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Development and Change of Cortical Field Potentials During Learning Processes of Visually Initiated Hand Movements in the Monkey*

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Summary. Field potentials on the surface and at 2.5–3.0 mm depth in the cerebral cortex were recorded in various areas with chronically implanted electrodes and the potentials which preceded hand movements in response to a light stimulus were observed during the process of learning the skilled conditioned movement. A naive monkey had to lift a lever by wrist extension within duration of the light stimulus lasting for 900, 700 or 510 ms depending on the stage of the learning process.

In addition to some responses in the striate gyrus, significant short-latency responses to the light stimulus appeared bilaterally in certain areas of the prefrontal and prestriate cortices at an early stage of learning in which the monkey still lifted the lever randomly, and they became gradually larger as the monkey was trained further. Short-latency responses were also often noted in the bilateral premotor cortices during an early stage of learning.

When the monkey started to respond to the stimulus by the appropriate movement, early surface-positive (s-P), depth-negative (d-N) premovement potentials appeared in the forelimb motor cortex, and the responses in the premotor cortex increased in size. As the movement became faster and more skillful, late s-N, d-P premovement potentials, that are known to be mediated by the neocerebellum and superficial thalamo-cortical projections, emerged after the early s-P, d-N potentials and became more marked, larger and steeper in the forelimb motor cortex contralateral to the moving hand. All the premovement potentials in the different cortical areas thus developed into steady and constant states and remained so for many months thus maintaining their established patterns.

Such successive appearances of premovement field potentials in various cortical areas were related to learning processes of the movement and the implication of these findings was discussed.

Key words: Cortical field potential – Visually initiated movement – Motor learning – Monkey

Introduction

Field potentials which preceded visually initiated hand movements were recorded and analysed with chronically implanted electrodes on the surface and in the depth of the premotor, forelimb motor and somatosensory cortices of the monkey (Sasaki et al. 1981a; Gemba et al. 1981). It was also demonstrated that the neocerebellum directly participates in producing the surface-negative (s-N), depth-positive (d-P) component of the premovement potentials in the forelimb motor cortex and thus activates the motor cortex through superficial thalamo-cortical (T-C) projections to initiate the movement (Sasaki et al. 1981a, 1982). The premovement potentials in these cortical areas were recorded after monkeys had been sufficiently trained to perform the movement quickly without much failure and the potentials revealed steady and fairly constant characteristics in respective cortical areas for many months.

In the present study, premovement cortical potentials were recorded in every session of training from the beginning to the steady state in the learning processes of the movement and they were compared for different stages of the learning process. Recording sites of the cortex were extended from the premotor, motor and somatosensory cortices previously investigated to the most dorsolateral parts of the frontal, parietal and occipital cortices on bilateral

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sides. The preliminary data have been reported elsewhere (Sasaki and Gemba 1981).

Methods

Fourteen adult monkeys (*Macaca fuscata*) were used for the present study. Most of the methods for recording cortical field potentials with chronically implanted electrodes were the same as previously reported (Hashimoto et al. 1979; Gemba et al. 1981). Silver needle electrodes (0.25 mm in diameter) insulated except at their pointed tips (about 0.2 mm in exposed length) were placed on the surface and at a depth of 2.5–3.0 mm in eight to ten different loci in each hemisphere and fixed to the bone with dental cement. A few weeks after implantation, training was started for visually initiated hand movements. The monkey was conditioned to lift a lever by a wrist extension within the duration of the light stimulus, which lasted for 900 ms in the beginning and was later shortened to 700 and then to 510 ms. The light stimulus was delivered with a small green light diode in front of the monkey at a random time interval of 2.5–6.0 s. For a successful movement the monkey was rewarded with a bit of juice 600 ms after the lever elevation.

Initially, the monkey lifted the lever at random so that the movement sometimes occurred incidentally during the light stimulus. After training for some weeks (3–8 weeks in 14 monkeys), the monkey began to lift regularly the lever during the 900 ms duration of the light stimulus. It was considered that the monkey had learned the conditioned movement although the movement was still slow and unstable, and was called stage III. The previous stages when the monkey performed the movement randomly, were divided into stage I and II for convenience, the former being the earlier days of training with relatively small premovement potentials and the latter showing the marked potentials in the frontal and occipital association areas as will be seen in Results. The division of stages I and II did not depend on different behaviour of the monkeys but on relative sizes of the cortical potentials. After stage III, the monkey repeated the movement and gradually became fast and skillful in lifting the lever so that the light stimulus could be shortened to 700 ms and then to 510 ms. The accomplished steady state, which was called stage IV, continued for more than several months.

