

## OVERLAPPING AREAS IN THE MOTOR CORTEX OF THE BABOON

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The use of variable parameters of electrical stimulation in experiments on the motor cortex gives opportunity to reinvestigate the definition of cortical areas (Fulton, 1949; Livingston, 1949). In the classical experiments of Ferrier (1873, 1876) and subsequent workers (Grünbaum & Sherrington, 1901, 1903), the inductorium disclosed circumscribed foci for a large number of movements forming a motor map of relatively constant pattern. On the other hand, from clinical observations Hughlings Jackson (1890), and more lately Walshe (1943), recognized widely overlapping fields of origin—a belief supported by the well-known stimulations of the brain cortex by Penfield & Boldrey (1937).

In observations on the motor cortex of the red monkey (*Erythrocebus patas*) we found that single pulses of adequate duration (5-25 msec.) elicited solitary movements of thumb and index from a large area which overlapped, medially, another large area from which similar movements of the hallux could be provoked. With pulses 1 msec. in duration at a frequency of 100 c.p.s., on the other hand, this same cortical territory yielded the usual wide range of fragmentary movements of all parts of the body. The observations were extended to the baboon (*Papio papio*), which seems to have a brain intermediate in complexity between other old-world monkeys and the great apes (Brown & Sherrington, 1911; Fulton & Keller, 1932).

### METHODS

Eight motor areas were examined in six immature baboons (*P. papio*), four male and two female, weighing between 4.0 and 6.0 kg. No immaturity of motor performance, however, was evident in their highly skilled and agile gage behaviour.

They were anaesthetized with nitrous oxide followed by intraperitoneal hexobarbitone sodium (50 mg./kg. body weight). The effect of the first injection would generally last for about an hour, during which the surgical preparation would be completed, and a lighter level of narcosis would then be maintained, and varied as required by the experiment, by injections of 10-20 mg./kg. hourly. The trachea was cannulated. After craniectomy to expose one or both Rolandic regions

widely, the head was fixed in a clamp which gripped zygomata and palate, but permitted movement of the jaw. The scalp edges were lifted up by sutures towards an overlying metal ring. After opening the dura the pocket thus formed was flooded with liquid paraffin at body temperature, and the brain photographed. Prints were then shortly available for accurate charting during the period of stimulation. Under these conditions the cortex is well coloured, the arteries pulsate freely, and the brain does not bulge into, nor fall away from, the opening in the skull.

The electronic stimulator we used was designed by Dr A. H. S. Holbourn and delivers square pulses of current continuously variable in duration from 3 sec. to 50  $\mu$ sec., and in strength from 5  $\mu$ A. to 15 mA. The impedance of the output valve and the incorporation of large series resistance (overall voltage 400) ensured that the current flowing between the electrodes remained steady at any setting, and was largely independent of tissue-resistance and reactance; non-polarizable electrodes were unnecessary. Pulses could be delivered at any frequency between 2/min. and 500/sec. Its calibration was frequently checked. It was driven from a stabilized power supply.

Monopolar and bipolar stimulation were both used. For the former, the stigmatic electrode (Sherrington's pattern) was the cathode, and was of silver wire tipped by a ball 0.75 mm. in diameter, spring-mounted and moved by a rack-and-pinion mechanism firmly clamped to the head-holder. The indifferent electrode (anode) was of silver foil tucked under the dural edge, or a silver plate beneath the scalp. In bipolar experiments the electrode-tips were 2.0-3.5 mm. apart.

The preparation lay prone, with the opposite elbow semi-flexed, the forearm semi-pronated and the thumb and fingers semi-extended by light traction with thin latex strips. The opposite hindlimb was abducted at hip, with knee and ankle at right-angles. All movements started from this initial posture. Three observers watched the responses.

## RESULTS

### *The effect of single shocks*

Stimulation by single shocks sufficiently infrequently provides conditions which tend to minimize facilitation and extinction, evoking, from any point or zone of the cortical surface, the smallest possible response. It was found by experience that a facilitatory building-up of responses did not occur if the single pulses were delivered at a frequency of 1 c.p.s. or less. At first, a full minute's interval was allowed between successive stimulations of three or four shocks each. After the first four experiments this interval was reduced when it had become clear that stable responses at 1 c.p.s. would continue for 2 min. at least.

The optimum pulse-duration was about 5 msec. Longer pulses had no greater effect. Shorter pulses, on the other hand, were ineffective in the unfacilitated state unless the current-strength were increased, and were not used because of the risk of stimulus spread. The results were the same with bipolar as with unipolar stimulation, and were unaltered whatever the orientation of the indifferent electrode.

