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The Initiation of Voluntary Movements by the Supplementary Motor Area*

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Summary. The hypothesis is formulated that in all voluntary movements the initial neuronal event is in the supplementary motor areas (SMA) of both cerebral hemispheres.

Experimental support is provided by three lines of evidence. 1. In voluntary movements many neurones of the SMA are activated probably up to 200 ms before the pyramidal tract discharge. 2. Investigations of regional cerebral blood flow by the radioactive Xenon technique reveal that there is neuronal activity in the SMA of both sides during a continual series of voluntary movements, and that this even occurs when the movement is thought of, but not excuted. 3. With voluntary movement there is initiation of a slow negative potential (the readiness potential, RP) at up to 0.8 s before the movement. The RP is maximum over the vertex, i.e. above the SMA, and is large there even in bilateral Parkinsonism when it is negligible over the motor cortex.

An account is given of the SMA, particularly its connectivities to the basal ganglia and the cerebellum that are active in the preprogramming of a movement. The concept of motor programs is described and related to the action of the SMA. It is proposed that each mental intention acts on the SMA in a specific manner and that the SMA has an 'inventory' and the 'addresses' of stored subroutines of all learnt motor programs. Thus by its neuronal connectivities the SMA is able to bring about the desired movement.

There is a discussion of the manner in which the mental act of intention calls forth neural actions in the SMA that eventually lead to the intended movement. Explanation is given on the basis of the dualist-interactionist hypothesis of mind-brain liaison. The challenge is to the physicalists to account for the observed phenomena in voluntary movement.

Key words: Supplementary motor cortex – Voluntary movement – Neuronal initiation – Motor programs – Mind-brain interaction

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* Dedicated to Prof. Richard Jung on the occasion of his 70th birthday

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Zusammenfassung. Es wird die Hypothese begründet, daß allen Willkürbewegungen neurale Koordination der *supplementären motorischen Areale (SMA)* in beiden Großhirnhemisphären vorausgehen.

Drei experimentelle Grundlagen werden besprochen. 1. Viele Neurone des motorischen Supplementärfelds SMA werden bis zu 200 ms vor der Pyramidenentladung aktiviert. 2. Hirndurchblutungsmessungen mit der Xenontechnik zeigen einen vermehrten Blutfluß über beiden SMA, auch wenn die Bewegung nur gedacht, aber nicht ausgeführt wird. 3. Das Bereitschaftspotential vor Willkürbewegungen beginnt etwa 0,8 s vor der Bewegung und zeigt ein Maximum am Scheitel über beiden SMA, das auch bei Parkinsonpatienten mit sehr geringem Bereitschaftspotential über dem motorischen Cortex erhalten bleibt.

Durch Verbindungen der SMA zu Stammganglien und Kleinhirn entstehen wahrscheinlich Bewegungsprogrammierungen, die mit der SMA-Aktivität korreliert werden. Es wird angenommen, daß jede Bewegungsintention auf die SMA wirkt und daß deren Inventar für gespeicherte und erlernte motorische Programme die intendierten Bewegungen steuert, die durch neuronale Verbindungen der SMA entstehen. Die psychische Intention, die mit der SMA-Tätigkeit Bewegungen startet, wird mit der dualistisch-interaktionistischen Hypothese der Hirn-Seele-Verbindung erklärt.

Schlüsselwörter: Motorischer Supplementärcortex - Willkürbewegungen - Neuronale Initiierung - Motorische Programme - Hirn-Seele-Beziehung

Introduction

I have the indubitable experience that by thinking and willing I can control my actions that so become describable as voluntary movements. However in normal waking life this prerogative is not exercised for most of my actions. Kenny (1963) in his discussion on motives gives the sequence as: motive → intention → voluntary action, and further goes on to make the important statement: "that intending to do something is itself a voluntary action whereas having a particular motive is not." Empirical evidence for this will be given later. Voluntary movements can be of the widest diversity and complexity, involving an immense repertoire of learnt motor programs (Brooks 1979), which can be assembled simultaneously or concurrently according to desire or intention. However, only occasionally do we bother to exercise voluntary control over our actions. Mercifully, almost all run automatically, for example breathing, walking, knitting, and one is sometimes tempted to say talking! But all of these can be voluntarily controlled if we so wish. Even breathing can be controlled within limits. We may hyperventilate, or breathe to a chosen rhythm, or cease breathing for as long as 1 min. The criterion for distinguishing voluntary from automatic action will be presented at the end.

There is general agreement that voluntary control is exerted through the motor cortex of the cerebral hemispheres and the pathway (the pyramidal tract) from there to the motoneurones. Though the motor cortex thus is essentially concerned in voluntary movement, it will be argued that it is not the initiator. It is only the final relay station of immensely complicated activities in widely dispersed areas in the cerebral cortex, the cerebellum and the basal ganglia. The pyramidal cells of the motor cortex with their axons passing down the pyramidal tract are important because they provide a direct channel out from the brain to the motoneurones that in turn cause the muscle contractions. This very direct connection of the motor cortex with motoneurones is of the greatest importance in ensuring that the cerebral cortex in general, via the motor cortex, can very effectively and quickly bring about the desired movement. Nevertheless there are 2 fundamental problems that will be discussed. (1) How can the willing of a motor movement set in motion neural events that lead to the discharge of motor pyramidal cells? (2) How do the cerebellum and other subcortical structures contribute to the finesse and skill of movement?

The Initiation of Voluntary Movement

An Hypothesis

I am going to present a precise neurological hypothesis with respect to the first problem. The second problem will be lightly touched on later. I will firstly state the hypothesis and then present the empirical evidence.

The hypothesis: *In all voluntary movements the initial neural event is generated in the supplementary motor area (SMA) of both hemispheres.* Figure 1 shows the diagram by Penfield who discovered and named it the supplementary motor area. The initial neural event would be the excitatory responses of the neurones and modules of the SMA. Somehow in the willing of the action this excitation of the SMA is brought about. That raises the vexed questions of the mind-brain problem, but I will sidestep them for the present. Later there will be a discussion of the mind-brain problem in relation to the philosophical problem of intention, and how it is transformed when considered in the light of the SMA hypothesis.