All cortical potentials and EOGs (electrooculograms) were referred to indifferent electrodes (two electrodes buried in the bone just behind the ears on both sides) and amplified with ac amplifiers with a 2.0 s time constant respectively, and stored through multichannel data recorders on cassette tapes. The data were averaged 100 times with the pulse of onset of the light stimulus and also with the pulse of the movement (time of lever elevation). Subtraction of the depth potential from the surface potential (S-D) can reveal the true electrical dipole activity of the cortical site being recorded (Sasaki et al. 1970; 1981b), and Figs. 3–5 exclusively show S-D records. EOGs recorded from electrodes buried in the rostrolateral edges of the frontal bone above the orbits on bilateral sides were usually negligibly small as shown in Fig. 1 and will not be presented in the other figures of this paper. EMG (electromyogram) was recorded from wrist extensor muscles by two electrodes placed on the skin over the muscles. It was amplified, rectified and averaged as shown in Fig. 1. Reaction times (RT) were plotted in a histogram for 100 successful movements and presented together with cortical potentials averaged over the same 100 samples. The histogram presents a time course similar to the averaged EMG, and is generally better in revealing different patterns of movement in the different stages than the EMG, e.g., random and reaction-time movements. Therefore, RT histograms are exclusively presented in Figs. 3–5. In the case of averaging with the pulse of movement, reaction times were plotted at onset times of the light stimuli preceding the movement (Fig. 4).

After electrophysiological investigations lasting from several months to two years, the monkeys were sacrificed and the sites of the recording electrodes were verified morphologically. Classification and nomenclature of the cortical areas were made according to Brodmann (1909). In two monkeys, as shown in Fig. 5, the unilaterel cerebellar hemisphere, including the interpositus and dentate nuclei on the same side to the moving hand, had been extirpated before the monkeys were trained in order to study the role of the neocerebellum in the learning process of the movement. The extent of the operation in these monkeys was histologically checked at the autopsy (Sasaki et al. 1982).

Results

Field Potentials Preceding Visually Initiated Hand Movements and their Distribution in Various Cortical Areas

Visually initiated hand movements are preceded by characteristic field potentials in premotor and forelimb motor cortices, as reported previously (Gemba et al. 1981). Figure 1 exemplifies premovement potentials in a region of the prefrontal cortex (a border region of areas 8 and 10) on contralateral (A) and ipsilateral (Ipsilateral A) sides in addition to those in premotor (B) and forelimb motor (C) cortices contralateral to the responding hand. Cortical areas are illustrated in the inset diagram by alphabetical symbols which are common with the headings of respective potential columns. In Fig. 1, field potentials on the cortical surface (S), and at depth (2.5–3.0 mm) (D) and surface minus depth potentials (S-D) are shown along with the EOG, EMG and histogram of reaction times (RT). All the data were made from 100 samples of the same animal on the same day after it had been sufficiently trained to lift the lever within the 510 ms light stimulus. In the examined part of the prefrontal area (A), surface-positive (s-P), depth-negative (d-N) field potentials emerged at about 40 ms latency after onset of the light stimulus and these were followed by s-N, d-P potentials. Such potentials were recorded on both sides, usually with equivalent sizes (A and Ipsilateral A). In the premotor cortex (B), s-P, d-N potentials were recorded at about 40 ms latency, bilaterally. In the forelimb motor cortex contralateral to the moving hand (C), early s-P, d-N potentials at about 40 ms latency were followed by late s-N, d-P potentials.

The distribution of such visually initiated premovement potentials is summarized in Fig. 2 with data obtained from 14 monkeys. Different potential profiles are illustrated by respectively different symbols. The potentials in a certain part of the prefrontal

