several authors (Umbach and Ehrhardt 1965; Jasper and Bertrand 1966; Bates 1969, 1973; Bertrand et al. 1969; Albe-Fessard 1974; Ohye and Albe-Fessard 1978; Ohye 1982). Some of them also described neurones at this level that increased their firing rate about 1 sec before the performance of motor acts (Umbach and Ehrhardt 1965; Jasper and Bertrand 1966; Crowell et al. 1968; Raeva 1972; Hongell et al. 1973; Fukushima and Schramm 1975; Ohye 1982). They are possibly to be compared to the reticularis units described in the present paper.

The most important new result for the VL units described here is the existence of a particular zone (Voa and Vop) where neurones are linked both to motor and rhythmic activity.

In parkinsonian patients, even though the spontaneous activity of these cells was not rhythmic, it could be changed to a rhythmic one during the initiation of voluntary movements and during the phase which followed motor tests. The provoked rhythm, being at 5 ± 1 Hz, is similar to that of parkinsonian tremor.
In patients having no tremor (akinetic and rigid forms of parkinsonism, torticollis) short periods when 5 ± 1 bursts could be recorded have also appeared in some Voa-Vop units when repetitive motor tasks were executed. Rhythmicity of this sort has been described in animals having no motor pathology (Andersen et al. 1964; Cordeau 1966; Massion 1969; Purpura 1970). These data suggest that Voa-Vop neurones exhibiting a 'latent' rhythmogenic 5 ± 1 Hz tendency play a significant part, not only in the genesis of pathological tremor, but in the control of voluntary movements. According to our previous reports (Raeva 1972, 1977a), the same type of rhythmic units were also found in the medial part of the globus pallidus and in the antero-medial part of the putamen.

These findings clearly confirm the complex polyfunctional nature of Voa-Vop neurones, which are characterized by a high reactivity to ascending aferents as well as to descending cortical influences. Thus, in man, the VL proves to be not merely a relay but an important integrative centre for processing somatosensory information originating from the lower levels of the CNS towards the motor cortex. A similar viewpoint is shared by other investigators who obtained similar results in non-anaesthetized monkeys (Evarts 1973; Evarts and Thach 1969).

(3) Using tests consisting of various forms of motor and proprioceptive stimulation, it has been found that the VL of the human thalamus itself may be divided into two functionally different zones whose borders are similar to those proposed in Walker's classification (1938), even if the delineation of the nuclear zones determined electrophysiologically is not as clear as that described by the anatomists. Neurones in the antero-lateral part of the VL (Voa-Vop) appear to be multifunctional while neurones in the posterior zone (Vim) are specific.

(4) From a practical point of view the data obtained show that microelectrode investigations during stereotaxic operations may be of great utility in the choice of the thalamic region to be destroyed and for the elucidation of the mechanisms of human pathological motor activity.

Résumé

Localisation chez l'homme d'unités thalamiques déclenchées pendant des 'commandes verbales', des mouvements volontaires et un tremblement

Des enregistrements par microélectrodes ont été réalisés dans le thalamus rostral (noyau réticularis) et latéral (n. ventral latéral) chez des patients parkinsoniens ou dyskinésiques opérés par la méthode stéréotaxique sous analgésie locale. Des mouvements volontaires ont été systématiquement provoqués par un ordre verbal, les activations correspondantes des différents neurones rencontrés ont été étudiées et comparées aux électromyogrammes des muscles intéressés, à l'aide d'un programme informatisé. Dans le noyau réticularis, et les zones thalamiques juste adjacentes, une partie des cellules réagissaient pendant l'initiation d'un mouvement volontaire (100 à 200 msec avant le mouvement). D'autres cellules du même noyau étaient activées pendant la commande verbale (700 à 1000 msec avant le mouvement). Nous les avons désignées sous le nom d'unité 'commande verbale'. Dans la partie antérieure du n. ventral latéral (Voa-Vop de la nomenclature allemande), la majorité des unités correspondaient pendant la phase d'initiation ou la phase de réalisation du mouvement volontaire. Elles correspondaient au type 'mouvement volontaire' décrit par Jasper et Bertrand (1966). Chez les parkinsoniens tremblants les unités étaient fréquemment spontanément rythmiques. Lorsqu'elles ne l'étaient pas, elles pouvaient le devenir (fréquence de 5 ± 1) pendant la préparation ou la réalisation du mouvement, et aussi, dans quelques cas, comme un effet de rebond après le mouvement. Chez des patients ne présentant aucun tremblement (parkinsoniens akinétiques ou rigides, torticollis) des unités cellulaires non rythmiques ont pu fréquemment être transformées en unités rythmiques par la répétition de tâches motrices. Dans la partie postérieure du n. ventral latéral (Vim) la majorité des cellules étaient activées par des afférences proprioceptives provenant d'une région localisée du corps. Elles étaient aussi entrainées pendant le mouvement volontaire du membre correspondant. La majorité de ces cellules présentaient des activités à 5 ± 1,
correlées en phase et en fréquence avec le tremblement. Ces activités rythmiques disparaissaient pendant le mouvement. La localisation anatomique des 3 principaux types neuronaux 'commande verbale', 'mouvement volontaire', 'rythmique à 5 ± 1' a été déterminée. Les unités 'commande verbale' sont localisées antérieurement et latéralement par rapport aux deux autres types. Ceux-ci par contre ont la même distribution spatiale. Ce fait est en faveur d'un rôle commun des deux derniers types d'unités dans les mécanismes centraux du tremblement et des mouvements volontaires.

We are grateful for the courtesy of Professor A. Konovalov, Director of the Institute of Neurosurgery of the USSR Academy of Medical Sciences where most of the data presented here were obtained. We are indebted to Professor N. Vasin, surgeons V. Shapovalov and N. Grochovsky for carrying out the stereotaxic operations in which we could use the microelectrode method. We also thank our colleagues N. Wainberg, Uy. Tichonov and A. Lukashev for their technical and computer assistance.

The author wishes to express deep gratitude to Professor D. Albe-Fessard who introduced us to the wonderfully interesting world of neuronal investigations of human brain function, and sincere thanks for her help in the preparation of this paper.

References


