Hughlings Jackson Lecture

ON

QUANTITATIVE MANAGEMENT OF CONTRACTION FOR "LOWEST- LEVEL" CO-ORDINATION

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[After some prefatory remarks in reference to the commemorative occasion, the lecturer proceeded]

There, at that lowest level, and at its simplest, is the old-fashioned if time-honoured entity, the motor centre. I hesitate to invite recontemplation of it, it is such oft-worn ground, but in light of some fresh detail it seems to accrete endowment. With it, an initial problem and nowhere more essential, is quantitative adjustment.

MOTOR-UNITS

Sampled by afferent stimulation, the motor centre soon reveals that every reflex fractionates its muscle. The fractionation is not pushed so far as separate muscle-fibres. Soleus has 30,000 muscle-fibres, and the long extensor of the digits 55,000¹; but nervous co-ordination, as Hughlings Jackson has said, is "based on the anterior horn cell." That cell by its motor nerve-fibre innervates a whole packet of muscle-fibres, 150 and more. This packet of muscle-fibres together with its motor nerve-fibre constitutes what has been for short called a "motor-unit." It is with these units that reflex fractionation deals. It gives numbers not unmanageable—soleus (cat) consists of 230, extensor longus of 330, medial gastrocnemius 500.² Such motor-units yield a contraction-wave of 2.5 g., and even of 8 g. A coarse unit, it would seem, to grade with. The more since its contraction runs on the "all or nothing" plan, so that to grade the strength of the stimulus of the contraction-wave is not a means of grading the strength of the contraction-wave itself. The contraction-wave is in so far a fixed quantity independent of the strength of its stimulus. In reflex action, however, we know that the single contraction-wave as an isolated event scarcely happens. What happens, of course, is the overlapping succession of the contraction-waves to form tetanus. This tetanus, when once the mechanical fusion of the component waves is complete, yields in its turn a tension value fixed, in so far that no increase of strength or rate of stimulus will change it further. Such fixity of value for the tetanized motor-unit allows reflexes which can ensure it, to be tested for their share of a given muscle.³ In this way it is found that in the limb no afferent nerve possesses the whole of any one muscle, and that every afferent nerve has some reflex share in practically every muscle.

The motor-units which make up tibialis anticus (cat) number some 360, and its spinal motor-horn cells are in effect the expanded receptive central ends of these motor-units. Some of the motor-units are larger than others, and to these attach doubtless the larger motor-horn cells. The overlap of central terminals on these large cells, if their density on the cell surface is as elsewhere, must be specially extensive, so that the large motor-units will be the more widely at call and the more often in play. Of the 360 motor-units thus making tibialis anticus the internal saphenous nerve under faradization can tetanize some 110, the popliteal 290, a dorsal digital 125, and so on. That most at least of the motor-units are fully tetanized is shown by the fact that when submitted to additional excitation they show no additional contraction. Motor-units and their motoneurones thus fully tetanized

are classed as "maximally" excited, or, in brief, "maximals." We may suppose the central terminals of these afferent nerves to play directly upon the motoneurones, since in the case of this relatively simple reflex, present work discounts the invariable mediation of an internuncial neurone between afferent root and ventral horn cell.

When we find in an experiment that full tetanic stimulation, say, of a plantar nerve tetanizes 180 of the 360 motor-units and stops at that, may we suppose that the anatomical limit of the number of motoneurones reachable by the afferent has been attained? Hardly, for the number thus found may, within limits, fluctuate quite rapidly within the course of an experiment.⁴ A slight subconvulsive dose of strychnine will enlarge it, perhaps 25 per cent. Conversely, with spinal shock it shrinks; and so on.

The temporary upper limit represents, therefore, not the anatomical total which the nerve can reach, but some, often large, proportion of that total, a proportion circumscribed by functional condition. And there is abundant evidence that besides those motoneurones which the afferent nerve thus excites, there are others, a subliminal fringe,⁵ which it acts on but fails to bring to discharge. The proof of this is that an excitation similarly subliminal from another source when brought to bear concurrently on this subliminal fringe does bring it to discharge. We see that part of the explanation of the variation in the number of motor-units a given afferent nerve at different times will excite may lie in subliminal excitation from some other reflex or central source being in action or not on some of the motoneurones at the time.