Of immediate interest is the way in which the initiated activity in the SMA is transmitted to the neural machinery so that eventually the motor cortex is triggered to fire the pyramidal tract discharge for bringing about the desired or intended movement. The SMA hypothesis is based on 3 independent lines of evidence that have been published in the last few years. I will present them after a brief account of the SMA.

The Supplementary Motor Area

The supplementary motor area (SMA) was defined by Penfield (Penfield and Jasper 1954) as an area that on repetitive stimulation evoked motor responses quite different from the localised contralateral muscle contractions evoked from the motor cortex. Usually there were complex synergistic movements of the contralateral limbs and body and often vocalization and occasionally ipsilateral movements. The area so defined is that part of the premotor cortex (area 6) that lies on the medial side of the cerebral cortex just anterior to the motor cortex and extending down to the depth of the cingulate sulcus (Fig. 1). Similar responses except for vocalization were evoked in the monkey. There is evidence for an SMA in a wide range of mammals. It is doubtful (Wiesendanger et al. 1973) how far the stimulation responses can be

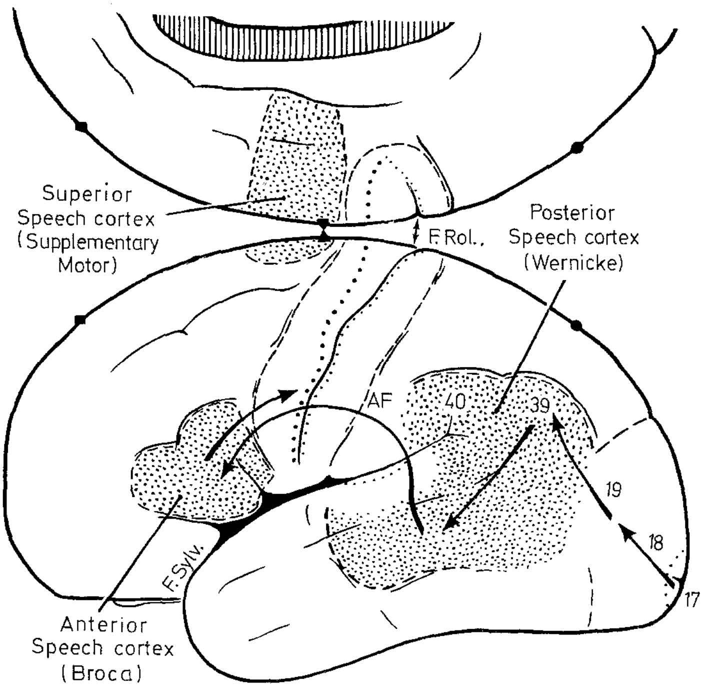

Fig. 1. Cortical speech areas and supplementary motor area of dominant left hemisphere. Note that the view is of left hemisphere from both lateral and medial aspects. *F. Rol.* is fissure of Rolando and *F. Sylv.* is fissure of Sylvius (modified from Penfield and Roberts 1959)

converted into the somatotopic map depicted by Woolsey et al. (1952). Certainly the topography would be seriously blurred in the translation from the complex synergistic responses.

Ablation in patients has provided little of significance in respect of the role of the SMA in movements or posture. After unilateral ablation, the arm contralateral to the ablation suffered from disability in initiating movements and was somewhat neglected with a decreased capacity for speed and rapidly alternating movements (Penfield and Jasper 1954). Moreover removal of SMA on the dominant side resulted in aphasia of several weeks duration (Penfield and Roberts 1959), hence this SMA is also referred to as the supplementary speech area (Fig. 1). In interpreting these results it is important to recognize that one SMA can substitute for the other.

Experimental Basis for the SMA Hypothesis

1. Recording from single neurones in the primate SMA during voluntary stereotyped movements (Brinkman and Porter 1979).

The movements are trained motor programs of brief pulling movements on a lever that are voluntarily initiated by the monkey. The animal was not restrained in arm usage, pulling with the right or left hand in random sequence. If the SMA is concerned in the voluntary initiation of the movement, it would be expected that many neurones would be firing impulses well before the motor cortical cells that eventually bring about the movement. In Fig. 2A the SMA unit is seen to commence firing approximately *250 ms before the action potential* of the muscle

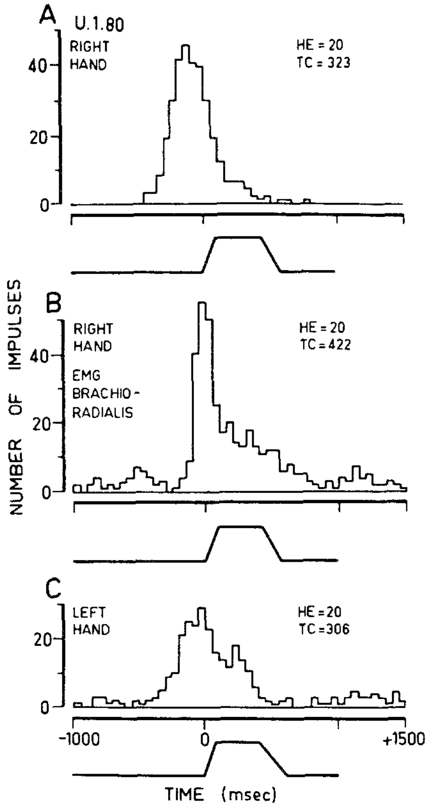

Fig. 2. This illustrates the discharges patterns of a neurone associated with flexion of the elbow during the lever pull for both the right (**A**) and left hand (**C**). **B** is the periresponse time histogram demonstrating the EMG activity of a representative elbow flexor, m. brachioradialis, in the right arm during the same 20 pulls as those in **A**, and shows that the neurone increased its discharge well before EMG activity increased. This was the case for the majority of neurones in which the discharge pattern could be compared with EMG changes (Brinkman and Porter 1979)

producing the movement (B), and this early start is also seen when the other hand was employed (C). The movements were self-paced and there was usually a food reward after each successful response. In the generation of a movement the motor pyramidal cells fire down the pyramidal tract, usually beginning at 40 to 60 ms before the muscle response, the earliest being at 140 to 120 ms (Evarts 1972). Hence at a conservative estimate the SMA neurone of Fig. 2 would commence firing approximately *100 ms before the earliest pyramidal tract firing.* The early discharge of SMA neurones was a common finding. In 10 of the 28 illustrations of Brinkman and Porter (1979) the average was approximately 450 ms before the onset of the movement (range 170 to 650 ms).