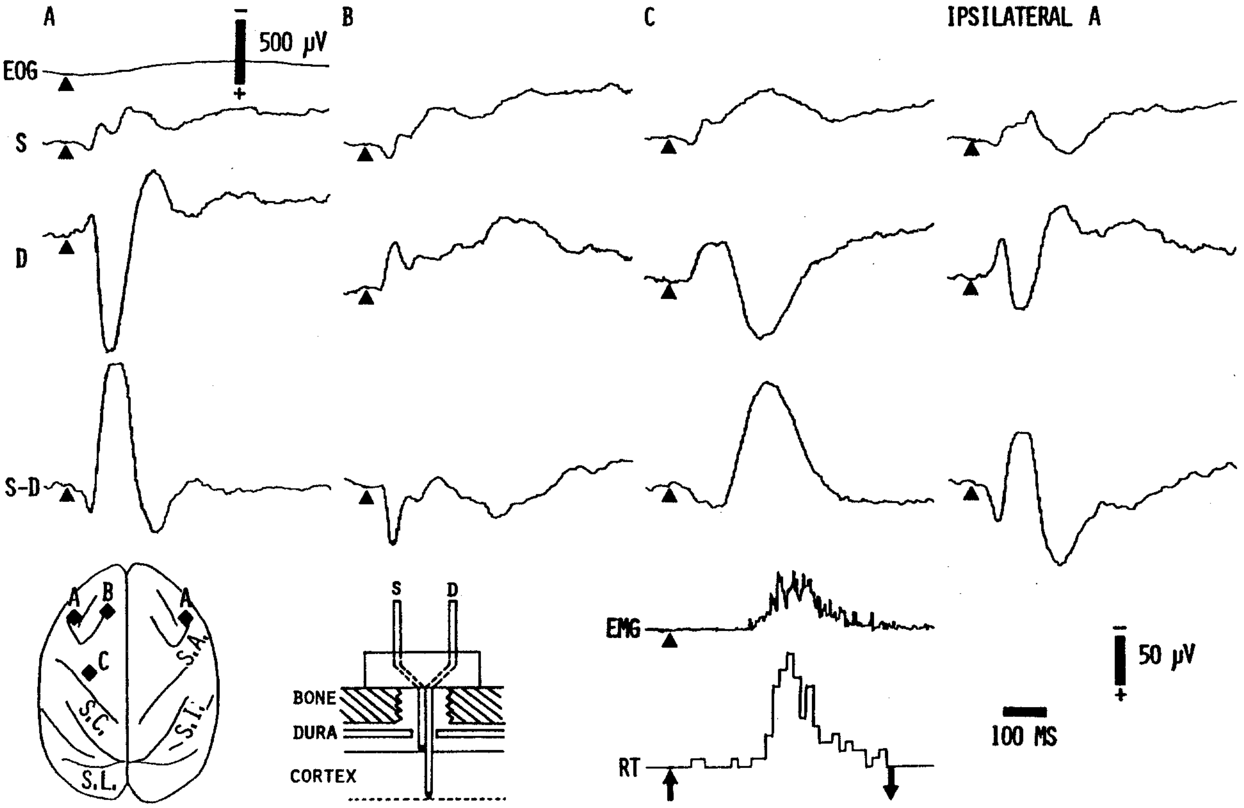

Fig. 1. Premovement field potentials in four cortical sites of a monkey which had been sufficiently trained with a visually initiated hand movement. The sites are indicated by common alphabetical symbols on the left inset diagram and respective potential columns. The site A of the right hemisphere was ipsilateral to the responding hand and its potentials are given in the Ipsilateral A column. Potentials of S and D rows were obtained from electrodes on the cortical surface (S) and at 2.5–3.0 mm depth (D), respectively, as illustrated in the right inset diagram. S-D row gives surface minus depth potentials. EOG (electrooculogram), EMG (electromyogram) and cortical potentials were averaged 100 times by the time pulse of onset of light stimulus indicated by *triangles*. Reaction times (RT) from the stimulus onset to the movement (moment of lever elevation) are plotted with 16 ms bins, and the onset and end of stimulus are given by upward and downward *arrows* under the histogram. There was a 100 ms scale for all potentials and the reaction time histogram, a 500 µV scale for EOG and a 50 µV scale for all cortical potentials. SA – arcuate sulcus; SC – central sulcus; SI – intraparietal sulcus; SL – lunate sulcus

cortex (Fig. 1A) and those in the prestriate cortex (area 19) (Fig. 3F) were usually similar to each other in configurations of early s-P, d-N and late s-N, d-P potentials, but the early component in the prestriate cortex was sometimes negligibly small as shown in Fig. 3F IV. The potential profiles of these cortical areas seem to resemble those of the contralateral motor cortex, i.e., the latter revealed early s-P, d-N and late s-N, d-P deflections (Fig. 1C). However, the potentials of the motor cortex are illustrated by the other symbol (open square), since the late s-N, d-P ones are known to be specifically mediated by the neocerebellum (Sasaki et al. 1981a; 1982). The latency of the late potentials measured on the baseline was longer for the motor cortex (105–130 ms in 14 monkeys) than for the prefrontal and prestriate cortices (65–110 ms in eight monkeys). Also, the time course of the potentials was usually longer in the former than in the latter.

In general, similar premovement potentials were obtained in both cerebral hemispheres, though the late s-N, d-P potentials in the contralateral forelimb motor cortex were seen exclusively on that side. The potentials in the somatosensory cortex were also predominant on the contralateral side, occasionally small potentials being noted on the ipsilateral side in some cases (Gemba et al. 1981). The distribution of the premovement cortical potentials on visually initiated hand movements is considerably different from that related to self-paced hand movements (cf. Gemba et al. 1980a).

Development and Change of Premovement Field Potentials in Different Cortical Areas During Learning Processes

From the commencement to the later steady stage of the learning process of the visually initiated hand movement, cortical field potentials were recorded in