At the opposite extreme from the subliminal fringe there obtains what we may perhaps term "supramaximal" excitement, a subclass of maximal. By combining tetanizing excitations, say, via two different afferent nerves, the excitement of some motoneurones can be brought to "supramaximal" in the sense of more than sufficient for full tetanic contraction of the muscle-fibres of their units. This is detectable by "occlusion" of contraction⁴; and it commonly happens under faradic stimulation of even a single afferent nerve because of central overlap between its constituent fibres.

GRADES OF EXCITEMENT IN THE MOTOR CENTRE

Therefore among the reflexly excited units of the motoneurone pool there obtain, and often at the same time, three different grades of excitement—*subliminal*, *maximal*, and, if we distinguish it from maximal, *supramaximal*. What then of the gap between maximal and subliminal? Three years ago Adrian and Bronk⁶ on the one hand, and on the other Denny-Brown,⁷ by different methods and independently, succeeded in observing reflex firing in the individual motor-unit. They found rates ranging down to 6 per second and 7.5 per second in slow extensor muscles, and down to 15 per second in the motor phrenic. Now these rates are not sufficient to secure in the muscle-fibres a complete tetanus; they are not of maximal grade, in the sense we use that term. They are *subtetanic* in the sense of being incompetent for full tetanus. Different rates, faster and slower, of subtetanic grade were observed to occur concurrently among motor-units firing at the same time in the same muscle.⁷ The rates did not correspond with the rate of the break-shock series applied to the afferent nerve.^{7 8} These examples were taken from crossed reflexes; there exists there, of course, the circumstance that an internuncial neurone mediates between the afferent nerve-fibre and the ventral horn cell. In the simple flexion reflex the central connexion is more direct, and there the rate of firing of the motor-unit shows much closer correspondence with that of the repetitive stimulus, at least in some of the motor-units and if the repetitive

stimulus be not too quick and strong. But the motor-unit here is prone to fire more than once in response to a single centripetal volley⁹ delivered by a single stimulus. This repetitive after-discharge is still greater in some crossed reflexes, and may reach extraordinary proportions. The point is that the firing of the motor-unit does not necessarily agree closely in all cases with impulse volleys entering from the afferent nerve.

Turning from artificial stimulation to natural, we know now, thanks to the discoveries of Adrian and his collaborators, that natural stimulation—for instance, pressure on the foot¹⁰—will, no less than does the artificial faradic stimulus, develop its reflex by means of impulse-showers, but these are far more diversely arranged. The trains of centripetal impulses engendered by such “natural” stimulations are not only of different rates among themselves, but vary in regularity, and differ in different fibres with heights of frequency related to intensity of the stimulation at different sense organs, and with different periods of crescendo and of adaptation and fatigue. It will resemble a noise rather than a musical note. This complex stream, pouring upon internuncial neurones or directly upon the motoneurone pool, proceeds, however, from a truly functionally related set of receptors. As compared with the centripetal stream sent in by the faradic stimulus to the bared nerve, the natural will have impulses less synchronized and in more dissimilar individual trains. It will exert consequently richer inequality of excitation on the motoneurone pool. In general correspondence with this—though, since the firing of the individual motor-unit may not closely agree with that of the afferent fibre, particular correspondence there need not be—there will result considerable diversity in the firing of the motor-units, and the more so that grade of excitement of the motoneurone governs rate of firing of the motor-unit. The rate of firing of the muscle-fibre can be taken as a guide to the rate of excitation of the motoneurone. The quicker the firing the greater the rate of excitation. Thus, in the phrenic nerve the individual motor-fibre fires more rapidly the stronger the inspiratory action⁶; in the extensor motor-unit firing steadily, weak inhibition⁷ by an inhibitory afferent slackens the firing until withdrawal of the inhibition, when the former quicker rate returns.

Clearly in reflex actions, and especially in the more natural and less simple of them, a whole gamut of excitements will obtain in the motoneurone pool. Besides the “maximal” (including “supramaximal”) and “subliminal” classes of motoneurone excitement earlier referred to as obtaining together in the reflexly excited motoneurone pool, there will alongside of them be intermediate grades which, since they produce imperfect tetani—*subtetani*—in their muscle-fibres, may be termed *subtetanic*. Where in the motoneurone pool the grade of excitement is greatest is where the successive arrival of converging impulses is quickest and thickest.