It has to be realized that, if the SMA neurones initiate a vast variety of voluntary motor programs, there would be a wide variety of neuronal responses in relation to the movement. This was indeed observed in the 229 movement-related neurones in the SMA. Figure 2 illustrates the simplest relationship. Other SMA neurones were activated during or later than the movement, or in 2 bursts before and after the movement. It was remarkable that some neurones with a high background rate were inactivated during the movement. All of these divergences from the simple relationship of Fig. 2 would be expected on the hypothesis that the SMA is concerned in the initiation of voluntary motor programs involving complex hand and arm movements with many muscles contracting

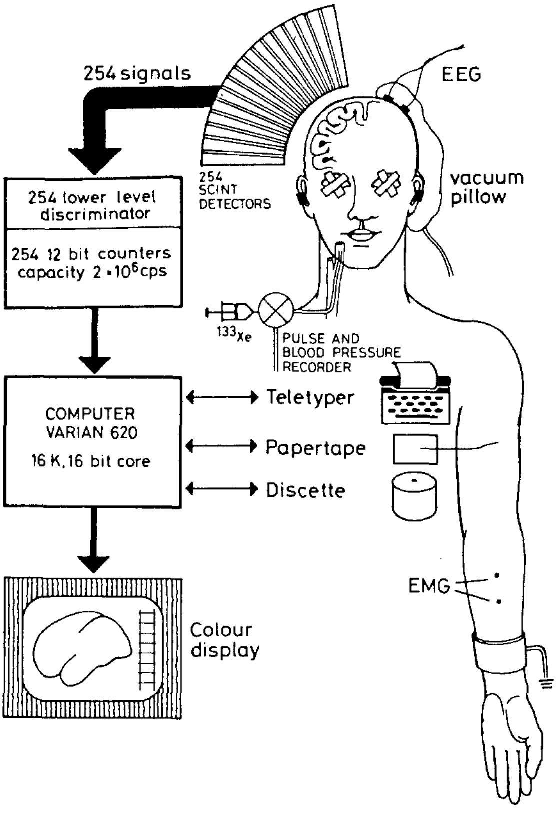

Fig. 3. Block diagram of the equipment and the principles of the method. The head is fixed to the collimator by a vacuum pillow. The 254 collimator tubes are arranged radially in a 50 mm-thick spherical lead segment. The spatial resolving power of the camera when used for rCBF measurements is one channel. The center-to-center distance of 2 adjacent collimator tubes is 10 mm. Signals from the 254 cortical regions are processed on-line, the isotope clearance curves, the rCBF values, and background radioactivity can be recorded in the 3 different formats for further processing or displayed on the TV screen (Roland et al. 1980a)

or relaxing. However much more investigation is needed, particularly on the temporal relationship of SMA discharge to pyramidal tract discharge.

2. Recording of the blood flow in the cerebral cortex with special concentration on the SMA. The blood flow can be assumed to be a reliable indicator of neuronal activity (Roland et al. 1980a and 1980b).

The *regional cerebral blood flow (rCBF)* was determined by an assemblage of 254 collimator tubes after internal carotid infusion of radioactive Xenon (^{133}Xe) (Fig. 3). This collimator assemblage could be applied over 1 cerebral hemisphere or over the vertex in order to record optimally from cortical regions near the midline and deep on the medial surface, which would be desirable for the SMA. A very subtle sequence of finger movements was chosen as the standard movement, the thumb touching each digit in turn, the successive touchings being 2, 1, 3, 2 for digits 1, 2, 3, 4 and then in reverse (2, 3, 1, 2) to complete a cycle which can be continued indefinitely. The subject practises to achieve dexterity. The complexity is much greater than for simple flexion-extension sequences of a finger, and mental concentration is required throughout. It can be assumed that the movement continues to be under voluntary control during all sequences. Figure 4A shows mapping of the regions in which there was a significant increase in rCBF during the *motor-sequence test* with percentages of increase shown.