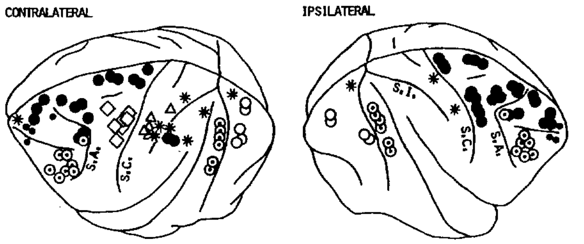

Fig. 2. Distribution of visually initiated premovement potentials in the dorsolateral aspects of hemispheres contralateral and ipsilateral to the responding hand. They were summarized from 14 monkeys at the well trained stage. Different symbols represent different kinds of potentials. Relatively simple surface-positive (s-P), depth-negative (d-N) potentials like Fig. 1B are shown by *filled circles*; s-P, d-N followed by s-N, d-P potentials like Fig. 1A and Ipsilateral A by *open circles with a dot in the centre*; s-P, d-N followed by s-N, d-P potentials of the contralateral forelimb motor cortex by *open squares*; those of the contralateral somatosensory cortex by *open triangles*; and those of the primary visual cortex by *open circles*. Loci without marked potentials are indicated by *asterisks*. Some of the electrode sites could not be plotted in the figures as they were too crowded in several areas. Sizes of potentials were not considered but only very small potentials were given by *small symbols*

every session of training. The training was undertaken on 2–5 days per week depending upon the situations of respective monkeys. In fact there were considerable differences noted among the 14 monkeys tested in this study in respect to the number of days required for training. However, it should be emphasized that the development and the successive occurrence of premovement field potentials in certain cortical areas appeared in the same manner and order in all the monkeys. Therefore, learning processes can be divided into four stages for the convenience of description. Figure 3 presents changes of premovement potentials in seven cortical areas on the contralateral side to the operant hand at four stages (I–IV) in the same monkey. Only S-D potentials are presented respectively with 100 averages with respect to the time pulses of the stimulus onsets. Figure 4 gives the same data as Fig. 3C–F but averaged with respect to the time pulses of the movements.

Figure 3 column I (stage I) gives premovement potentials recorded on the second day of training in the monkey. The monkey was still naive and lifted the lever randomly at its own pace as noted in the reaction time histogram (RT). Nevertheless some premovement potentials were already elicited in stage I, i.e., in prefrontal (A–C), premotor (D), prestriate (F) and striate (G) areas. Appearance of the potentials on such an early day was encountered rather infrequently, being confirmed in only three out of 14 monkeys. However, even if it took some days (3–20 days in 11 monkeys), significant premovement potentials emerged first in these prefrontal and prestriate loci, and simultaneously or a little later in the premotor cortex. Some responses were also recorded in the primary visual cortex from this early stage (Fig. 3I column G). In this stage, premovement potentials in the motor cortex revealed by movement pulse averaging (Fig. 4I, E) looked similar to those of self-paced movements reported previously (Hashimoto et al. 1979; Gemba et al. 1981), but were barely visible with stimulus pulse averaging (Fig. 3I, E). For the early stages, no marked premovement potentials were noted by movement pulse averaging in areas other than the motor cortex (Fig. 4I and II).

Within a few weeks after appearances of the potentials shown in stage I, the early s-P, d-N and late s-N, d-P premovement potentials in the prefrontal and prestriate cortices, especially the late potentials, became much larger though the movement still occurred randomly as noted in the histogram (Fig. 3II column) and in slowly increasing premovement potentials in the motor cortex (Fig. 4II, E). Behavioural manifestation was much the same as at the previous stage I, but such situations are called stage II, at which the monkey might pay at least more attention to the light stimulus than at stage I and recognize the light stimulus to be more "meaningful", as revealed by the enhanced potentials in the prefrontal and prestriate cortices. Next the monkey learned to lift the lever in response to the stimulus as indicated by the occurrence of some reaction times within the 900 ms stimulus duration (RT histogram in Fig. 3III column, stage III). The stage III usually began "suddenly", i.e., the monkey was able to respond to the stimulus on one day and then retain this ability on successive days. Three to eight weeks were noted from the commencement of training to this stage in 14 monkeys. This stage is characterized by the appearance of marked s-P, d-N field potentials at a latency of about 40 ms in the forelimb motor cortex (E of Fig. 3III). However, small s-P, d-N potentials were occasionally seen already at stage II in the motor cortex of a few animals (Fig. 5II, D). The s-P, d-N potentials in the premotor cortex often became larger at stage III. The potentials in the prefrontal and prestriate areas grew considerably and reached steady levels at stage III and this maximum size was maintained throughout the following months. Yet, during stage III, the movement response was still slow and the reaction time was unstable, as revealed by the histogram, and the light stimulus had to be given for 900 or 700 ms to encourage the monkey. Accordingly, the larger potentials in the prefrontal and prestriate cortices still appeared small by movement pulse averaging (Fig. 4III, C and F).