ADJUSTMENT OF EXCITEMENT

If we reduce the stimulation of the afferent nerve fewer fibres in it are excited; the field and density of the exciting central terminals are reduced. Supposing we picture the reflexly excited motoneurone pool of a muscle and imagine such a withdrawal of excitation so as to reduce existing excitements by a given, say the just subliminal, amount. We may sample this withdrawal for its effect motor-unit by motor-unit along the scale of excitation of the chart. One consequence is that the total excited field somewhat shrinks. The old subliminal fringe drops out of action altogether, to be replaced by another, in this case not less plentiful, recruited from “subtetanics.” All along the firing line firing somewhat slackens. Units well up in the “maximal” class continue to give the same contraction-tension as before; other “maximals” lower down degrade

into the subtetanic class, and yield less tension. In the subtetanic class all slip lower, yielding individually less tension, and some cease to discharge, entering the subliminal fringe. In records where two motor-units are firing, one somewhat faster than the other, it can be seen that if the faster slacken somewhat its slower companion may disappear altogether—that is, cease firing. On weak reflex excitation causing the remaining one to quicken again, its companion which had stopped reappears, starting firing again. The waxing and waning affect the two in the same direction, and what will slow one will stop the other. Sometimes, however, one will persist unaltered while another stops.

The total result is a decrease of contraction, which is traceable to several factors. A question rises. Do the motor-units composing a single muscle undergo adjustment concurrently in opposite directions? Are some accelerated while others are slackened? Under certain conditions, rather artificial, this can be observed. Such combination is perhaps more likely with “higher-level” co-ordinations, such as Dr. Blake Pritchard has been investigating, than with the “lowest-level” adjustments I am concerned with now. Though even here there can occur quite fractional inhibitions.

As regards weak reflexes, since a central excitation field reduced to its minimum is entirely subliminal,^{11 12} clearly in weak reflexes the subliminal fringe will constitute a larger proportion of the excited field; and this has been often observed.

As regards strong reflexes, in them excitement of the “maximal” class embraces in certain exceptional examples the motor-units of a whole muscle.⁴ Often in strong reflexes “maximal” motor-units are plentiful enough to include all of the motor-units engaged by a weaker reflex; this latter’s contraction-tension can then be entirely concealed by the former’s.

We have to distinguish, therefore, in our type motor-centre of a muscle certain broad classes in the grades of excitement of the motor-units. Grouping together what was termed above the supramaximal with the maximal so as to make one class—namely, maximal—we have then the three broad classes: subliminal, subtetanic, and maximal. Of these each contributes to active adjustment of the reflex contraction, and each somewhat in its own way.

SUBLIMINALS, SUBTETANICS, AND MAXIMALS

The *subliminal fringe* group adjusts mainly on the basis of extensity, increasing or diminishing the total number of motoneurones. It, so to say, mediates between excitation and the quiescent pool outside. It also feeds the supraliminal field. Its relation to this latter is sometimes illustrated under conditions strikingly simple. Thus, to take a particular case,¹³ two similar volleys are fired into a flexion centre in quick succession. The first excites a reflex twitch in 70 motor-units. The second, following quickly, finds those 70 motoneurones refractory because they have just fired. But in 45 other motoneurones which the first volley excited, though not to the extent of firing them, the second volley finds still some subliminal excitement left by the first, and, itself subliminal for them, yet adds an increment of excitement sufficient for their firing. The myograph gauges their number from their contraction. The exciting volleys are then strengthened, so as each singly to fire 180 motor-units instead of 70. But these two stronger volleys in sequence discover little fringe. Therefore evidently the 45 subliminals of the weaker reflex must have become some of the 180 supraliminals of the stronger. In such an experiment, the summation being confined to two stimuli, opportunity for revealing the whole fringe is small. Temporal summation by its mere iteration possesses powers less limited than spatial summation can attain alone.

Subliminal fringe is absent in some strong reflexes, at least as concerns a particular muscle. That is not to say it is absent altogether, for a reflex employs concurrently several synergic muscles each with opportunity for fringe.¹⁴ Subliminal reflexes converging with allied effect on the same muscle can produce large quantities of contraction (Eccles and Granit¹⁵).

The large fringes of weak reflexes are an effective factor in co-ordinative liaison and combination between such reflexes, and between them and others. Thus, nothing is more frequent than in the course of an experiment with, for instance, the ankle extensor attached to the myograph, to see, if head and neck be passively turned into the so-called favourable position, the same limb-stimulus evoke a much greater reflex than before, although the new posture of head and neck itself may have evoked no reflex from the muscle. It facilitated by means of subliminal fringe, on which summation built when the local reflex was repeated.