A part of the middle third of the precentral gyrus had the lowest threshold (1.0-1.6 mA.). Each shock caused a flick of the opposite thumb. The movement was generally of flexion and adduction, but sometimes of extension, and was associated, but not invariably, with abduction of index, with flexion or adduction of minimus, or with both. The details of the movement differed slightly from one preparation to the next, but were rather stable throughout each individual

experiment. No other movements could be evoked from this area at this strength, and no movements at all from the rest of the motor area (Fig. 1).

A small increase in strength resulted in enlargement, in a medial direction, of the area from which this thumb-complex could be evoked (Fig. 2). The

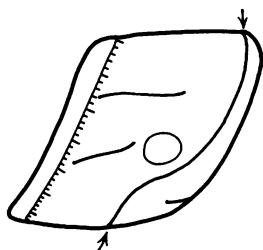


Fig. 1.

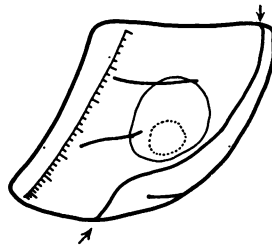


Fig. 2.

Fig. 1. Left Rolandic region, thumb-index-minimus area. Strength 1.6 mA., duration 4.5 msec. Scale in mm. Arrows mark central fissure.

Fig. 2. Same experiment as in Fig. 1. Enlargement of thumb-index-minimus area, solid line, strength 1.8 mA., duration 4.5 msec. Broken line indicates area in Fig. 1.

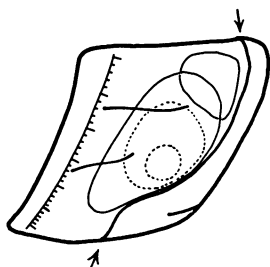


Fig. 3.

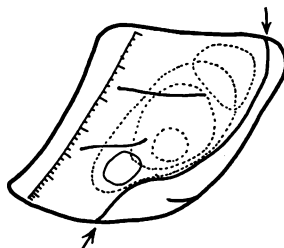


Fig. 4.

Fig. 3. Same experiment as in Figs. 1 and 2. Strength 2.05 mA. Thumb-index-minimus area indicated by lower continuous line. Broken lines indicate areas in Figs. 1 and 2. Upper continuous line indicates toe area, now overlapped by thumb-index-minimus area.

Fig. 4. Same experiment as in Figs. 1-3. Strength 3.7 mA. Continuous line indicates mouth area. Thumb and toe areas, though now actually larger, are indicated as in Fig. 3, but with broken lines.

movements obtained from its edges resembled those obtained from its lowest threshold lateral part with the weaker shocks. The remaining parts of the motor area do not respond at all at this strength.

Further increase in strength enlarges the area still further medialward, and at this stage flick movements of the toes occur when a medially contiguous area is stimulated (Fig. 3). These movements, like those of the hand, are variable from animal to animal: sometimes hallux, alone or with the long middle toe, flexes; sometimes the four lateral toes dorsiflex, alone or with abduction of hallux. As the shocks are made still stronger, these areas for the

thumb and toe complexes, expanding respectively medialward and lateralward, overlap more and more. A third area then appears: movements of the tongue, and sometimes of the crossed lower face as well, answer stimulation of the lateral part of the gyrus (Fig. 4). And with stronger shocks still, the three areas overlap so extensively that flick movements of all three regions together can be obtained by stimulating at any point over the greater part of the motor area.

With the stronger shocks, the thumb complexes elicited from the lowest threshold region of the thumb area were more vigorous, involving all the digits (usually in dorsiflexion) and sometimes the wrist as well; with stronger shocks still (5 mA.) the elbow may flex as well.

The level of narcosis was found to be of critical importance. In every experiment, and several times during each experiment, these stimuable areas would shrink, or disappear altogether, during the few minutes that followed each (hourly) injection of hexobarbitone, to reappear (thumb first, face last) and enlarge gradually as the anaesthetic lightened again. The level of narcosis could be gauged more readily from the size of these areas for any given current strength than from any other signs. Conjunctival, pupillary and swallowing reflexes were present throughout.

From four of the motor areas examined, the cortical region of the lowest threshold for the 'thumb complex' was at the conclusion of the experiment resected subpially, without reducing the responses obtained from the fringes of the enlarged area found with the stronger shocks.