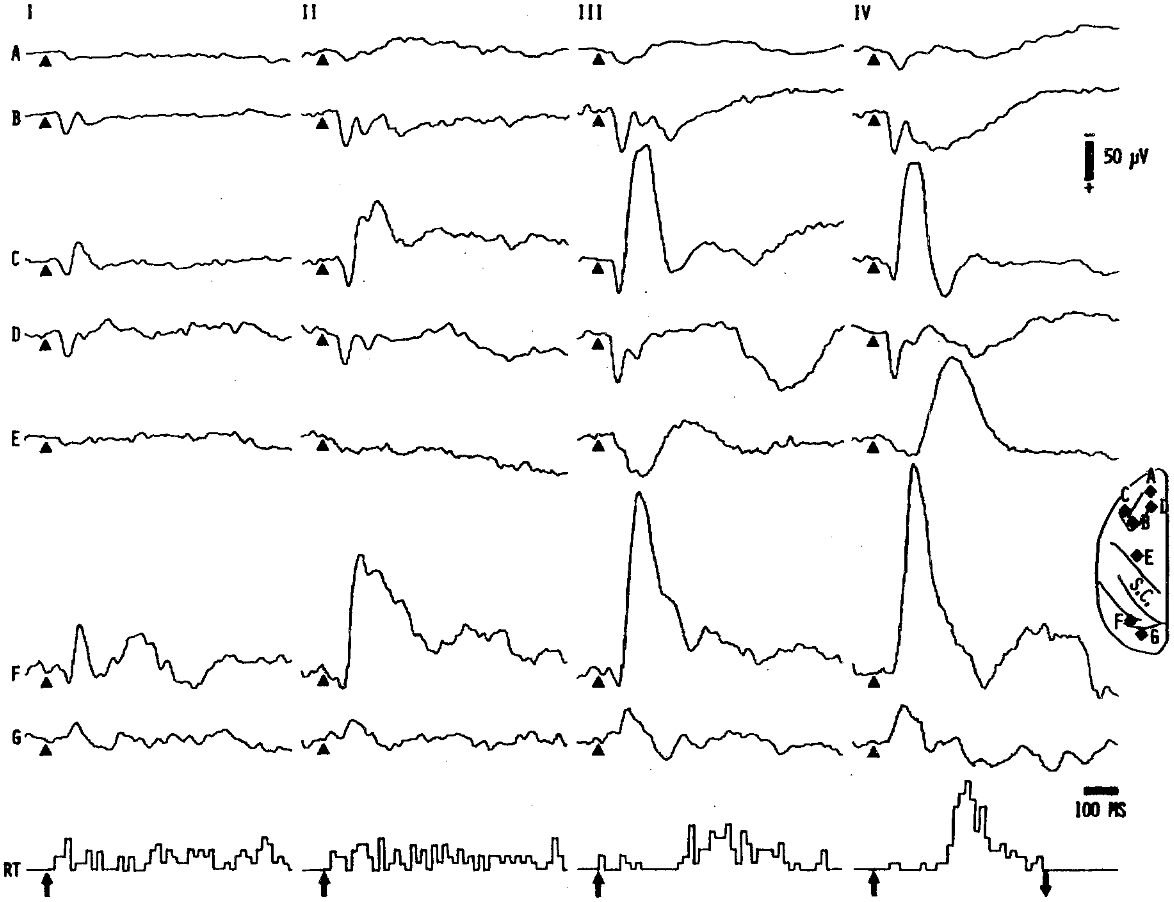

Fig. 3. Premovement S-D potentials in seven cortical loci on the left hemisphere of a monkey performing the right hand movement. I–IV columns present four sessions at different stages in the learning processes; I was taken in the 2nd session, II was 21 days after I, III 3 days after II, and IV 35 days after III. Two sessions were regularly performed in 1 week for this monkey, which lifted the lever several hundred times in one session. Potentials were averaged 100 times from every session for respective cortical loci indicated by *alphabetical symbols* in the inset diagram and the potential row. Light stimulus was given for 900 ms at I–III stages but 510 ms at IV. Only the movements which occurred during the light stimulus were counted in the histogram and averaged potentials (the later part of 900 ms is curtailed in columns I–III). *Triangles* and *upward arrows* indicate the onset of the light stimulus, whereas *downward arrows* mark the end of the stimulus. Other symbols and indications are the same as Fig. 1. For all potentials: 50 μV; for all traces: 100 ms

After stage III, the movement became gradually faster and more skillful with fewer failures as the monkey further repeated the movement in every session for several weeks, and the monkey reached a steady stage as shown in Figs. 3IV and 4IV (stage IV). This stage was invariable accompanied by a gradual increase in the late s-N, d-P potentials of the contralateral motor cortex. Better synchronization of the potentials related to less variable reaction times in stage IV contributed to some extent to the enhancement of the average (Fig. 3E). In fact, averaging of the same data by the movement pulse revealed some late premovement potentials at stage III, although they were smaller and blunter than those at stage IV (Fig. 4E). The late potentials have been shown to be mediated by the hemispherical part of the cerebellum (neocerebellum) and superficial thalamo-cortical (T-C) projections (Sasaki et al. 1981a, 1982).