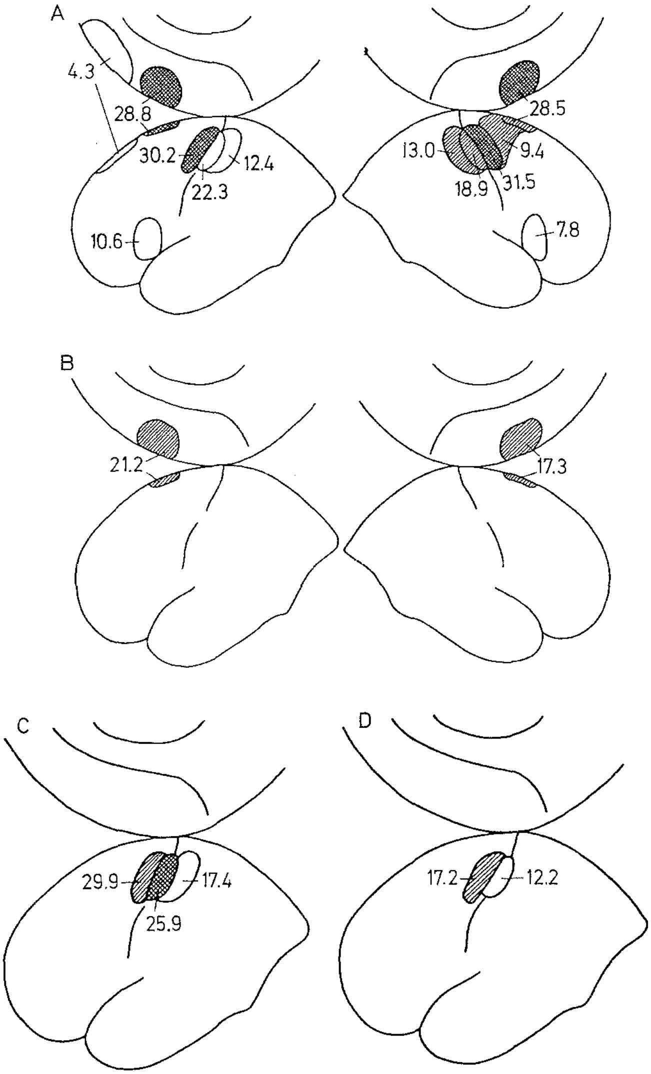

Fig. 4. (**A**) Mean increase of the rCBF in percent during the motor-sequence test performed with the contralateral hand, corrected for diffuse increases of the blood flow. The individual focuses of rCBF increase have been transferred to a brain map of standard proportional dimensions. The size and location of each focus shown is the geometrical average of the individual focuses. Cross-hatched areas have an increase of rCBF significant at the 0.005 level. *Hatched areas* have an increase of rCBF significant at the 0.005 level, for other areas shown the rCBF increase is significant at the level 0.05. *Left:* left hemisphere, 5 subjects. *Right:* right hemisphere, 10 subjects (Roland et al. 1980a). (**B**) Mean increase of rCBF in percent during internal programming of the motor-sequence test, values corrected for diffuse increase of the blood flow. *Left:* left hemisphere, 3 subjects; *right:* right hemisphere, 5 subjects (Roland et al. 1980a). (**C**) Mean increase of the rCBF in percent during forceful repetitive flexions of the contralateral index finger, corrected for diffuse increases of the blood flow. Data from the right and left hemispheres have been pooled and subsequently averaged. Here the pattern of increases is shown on a left hemisphere for 5 subjects (Roland et al. 1980a). (**D**) Mean increase of rCBF in percent during a sustained isometric contraction of the contralateral index finger and thumb. Values corrected for diffuse increase of the blood flow. Data from the right and left hemispheres have been pooled and shown on a left hemisphere, for 7 subjects (Roland et al. 1980a)

There is mapping on the left hemisphere of the rCBFs when the motor-sequence test was carried out by the right hand, and on the right hemisphere for the left hand. There was a large increase in rCBF of the motor cortical areas for each hand in each hemisphere, with less rCBF more posteriorly in the sensorimotor and sensory hand areas. Of particular interest is the large increase in rCBF over the whole of the SMA of *both* hemispheres when the motor-sequence test was carried out by *one* hand. The rCBFs for the ipsilateral SMA's are not shown in

Fig. 4A. Roland et al. (1980a) illustrate for the right hemisphere a mirror image of the rCBF of SMA shown for the left hemisphere in Fig. 4A, there being, as expected, no increase for the motor and sensorimotor areas on the ipsilateral side. The mean increase for the motor-sequence test in the (ipsilateral) SMA (27.3%) was almost the same as for the SMA contralateral to the hand movement (28.8% in Fig. 4A). This bilateral activity of the SMA has already been seen in Fig. 2.

Figure 4B is of the greatest interest because the subject was indulging in what was called "internal programming" of the motor-sequence test, the subject rehearsing the movement sequences without carrying out any movements. Motor silence was established by the observed electrical silence of the muscles and the absence of all bodily movements. It was remarkable that there was a considerable increase in rCBF over the supplementary motor areas, though it was less than with the movement sequences, and that there was no significant increase in any other regions of the cerebral hemispheres.

By contrast Fig. 4C shows that, with an ongoing series of repetitive finger flexions and extensions, there was an increase in the rCBFs over the motor and sensory hand areas matching that for the motor-sequence test in Fig. 4A, but there was no significant increase over the SMA. Similarly for a sustained isometric contraction when a spring was compressed between thumb and index finger (Fig. 4D) there was an increased rCBF over the motor and sensorimotor areas, but no significant increase over the SMA. Actually the small mean increases of the rCBFs over the SMA (2.0 and 3.1%) in Figs. 4C and D were not significant.

These measurements of rCBFs are of great importance in demonstrating the role of the SMA in bringing about motor responses. The internal programming test shows that the mental rehearsal of the motor-sequence test is associated exclusively with the SMA. On the other hand, with simple repetitive actions or a steady contraction, the SMA is not significantly activated. It is obvious that these actions require much less mental concentration than the motor-sequence test, as was pointed out by Roland et al. (1980a). Thus the motor cortex is not associated with the on-going programming of the motor-sequences, but only in their later execution. The subjects were well trained in the motor-sequence test. As Roland et al. (1980a) state most succintly:

> "The information about the type of movements - - - must therefore, have been stored in a memory before the rCBF measurements started. The cerebral events during internal programming of the motor-sequence test are formally a recall of this information and the formation of a queue of time-ordered commands. The formation of a motor subroutine, specifying the sequence of isolated ballistic flexion-extensions and oppositions of the fingers, seems to be the most important contribution of the supplementary motor areas during the planning and execution of the motor-sequence test."

The conclusion to be drawn from these remarkable experiments is that the mental activities concerned in the "internal programming" are in liaison specifically with the neuronal activity in the SMA. It provides a corroboration of Kenny's (1963) statement: „intention is a voluntary act." The recording of an rCBF takes 1 min and so it cannot provide evidence for the temporal relationships of SMA and motor cortical activity as in Fig. 2. However, the priority of the SMA is demonstrated by the mental rehearsal test of Fig. 4B. Another disability of the rCBF measurements is that there is little spatial discrimination. The display is little more than the neuronal activity of the whole SMA (Fig. 4A). On the other hand its great significance is that it establishes the uniquences of the SMA in its liaison with the mental activities concerned in initiating voluntary movement. In the sequence: motive → intention → voluntary action, the SMA can be identified as the neuronal correlate of the mental actions of intention.

3. Recording of potentials over the cerebral cortex during freely initiated movements, the readiness potential (RP), particularly in Parkinsonian patients (Deecke et al. 1977; Deecke and Kornhuber 1978).