The detailed analysis of the electromyographic records from the intrinsic muscles of the hand is not now presented in detail. But it may be said that the measured latencies varied between 10 and 16 msec., which were the shortest and longest values in the whole series of experiments. In any one experiment, the largest difference between maximum and minimum latencies was 4 msec. If movement had been due to excitation of the regions of lowest threshold by deep cortical waves (Adrian, 1937) reaching them from outlying stimulated points, the latencies should have lengthened systematically, by at least 10 msec. for every 6 mm. Adrian found no such lengthening in the same muscles excited from different cortical points, nor have we observed it in our own experiments.

#### *Responses to repetitive stimulation*

If the frequency of the current pulses is increased, for example to 50 c.p.s., the simple pattern of representation of hand, toes and face ultimately dissolves into the greater wealth of representation of fragmentary movements of all parts seen in the classical motor map (Brown & Sherrington, 1911).

This effect of progressive increases in pulse frequency at different cortical points (pulse strength and pulse duration remaining unchanged) has been repeatedly observed. In general, it may be said that movements of more

proximal joints are brought in by frequencies above about 15 c.p.s., with diminishing summation-period for those movements as the frequency rises further. Stimulus rhythm up to about 10 c.p.s. is visible and palpable in the distal parts which alone are activated by the same pulses when given singly.

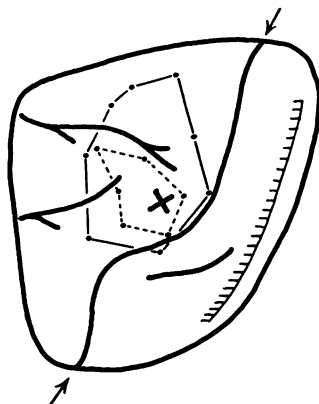


Fig. 5. Left Rolandic region, another experiment, 4.5 msec. pulses. Continuous line indicates thumb-minimus area when strength 2.35 mA., broken line when strength 1.4 mA. Cross marks point referred to in text.

This process of transition can be illustrated by an example from another set of observations. A point, indicated by the cross in Fig. 5, was stimulated with 4.5 msec. pulses, strength 1.0 mA., while the pulse frequency was gradually increased. The development of events was as shown in Table 1.

TABLE 1		
Time	Pulse frequency (c.p.s.)	Response
1843	—	100 mg. hexobarbitone injected
1852	1	Flick-flexion and adduction of thumb and flexion of minimus with each shock
1853	10	Flexion of thumb and minimus, with detectable stimulus rhythm
1855	10	Flexion of thumb and minimus, with detectable stimulus rhythm
1856	17	Flexion of thumb and minimus; rhythm irregular
1857	25	Immediate flexion of thumb and minimus; delayed movement of wrist
1858	25	Immediate flexion of thumb and minimus; dorsiflexion and ulnar deviation of wrist, latency 2.5 sec.
1859	37	Immediate flexion of thumb and minimus; dorsiflexion, ulnar deviation and hyperpronation of wrist, latency 2 sec.
1900	50	Immediate flexion of thumb and minimus; dorsiflexion, ulnar deviation and hyperpronation of wrist. Small interval between digit and forearm movements

When electrode positions are chosen well inside the 'leg area', and pulses are strong enough, singly, to elicit combined flick-movements of thumb and toe complexes, the thumb-complex component of the response gradually drops out as the frequency is increased and movements of the proximal parts of the leg are now added to those of the toes.

#### DISCUSSION

The configuration of the excitable motor areas delineated by single-pulse stimulation at an appropriate level of narcosis is akin to the composite map of Penfield & Boldrey (1937, fig. 25) derived from cortical stimulation of 163 conscious patients, with a frequency of 55-65 c.p.s. Before 1932 they had been using galvanic stimulation for localization and faradic for provoking epileptiform phenomena, when the importance of exact specification of the parameters of stimulation was not appreciated.

Hughlings Jackson (1890) had concluded from the study of oncoming and recovering paralysis, and of local epilepsy, that the representations of movements overlap and that the highly skilled movements of distal parts do so most widely. 'To me the "leg centre" is only part of the "motor region" where most special movements of the leg are represented, and where subordinate movements of the arm and of other parts of the body are also represented. (The same *mutatis mutandis* for other centres).'

Anatomical proof of overlap in the macaque's brain is provided in the recent study of Glees & Cole (1950). Small lesions in the 'hand area' caused degeneration diffused evenly throughout the cross-section area of the pyramidal tract, extending as far as the lumbosacral cord. Functional recovery followed in quantitative tests of motor skills pre-operatively inculcated. Their observations confirm the earlier observations of Sherrington (1889), who found that after a lesion in the arm area encroaching little if at all on the cortex of the leg area, Marchi's method showed degeneration in the cord as low as the sacral region of the cord. As in the case of the comparable clinical observations, recovery, in the experiments of Glees & Cole, is unintelligible in terms of a rigid mosaic of motor representation (Walshe, 1947).