As for cortical areas other than those mentioned above, premovement potentials were recorded in several other locations. In the area caudal to the lunate sulcus (area 17 and 18), s-N, d-P potentials appeared at an early stage of training and increased a little in size during the course of training (Fig. 3G). Such potentials were in some cases preceded by small s-P, d-N potentials. Latency of the potentials in this area was also about 40 ms. In the cortical area dorsal to the principal sulcus and rostral to the premotor cortex, relatively small s-P, d-N potentials were recorded at an early stage of training and they became enlarged a little later in training (Fig. 3A). Less active responses were noted more rostrally in this part of the prefrontal area. In the dorsal part of

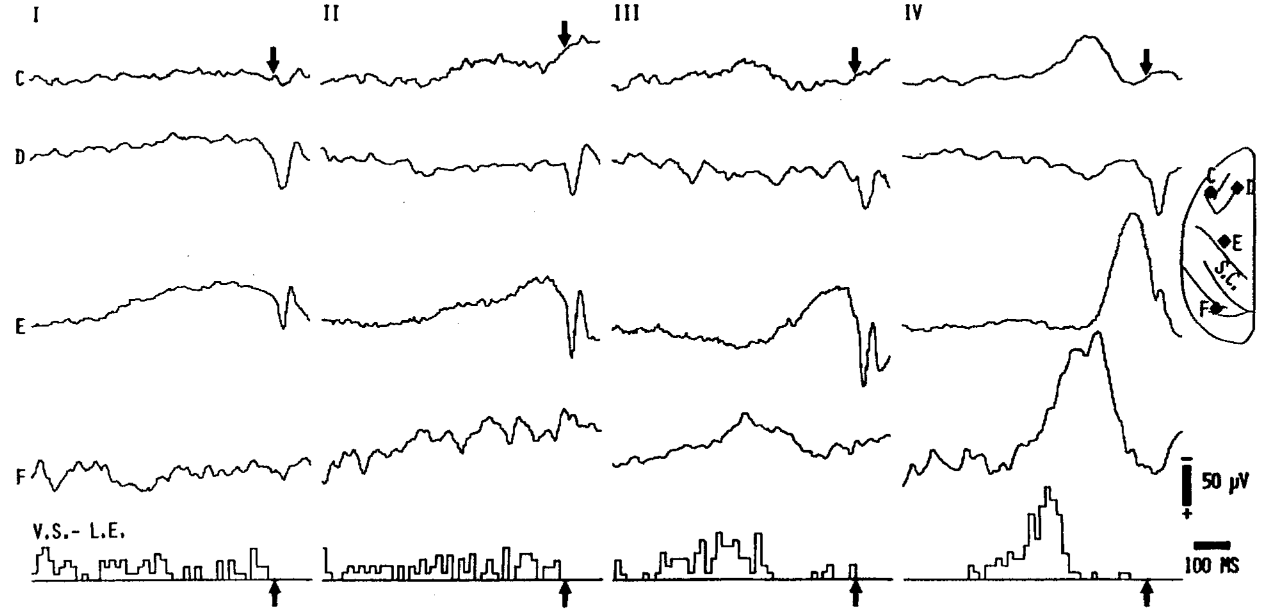

Fig. 4. The same data as Fig. 3C–F are averaged with time pulses of the movement (lever elevation) which are indicated by *upward* and *downward arrows*. Moments of onsets of the light stimuli are given in histograms (V.S.–L.E.) as preceding the movement pulse, and the early part of them in I–III columns are out of traces. Other indications are the same as Fig. 3

arcuate area, s-P, d-N potentials were usually observed as shown in Fig. 3B, being followed occasionally by s-N, d-P potentials (Fig. 2, an open circle with a dot in the centre).

In the somatosensory cortex contralateral to the operant hand, s-P, d-N potentials followed by s-N, d-P potentials emerged in some cases at a latency longer than 40 ms (Gemba et al. 1981), these being predominant at later stages of training. In the parietal association cortex, areas 5 and 7, conspicuos potentials were infrequently encountered in the present study, but s-P, d-N potentials could be recorded in a few cases from area 7, as illustrated in Fig. 2. The situation was different from that in the prestriate cortex (area 19).

Learning Processes in Cerebellar-Hemispherectomized Monkeys

After the cerebellar hemisphere had been extirpated on one side, two monkeys were trained to perform the visually initiated hand movement on the same side as the hemispherectomy. Histological examination verified later that the cerebellar hemisphere including the greater part of the dentate nucleus and