The readiness potential (RP) is the electrophysiological counterpart of the initiation of a voluntary movement. By an ingenious technique it is possible to average 250 or more records of the extremely small potentials recorded at several sites on the scalp in relation to some freely initiated movement such as a sharp flexion of the finger. The subject initiates these movements voluntarily at irregular intervals of many seconds, and there is recording by a scalp electrode relative to a remote indifferent electrode. The slowly rising negative potential, called the readiness potential, was widely dispersed over the scalp, usually beginning as long as 0.8 s before the onset of the movement at zero time, as illustrated in the 4 lower tracings of Fig. 5. We can assume that the readiness potential is generated by complex patterns of neuronal discharges that eventually project to the pyramidal cells of the motor cortex and so down the pyramidal tract to cause the movement. It can be presumed that during the readiness potential there is a developing specificity of neuronal activities, the motor program, that eventually activates the correct motor pyramidal cells for bringing about the desired movement.

In a bilateral Parkinsonian patient the bilateral akinesia (Fig. 5) is associated with an extreme reduction of the RP with both precentral recordings (over the motor cortex) during movement of one finger (left). By contrast there was a large readiness potential over the vertex, and fairly large parietal responses on both sides with a larger midparietal response. It can be concluded that both the vertex RP and the parietal RP's are produced independently of the precentral RP. Deecke and Kornhuber (1978) suggest that the vertex RP is likely to be produced by the SMA which is located exactly below the vertex recording and that the SMA ... "is definitely involved in voluntary finger movement". They further suggest that: ... "The abolition of the precentral Bereitschaftspotential (readiness potential) may therefore be an expression of such lack of striatofugal synaptic drive in motor cortex. The high RP amplitude at the vertex and in parietal leads may be the expression of a higher degree of independence of supplementary motor and cingulate areas from the basal ganglia input".

The hypothesis of the primacy of the SMA in a voluntary movement relates particularly to these findings in Parkinsonian patients. In attempting to carry out the voluntary movement there is no defect in the primary neural event, bilateral activation of the SMA, but the SMA has no appreciable direct connection to the

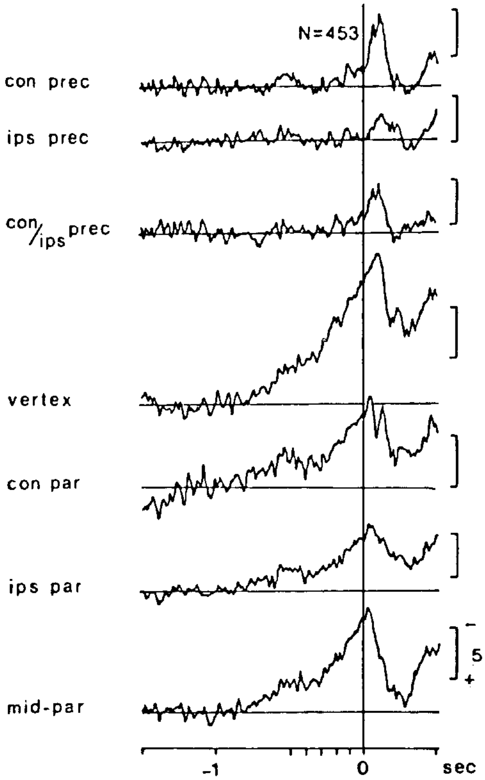

Fig. 5. Cerebral potentials (readiness potentials, RP) preceding voluntary finger movement in a patient with bilateral Parkinsonism. Averages of 453 left index flexions recorded in contralateral and ipsilateral precentral and parietal leads and the vertex, referred to linked ear lobes. Maximal RP at the vertex, but virtually no potential in contralateral or ipsilateral precentral leads overlying the hand representation of the MI motor cortex; con/ips prec represents subtracted ips from the con curve (Deecke and Kornhuber 1978)

motor cortex (Wiesendanger et al. 1973). As stated below, the SMA works largely through loops via the cerebellum and the basal ganglia, particularly the striato-fugal synaptic drive, as proposed above by Deecke and Kornhuber, and this is gravely deficient in Parkinsonism. It is important to recognize that the motor cortex, per se, is activated to give *the motor potential* only 50 to 60 ms before the movement (Deecke and Kornhuber 1977). The failure of the precentral RP in Fig. 5 can thus be attributed to the deficient response of the subjacent premotor cortex (area 6), which is bilaterally activated before the movement, and which must be dependent on striato-fugal drive.

Hitherto in discussing the neuronal mechanisms concerned in generating the readiness potential there has been speculation about the site of its generation and the spread therefrom. On the SMA hypothesis the readiness potential is initiated by neuronal activity in the SMA, which continues throughout the RP. The problem now is to trace the neuronal patterns emanating from the SMA to the association cortex, the basal ganglia and the cerebellum (Fig. 7).

The Connections of the Supplementary Motor Area (SMA)

As illustrated in Fig. 6, the SMA has a wide range of connectivity, both in giving and in receiving (Jones and Powell 1969 and 1970; Pandya and Vignola 1971; Brinkman and Porter 1979). Figure 6 is built up from studies by degeneration and

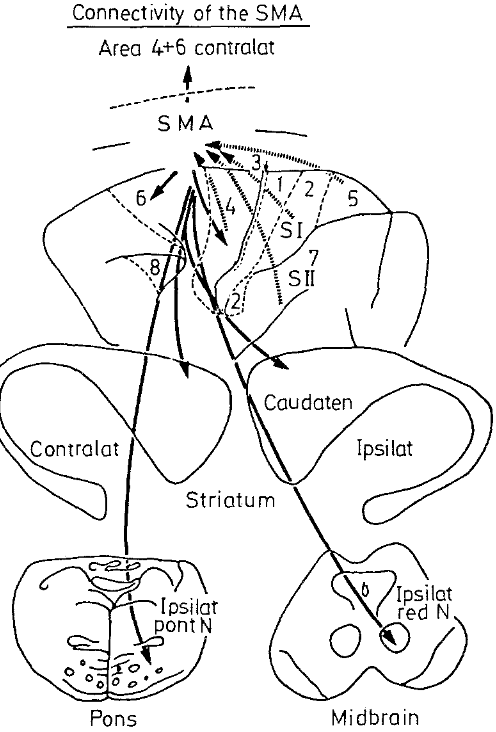

Fig. 6. Afferent and efferent connections of the SMA as revealed by anterograde degeneration and radio-tracer techniques (Wiesendanger et al. 1973)

tracer techniques (Wiesendanger et al. 1973). Projections to areas 4 and 6 were modest, but the bilateral projection to the striatum was widespread, and the SMA also received input from the ipsilateral somatosensory areas, 2, 5, and S II. The projection to the pontine nuclei gives the pathway to the cerebellum. Contralaterally there are projections to areas 4 and 6, and to the SMA (not shown).