In stimulation experiments Murphy & Gellhorn (1945) observed a wide overlap of representation in rabbit, cat and monkey under conditions of primary facilitation, but were surprised to find that proximal movements were evoked at least as widely, and even more widely than distal movements. Clark & Ward (1948) were also surprised to find that near-threshold stimulation excited distal segments less often than proximal. Like Penfield & Boldrey (1937) both groups of investigators employed relatively high frequencies of stimulation: 90 c.p.s. (Goodwin stimulator) and 60 c.p.s. (alternating current) respectively.

The experiments now reported have differed from those of other investigators chiefly in the choice of anaesthetic, which seems to be less of a circulatory depressant than Dial, and in the use of stimulus frequencies so low that each shock finds the cortex in an 'unfacilitated' state. In these circumstances large overlapping areas of the precentral gyrus yield flick movements of distal parts. With higher frequencies the pattern of representation approximates more and more to that of the classical maps.

The possibility that escape of stimulating current may have been the cause of the overlap found in our experiments remains to be discussed. We believe that the irregular shape of the areas and the eccentric disposition of their lowest threshold regions makes this unlikely; these spatial features are unaffected by altering the orientation of the indifferent electrode in unipolar stimulation or by changing to bipolar. Escape of current to the cortex of the lowest threshold regions (but not to the underlying white matter), or transcortical spread of excitation to it, is excluded by the experiments in which those regions were excised. Replacement of the dural flaps and stimulation of their surfaces never excited the underlying cortex. None of these controls, of course, is absolute. But even if escape of current were occurring, it remains true that at the strengths we used, single pulses evoked these distal movements alone, and none of the other movements, to reveal whose rich representation there was need only to increase the frequency of the same stimulating pulses.

#### SUMMARY

1. In six young baboons anaesthetized with soluble hexobarbitone stimulation of the brain surface with single pulses (1–5 mA., 5 msec.) elicited flick movements of thumb, index and minimus, of hallux and other toes, and of tongue and angle of mouth, from large overlapping areas centred on middle, medial and lateral thirds respectively of the precentral gyrus.

2. Thumb complex has the lowest threshold, face complex the highest.

3. If the frequency of stimulation is increased, this simple pattern of representation dissolves into the classical motor map.

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#### REFERENCES

- Adrian, E. D. (1937). *J. Physiol.* **88**, 127.  
Brown, T. G. & Sherrington, C. S. (1911). *J. Physiol.* **43**, 209.  
Clark, G. & Ward, J. W. (1948). *Brain*, **71**, 332.  
Ferrier, D. (1873). *West Riding Lunatic Asylum med. Rep.* **3**, 30.  
Ferrier, D. (1876). *The Functions of the Brain*. London: Smith Elder.  
Fulton, J. F. (1949). *Functional Localization in the Frontal Lobes and Cerebellum*. (*Withering Lectures*, 1948, Birmingham.) Oxford: Clarendon Press.  
Fulton, J. F. & Keller, A. D. (1932). *The Sign of Babinski*. Springfield.  
Glees, P. & Cole, J. (1950). *J. Neurophysiol.* **13**, 137.

- Grünbaum, A. S. F. & Sherrington, C. S. (1901). *Proc. Roy. Soc.* **69**, 206.
- Grünbaum, A. S. F. & Sherrington, C. S. (1903). *Proc. Roy. Soc.* **72**, 152.
- Jackson, J. Hughlings (1890). *Lumleian Lectures. R.C.P.* (Reprinted in *Selected Writings of John Hughlings Jackson*, p. 412. London, 1931: Hodder & Stoughton.)
- Livingston, R. B. (1949). *Helv. physiol. pharmacol. Acta*, **7**, 15 C.
- Murphy, J. P. & Gellhorn, E. (1945). *Arch. Neurol. Psychiat., Chicago*, **54**, 256.
- Penfield, W. & Boldrey, E. (1937). *Brain*, **60**, 389.
- Sherrington, C. S. (1889). *J. Physiol.* **10**, 429.
- Walshe, F. M. R. (1943). *Brain*, **66**, 104.
- Walshe, F. M. R. (1947). *Victor Horsley Memorial Lecture*. Edinburgh: Livingtone.