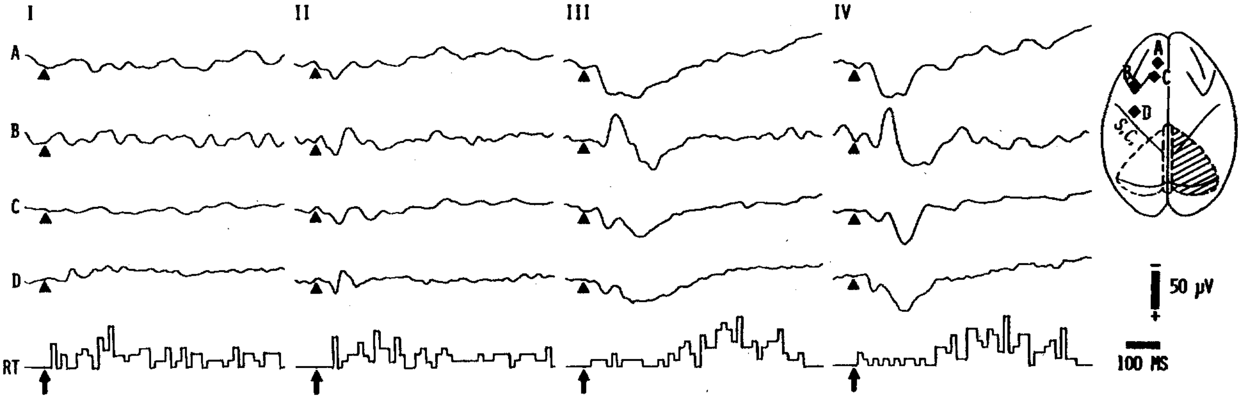

Fig. 5. Premovement S-D potentials in four loci of the left cerebral hemisphere of the monkey whose cerebellar hemisphere on the right side (shaded by *oblique lines*) had been extirpated before training the right hand movement. Averaged 100 times by the pulse of onset of the light stimulus lasting for 900 ms. The later part of I–IV columns is curtailed. Other indications are the same as previous figures. For all potentials: 50 µV; for all traces: 100 ms

a major part of the interpositus nucleus had been eliminated in each of the two cases. These monkeys revealed relatively severe cerebellar symptoms on the side ipsilateral to the operation, such as hypotonia, asthenia, dysmetria, motion and/or static tremor etc., especially in their forelimb (Gemba et al. 1980b). When such monkeys were trained to lift the lever with the disturbed hand, they needed a much longer time to touch and to lift the lever. Consequently, it took a longer time to train such monkeys to learn the visually initiated hand movement than it did normal monkeys. However, the successive appearance of premovement cortical potentials in various areas occurred in exactly the same order as in normal monkeys except the late s-N, d-P potentials in the contralateral forelimb motor cortex. The potentials were invariably and markedly observed at stage IV in normal monkeys, but were hardly recorded in the hemispherectomized monkeys for many months until the end of the experiment as shown in Fig. 5. This was confirmed by averaging the data with movement time pulse. In accordance with the lack of the potentials in the motor cortex, reaction time was shortened to a much less extent than in normal monkeys with training over the whole experimental period (Fig. 5IV). Relatively more frequent failure in lifting the lever within the 900 ms stimulus duration was encountered with these monkeys than with normal ones and this hardly improved with training over many months.

Discussion

Field potential analysis with chronically implanted electrodes in the cerebral cortex has enabled us to investigate phenomena of long-lasting, learning-related changes occurring in the cortex. The advantages, reliability and limitations of the analysis have previously been pointed out and discussed (Sasaki et al. 1981b). This method can reveal electrical dipoles produced mainly by EPSP currents in populated pyramidal neurones of the cerebral cortex in a relatively limited area under recording but ignores activities of cortical stellate neurones (Lorente de Nó 1947; Sasaki et al. 1970). Nevertheless, 14 monkeys used in the present study have revealed consistent data and disclosed sequential events occurring in various areas of the cerebral cortex during the process of learning a conditioned movement.

Marked premovement potentials were observed in a certain region of the prefrontal cortex and in the prestriate cortex from an early stage of the learning process and grew further to stage III, when the monkey learned to respond to the light stimulus by lifting the lever. This learning was accompanied by significant changes in the electrical activities of the forelimb motor cortex. The premotor cortex usually started to reveal its activities at a relatively early stage. Within the premotor area, the rostral part tended to start earlier than the caudal part. It was not expected that the parietal association areas, especially area 7, lacked marked premovement activities (Mountcastle et al. 1975; Lamarre et al. 1980). The method adopted in the present study would not be suitable to pick up activities of relatively small numbers of neurones. Another limitation of this method is that the neuronal activities in a deeply folded sulcus would inevitably be overlooked.

Activities of Association Cortices in Learning Processes

Enhanced premovement potentials in a part of the prefrontal cortex and in the prestriate cortex, and often those in the premotor cortex, always preceded the learning of the conditioned movement. After the monkey had come to respond to the light stimulus with the movement, the premovement potentials in these cortical areas showed steady characteristics (stage III and IV). This may indicate that these cortical areas are important in earlier stages of learning the conditioned movement, i.e., learning the meaning of the light stimulus, relating the stimulus with the movement to obtain the reward and so on. These association cortices and also the premotor cortex appear to function bilaterally for the learning process of unilateral forelimb movements, which is in contrast to motor and somatosensory cortices.

Since a part of the prefrontal cortex and the prestriate cortex are known to be closely related to the visual function (Chavis and Pandya 1976; Suzuki and Azuma 1977; see Creutzfeldt and Kuhnt 1973), activities of these areas during the early stages of the learning process will be concerned with the kind of stimulus used as the conditioning stimulus. If another kind of stimulus, like auditory or somesthetic, was used, different cortical areas might be active instead or in addition to these areas. The significantly altered electrical activity of this part of the prefrontal cortex and the prestriate association cortex in the course of attaining the visually initiated movement suggests that participation of such association cortices in higher order integration is primary and essential in the learning of conditioned movements in general.