The projection of SMA to the somatosensory areas, 5 and 3a (Jones and Powell 1969 and 1970; Brinkmann and Porter 1979) are not shown in Fig. 6, but would account for the large parietal RP's in Fig. 5. The cerebellar and basal ganglia (striatum) pathways are believed to be of great importance in the preprogramming of movements.

The projections from the cerebral cortex to the corpus striatum have a return line via the VA-VL thalamus. The cortical inputs would be both from the motor and premotor cortices and from the SMA. The output of the striatum is to the globus pallidus and thence via the VA-VL thalamus back to the cortex. Another important output is from striatum to the substantia nigra and thence back to the striatum and so again to the cortex via the thalamus. In Parkinsonism this path through the substantia nigra is degenerated with a consequent failure of voluntary movements (Fig. 5, upper traces), presumably due to the loss of the background excitation provided by the path via the substantia nigra. There are many other connectivities of the corpus striatum, but they are as yet but poorly understood functionally.

The other main circuit from SMA to motor cortex would be via the cerebellum. The projection of the SMA to the ipsilateral pontine nucleus in Fig. 6 is the first stage of the cerebellar loop: SMA→pontine nucleus→cerebellar cortex→dentatus nucleus→VA-VL thalamus→cortex, either motor or association (Allen and Tsukahara 1974; Allen et al. 1978; Eccles 1979; Sasaki 1979). There is also another loop via the pars intermedia of the cerebellar cortex, and either back to the cerebellar cortex of alternatively via the red nucleus to modulate the ongoing movement by spinal action (Allen and Tsukahara 1974; Eccles 1979).

Some 5% of SMA neurones project down the spinal cord in the pyramidal tract (Brinkman and Porter 1979), a projection that is also indicated by microstimulation of the SMA and retrograde transport to it of spinally injected horse radish peroxidase (Macpherson et al. 1981). Some 14% of SMA neurones are activated by peripheral afferent stimulation, an effect that presumably is by the pathways from areas 2, 5 and S II in Fig. 6.

There is much evidence that in the preprogramming of a movement, circuits through the basal ganglia and the cerebellum precede the activation of the motor cortex and the firing of impulses down the pyramidal tract. This would be of particular significance with quick 'ballistic' movements of the fingers, for example in typing or playing a percussion instrument. The total duration of the contraction may be no more than 200 ms, and the motor discharge is so brief in duration, down to 100 ms, that a ballistic movement cannot be modified by feedback from the periphery (Desmedt and Godaux 1979; Freund 1981). Thus the fine control of ballistic movements has to be exercised before the motor discharge is fired down the pyramidal tract. Its name derives from its resemblance to the firing of a gun. Even with the slower 'ramp movements' there can be an initial ballistic component that continues on to the slowly varying contractions of the ramp, which are under feed-back control by various reflex pathways activated by movement.

We are now introduced to the general concept of *the motor program* (Brooks 1979), which may be defined operationally as an assemblage of muscle contractions and relaxations for bringing about a particular learnt movement, for example writing a letter of a word, or even a whole word. To write a sentence involves a whole sequence of motor programs. The inventory of learnt motor programs is incalculable, for example in games, dancing, ballet and playing musical instruments. According to the SMA hypothesis the SMA does not contain most of the neural machinery of the motor programs. Rather what it does is to provide the entrée into the appropriate motor programs for implementing any particular intention. The motor programs are themselves complex neuronal organizations including circuits to the basal ganglia and the cerebellum. Both of these systems are immense neuronal machines, there being for example more neurones in the cerebellum than in the entire cerebral cortex. There is much evidence (Eccles 1977) that the cerebellum is an important repository of learnt motor programs, but its mode of action in this respect is still but little understood.

These circuits involved in motor programs can be assembled tentatively and very imperfectly in a composite diagram (Fig. 7), which illustrates the manner in which the SMA functions in respect of bringing about a voluntary movement in response to an *Idea* or *Intention*. As shown by the arrow the SMA is bilaterally activated across the mind-brain frontier (Fig. 2) and its output is partly to the association cortex, but most importantly to the basal ganglia and cerebellum by the pathways shown in Fig. 6. It is also necessary to realize that the basal ganglia and cerebellar pathways could act in the manner of reverberatory loops. This continued reverberatory action would be of particular importance in ensuring an effective preprogramming that is derived from the memory stores of motor programs. Roland et al. (1980a) even raise the possibility that the significant rCBF increases (10.6 and 7.8% in Fig. 4A) of the inferior frontal zones may be due to activity of the subjacent basal ganglia.

Discussion of the SMA Hypothesis

Much more investigation of the type initiated by Brinkmann and Porter (1979) is essential before it will be possible to define the SMA hypothesis more precisely. The two SMA's of the human cerebrum (Fig. 1) would have at a conservative estimate an area of 3000 mm^2 with more than 100 million neurones assembled in perhaps 30,000 modules. Such an area would have tremendous potentiality for pattern generation with special reference to the great repertoire of learnt motor subroutines. It would be a type of reference library. Though it seems to respond in a global manner as displayed by the rCBF indices (Fig. 4) and by the readiness potential over the vertex (Fig. 5), this can be considered as an illusion arising from the necessary crudeness of the recording procedures. The variety of unitary neuronal responses reported by Brinkman and Porter (1979) is to be expected when such a sampling technique is applied to the complex neuronal patterns that would arise in the SMA engaged in activating motor programs.

Voluntary movements can be of the widest diversity, involving an immense repertoire of learnt motor actions, which can be assembled according to desire or intention. In the development of the SMA hypothesis it is proposed that the SMA carries an inventory of this repertoire, so that directly or indirectly it can call up stored subroutines of learnt motor actions to give voluntary movements appropriate to any mental act of intention. Some of the pathways involved in this procedure are indicated in Fig. 7, but as yet we can only make the crudest diagrams. However Fig. 7 suggests an immense variety of research projects. It would be anticipated that there are stored subroutines in the cerebellum and the basal ganglia as well as in the association cortex. Furthermore these elemental subroutines must be blended together in the preprogrammed instructions forwarded to the motor cortex where there would be a final processing and coordination of information so that a well organized motor act is performed.

All of this activity precedes the excitation of the motor cortex with the resulting impulse discharges down the pyramidal tract (Evarts 1968 and 1972; Phillips and Porter 1977). It has previously been shown that neurones in the dentate and interpositus nuclei (Thach 1970, 1975 and 1978; Harvey et al. 1979), in the globus pallidus (DeLong 1971; Iansek and Porter 1980), and in the ventrolateral thalamus (Horne and Porter 1980) are intimately related to movements, with their discharges often preceding the movement as in Fig. 2. These neurones would be on the detours via the cerebellum (Fig. 7) and via the basal ganglia (Fig. 7) that have been extensively investigated by DeLong (1974) and DeLong and Strich (1974). Presumably these detours are involved in the preprogramming of movements initiated by the SMA.

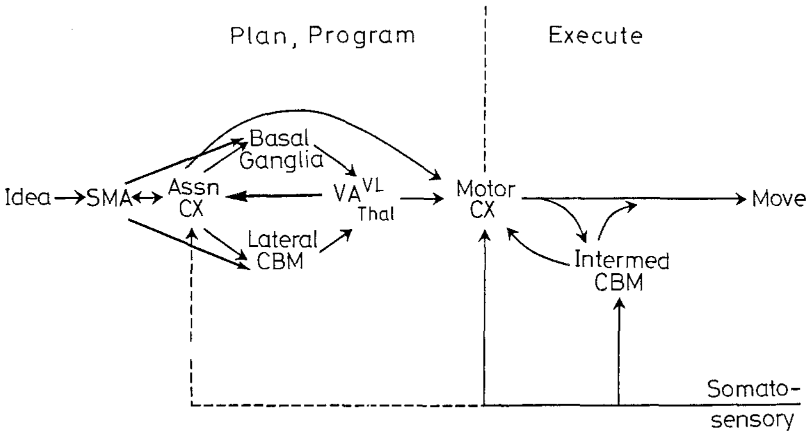

Fig. 7. Diagram showing the pathways concerned in the execution and control of voluntary movement; *ASSN CX,* association cortex; *lateral CBM,* cerebellar hemisphere; *intermed. CBM,* pars intermedia of cerebellum. The arrows represent neuronal pathways composed of hundreds of thousands of nerve fibres (modified from Allen and Tsukahara 1974)

In the light of this developed SMA hypothesis it is only to be anticipated that electrical stimulation of the SMA gave complex synergistic movements. This is all that could be expected when a crude and unnatural excitation is applied to the centre carrying the inventory of learnt motor actions. It is important to recognize that the bilateral activation of the SMA (Fig. 2), in order to bring about some unilateral movement, accounts for the bilaterality of the readiness potential in Fig. 5 for example.

It is important in the context of motor programs to mention linguistic expression–the tremendous variety in word pronunciation and tuning and in word linkage into sentences. It is not enough to make the usual statements that the Wernicke and Broca speech areas (Fig. 1) carry the stored programs of meaning and expression. On the SMA hypothesis the SMA plays a key role in the voluntary initiation of these programs, having the entrée into the repertoire of the motor programs of the Wernicke and Broca areas with the outcome of the desired linguistic expression. Penfield identified the role of the SMA of the dominant (speech) hemisphere in language and named it the supplementary speech area. He recognized its role both by stimulation and ablation in patients (Penfield and Roberts 1959). Stimulation resulted in vocalizations and ablation resulted in complete aphasia for about 2 weeks, with subsequent complete recovery. It can now be postulated that the recovery from aphasia is due to language initiation being taken over by the SMA of the minor hemisphere. Linguistic expression has not been left solely to the SMA of the linguistic hemisphere. In emergency the other SMA can stand in. We have already seen that both SMA's work cooperatively (Fig. 2).

Important research programs can now be outlined.

1. An intensive study of the microstructure of the primate SMA. Conceivably its unique relationship to the mental initiation of voluntary movement should have some identifiable structural counterpart.

2. The projections from the SMA need intensive study by tracer techniques (Wiesendanger et al. 1973). Goldman and Nauta (1977) showed that the dorsal bank of the principal sulcus projected to the caudate nucleus in a "spotty" manner. The cluster formation suggested a functional mosaic. Kunzle (1975) reported similar findings from area 4 to the putamen. Apparently there are as yet no studies of SMA projections to the basal ganglia. The tracer techniques should also be employed for SMA projections to the association cortex, the pontine nuclei and the inferior olive.

3. The discharges of SMA neurones should be studied as in Fig. 2, but for a wide range of learnt motor programs, and with a technique for studying the temporal relationships of SMA discharge to motor cortex activation.

4. Recording of neurones in the human SMA in response to trained subroutines as in the motor-sequence test and the readiness potential in the manner of Goldring and Ratcheson (1972) and Libet (1981) on the human motor cortex.

5. The ^{133}Xe investigations have great potentiality for disclosing more on the SMA activation in relation to motor programs. The motor programs in the first paper (Roland et al. 1980a) were excellently designed. But in the second paper (Roland et al. 1980b) the movements in relation to extrapersonal space were too complex to yield easily analysable results. It is hoped that a redesign of the testing procedures would give less complex results.

6. The ^{133}Xe investigations suffer from the disability that only the surfaces of the convexities of the cerebral hemispheres can be surveyed. The orbital surface of the frontal lobe, much of the medial hemispheric surface and important deep structures such as the thalamus and the basal ganglia are for example not investigatable. Thus there is a great future for tomography using such techniques as ^{14}C deoxyglucose or positron emission. But the spatial resolution of these techniques needs to be improved.