Boyd et al. (1977) reported an M (meaning) wave in the process of motor learning using squirrel monkeys and suggested that precentral and postcentral areas were the cortical sites of the M potential. The polarity of the M potential and its manner of appearance seem to resemble the late surface-negative (s-N), depth-positive (d-P) component of the premovement potentials in the prefrontal and prestriate cortices in the present study. However, according to the cortical localization of the M potential, it might correspond to the late component of the premovement potentials in the forelimb motor cortex which increased from stage III to IV in our study. But this late component obviously differs from the M potential, since this is entirely related to execution of the hand movement (Gemba et al. 1981). These problems might be caused by some difference in the cortical organization of squirrel and macaque monkeys.

Cerebro-Cerebellar Interactions in Learning Processes

In the later part of the learning process, the cerebro-cerebellar interaction was found to be recruited, activating the motor cortex through the neocerebellum and superficial thalamo-cortical (T-C) projections so that the movement was performed fast and skillfully. This conclusion is supported by the previous reports of cerebellar-hemispherectomized monkeys (Sasaki et al. 1981a; 1982), i.e., cerebellar hemispherectomy in the well-trained monkey immediately and completely eliminated the late s-N, d-P premovement potentials in the contralateral forelimb motor cortex with concomitant prolongation of the reaction time of movement by 90–250 ms. Such influences of cerebellar hemispherectomy appear to correspond to the degradation in the learning process from stage IV to III, i.e., from the state of utilizing fully the function of cerebro-cerebellar neuronal circuits to little or no organized state of the circuits.

The monkeys whose cerebelli had been previously hemispherectomized needed a longer time to learn the visuallyinitiated hand movement than normal monkeys as described in Results. Such slow attaining of stage III in the hemicerebellectomized monkeys may be mainly due to severe cerebellar symptoms as mentioned, but it might also be caused by disturbance of some programming functions of the cerebro-cerebellar neuronal circuits; both are, however, difficult to distinguish in the actual process of motor learning. It is not known what cortical areas send impulses induced by the visual stimulus to the neocerebellum, but data of previous acute experiments of cerebro-cerebellar interconnections in monkeys suggest the premotor cortex, some prefrontal areas and/oder the motor cortex (Sasaki 1979). The time course of the cerebellar participation in the later stages (stage III and IV) of the learning process will be dealt with in detail in another report.

Processes of Motor Learning

It is interesting to note that the latencies of premovement potentials in different cortical areas have largely equal values of around 40 ms (35–47 ms in different loci except the somatosensory cortex). The field potential analysis might overlook neuronal activities of small populations of neurones and/or those in deeply folded cortices which would possibly be excited at shorter latencies. However, the same ranges of latencies among the primary visual cortex, association areas in prefrontal and prestriate cortices, and premotor and motor cortices, suggest that the majority of impulses evoked by the visual stimulus arrive at these cortical areas almost simultaneously and in parallel during the late stage in which learning has been accomplished. Also, the latencies of discrete waves changed little in respective cortical areas during the learning process. In fact, it was consistently observed in every monkey that responsive cortical areas were successively added along the learning process. Moreover, respective premovement potentials increased in size gradually up to respectively certain levels at different stages without marked changes of the latencies. These facts indicate that visually evoked impulses arrive at the primary visual cortex at the beginning of learning, and simultaneously or several days later at the association as well as premotor cortices, then several weeks later at the forelimb motor cortex and thus let the motor cortex execute the visually initiated movement. At the later stages of motor learning, the neocerebellum will be recruited by the cerebral cortex to activate the motor cortex through the thalamus in order to perform the movement both quickly and skillfully.

The sequential participation of these different cortical areas with much the same latencies indicates that visually evoked impulses are conveyed in a stepwise and additional manner to the different areas by some "switching" mechanism, i.e., volleys of impulses evoked by the visual stimulus are first conveyed only to the primary visual cortex, and are then delivered in succession to the association cortices, the premotor cortex and then to the motor cortex along stages I–III of the learning process, additionally by a "switching" mechanism working somewhere in subcortical structures. The early components of premovement potentials recorded at latencies of about 40 ms in the different cortical areas were mostly s-P, d-N. According to depth profiles in the cortex, they must be either deep T-C responses or cortico-cortical ones, or admixed with both responses (Sasaki 1979; Sasaki et al. 1981b). The fact that the latencies are of the same order suggests that the early components are more likely to be mainly constituted by deep T-C responses than by cortico-cortical ones. Therefore, the "switching" mechanism should occur in the thalamus or its closely related structures. Thalamic nuclei, especially associational and/or intralaminar nuclei of the thalamus, might be candidates for such a function, since various paths of information flow, including those from the cerebral cortices, can converge into these nuclei which then project divergently onto various cortical areas both directly as well as indirectly (Hassler 1972; Kievit and Kuypers 1977; Akert and Hartmann-Von Monakow 1980).

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