The Mental Act of Intention

As shown diagrammatically in Fig. 8, the mental act of intention is placed in the category of Inner Sense in the subjective World 2. According to the SMA hypothesis the liaison brain for intention is composed of the SMA modules. But there is reciprocity of information flow across the frontier between mind and brain—between mental intention and SMA activity in this case. On the dualist-interactionist hypothesis of the mind-brain relationship there is an intimate two-way information flow, but the mental event of intention or desire is primary, though subject to incessant revision from the secondary ongoing neural events in the SMA. It is of particular interest that in Fig. 4B the 'internal programming' of the motor-sequences evoked a large increase in the rCBF restricted to both SMAs, with no other significant cerebral activity. The mental act of intention must be able to trigger the SMA responses and yet by a further act prevent the normal neuronal spread from the SMA that is indicated in Fig. 4A. The obverse of this is that, when motor routines of a simple kind are voluntarily instituted (Fig. 4C, 4D), presumably by the SMA, the continued activity is carried out by the motor cortex while the SMA relaxes. The motor performance of Parkinsonian patients exem-

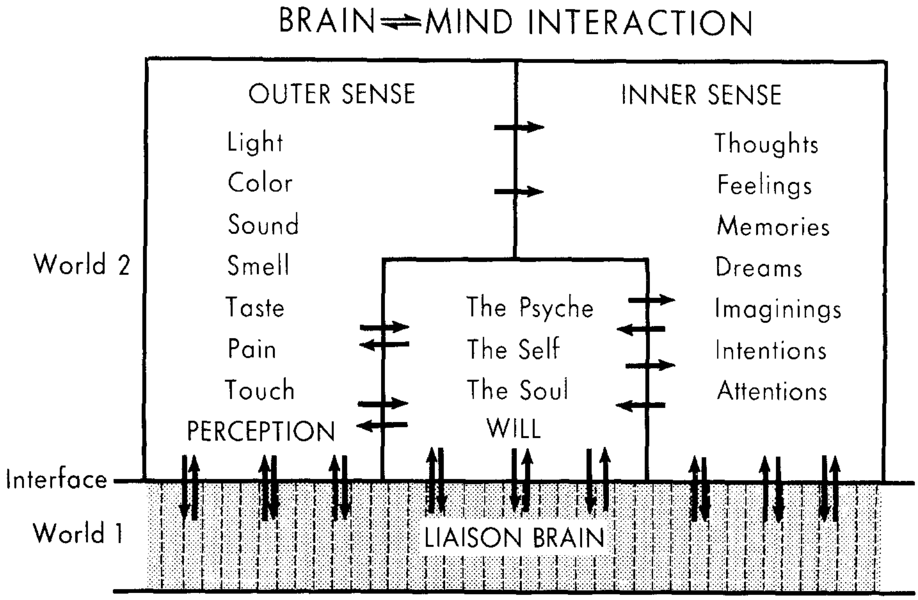

Fig. 8. Information flow diagram for brain-mind interaction in human brain. The three components of World 2: outer sense, inner sense and psyche or self are diagrammed with their communications shown by *arrows*. Also shown are the lines of communication across the interface between World 1 and World 2, that is from the liaison brain to and from these World 2 components. The liaison brain is the columnar arrangement indicated by the *vertical broken lines*. It must be imagined that the area of the liaison brain is enormous, with open modules numbering over a million, not just the 2 score here depicted. However for the SMA, which is the liaison brain for intentions there are probably no more than 30,000 modules

plifies this dichotomy. They have difficulty is starting up some movement, but, if that movement has an automatic character as in walking or swimming, there is no further difficulty.

The SMA hypothesis allows a sharp discrimination between voluntary and automatic movements. The former are initiated by the SMA and require continued SMA monitoring for their execution. The latter run on motor programs that do not require continual monitoring by the SMA, which is at rest as in Figs. 4C and D.

The mind-brain interaction postulated for voluntary movement has hitherto had a rather nebulous character because the unspecified site of action could be the whole of the association cortex. It is a great simplification and clarification to have, on the SMA hypothesis, the mental influences of intention restricted to the cortex of the SMA which is little more than 1% of the association cortex. There is a particular challenge to study the microstructure of the SMA to see if there is any unique structural design of the constituent modules (Eccles 1981) that could be related to its unique function. Moreover it should be possible to record from neurones of the human SMA in response to trained subroutines, as in the motor-sequence test. It cannot be anticipated that the knowledge gained by such investigations will provide decisive evidence on the opposed mind-brain theories—physicalism (materialism) or dualist-interactionism. But it will certainly be a challenge to the physicalists to develop their theory beyond the bland identification of mental with neuronal events.

The activated SMA can be envisaged as a complex of modular discharges interacting in circuits with a temporally patterned activity. The coded information in the SMA would be carried in scintillating sequences of dynamic patterns much as with a TV screen (Eccles 1981, Fig. 10). It may be asked: How can the intention to bring about a voluntary movement activate the appropriate modular patterns in the SMA so as to call forth the desired assemblage of motor programs? The answer is that from babyhood onwards we have been learning to carry out the skilled movements we desire.

So the general conclusions would be that the SMA represents the liaison area of the brain for intentions and that the dynamic patterns of its activity carry the information derived from the intention and relate it to the repertoire of the motor programs that are brought into action by outputs from the SMA to give eventually the required movements. We may ask: How can the physicalists account for the activation of SMA neurones when there is intention to move (Fig. 2)? It is begging the question to reply that this activation comes from some other as yet unidentified brain nucleus. No such extraneous activation is detectable in Fig. 4B when there is internal programming. For a dualist-interactionist, the explanation is simply that the intention is a mental influence that is exercised across the mind-brain frontier as illustrated in Fig. 8. The concept of the liaison brain for intentions is given precision by its identification with a relatively small cortical area, the SMA. The controversy between physicalists and dualist-interactionists has to be fought out on the basis of the most recent empirical discoveries, not on prejudice.

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