Thus again with Rademaker's¹⁶ supporting reaction from the sole of the foot and soleus postural stretch-reflex. Also with Bremer's¹⁷ cerebellar influences upon the extensor reflex of the limb; and these remind us that there can be inhibitory fringe as well, and that the withdrawal can give Hughlings Jackson's "release"; a theme so luminously treated of by Sir Henry Head. It is mainly by subliminal fringes of motoneurone excitation that the higher nervous centres exert the postural adaptations which are as necessary to the animal as its posture itself.

The "Subtetanics" Group.—An important attribute of these is that they effect grading of the reflex contraction in their motor-units by so spacing the successive contraction-waves that the integrated tension falls variously short of full tetanic. The shortage is of course greater the slower the wave-succession, and the scale of grading becomes progressively less open as full tetanus is approached. A given increment of frequency of firing of the motor-unit represents less increment of contraction-tension value in proportion as the frequency of firing in the motor-unit is already high, until at last it represents no increment at all (occlusion).⁴ I suppose, therefore, the weak reflex will contain more tremor, but I do not know that myographically. The subtetanic contraction is of course tremulous. With a power-unit like that of gastrocnemius, which averages a contraction-wave of some 8 g., its tremulous contraction must threaten the steadiness of the whole muscle. But lessening such defect is the circumstance that the various subtetanzed units are out of phase one with another. It may well be a specific office of co-ordination to keep them out of phase. If a number of the subtetanic units once get into step with each other, tremor must become gross. Denny-Brown has brought forward,⁷ and supported from his experiments, an interpretation on this basis of the clonus readily induced in the decerebrate rigidity of the laboratory. Clonus there, he says, is simply the tonic asynchronous discharge of the units thrown into synchronism. The tonic stretch-reflex of the laboratory can exhibit in the firing of its units all shades of transition between asynchronism and complete synchronism, and it can be made to pass from one to the other reversibly by suitable conditions of initial pose (Viets),¹⁸ and, as Pritchard¹⁹ has particularly shown, of tension. Conducive to the position taken by Denny-Brown²⁰ was his identification of the "silent period" of the galvanometer string following a knee-jerk as being inhibition of proprioceptive source evoked by the jerk itself from its own muscle. This inhibition damps the discharge of the jerk down in effect to one centrifugal impulse. In clonus not only do the motor-units get into step as regards contraction, but their getting into step and their keeping in step is accentuated

by their proprioceptive inhibitions getting into step likewise. Their beats in the clonus are punctuated by their proprioceptive self-inhibitions, forming a vicious circle keeping them in step. Inherent in the operation of the subtetanic motor-units is besides tremor some waste work, an uneconomy which has been dealt with by Bronk.²¹ Can we be sure that nature is in love with economy? In this instance the uneconomy seems more than offset by the advantage gained in delicacy and range of means of grading reflex contraction strength.

The "Maximals" Group.—In weak reflexes—for instance, in weak postural reflexes—there may be no "maximals" at all. A weak tonic postural reflex of soleus (cat), favourable to isolated examination of single motor-units, not rarely fails to exhibit a single unit firing in other than subtetanus. On the other hand, in strong reflexes there may be none but "maximals" in the entire motoneurone pool of a whole muscle, as driven in laboratory experiment. Though this is quite exceptional. In the "maximals" group each unit yields its maximal contraction. Motor-units added mean added contraction, and removed mean contraction lessened. All additional excitement received here lays aside its mechanical equivalent. That is to say, "occlusion" occurs here, and is therefore prominent in strong reflexes. It is the "maximals" group which by its growth limits more and more the further increase of the reflex muscular response. It brings into the relation between increase of reflex contraction and increase of reflex stimulation some resemblance to the approximately logarithmic ratio between increment of sensation and increment of stimulus. The maximals are economical in a sense, because contraction-tension is maintained at a smaller expenditure of energy in a stronger contraction than a weaker.

THE MOTOR CENTRE AS A SUMMATION APPARATUS

I would not pursue the subject to tiresome length. It arrives at this: that the motor centre—to use that old but expressive term—is more than a mere relay on the way out to its muscle, more than a mere passive place of assembly for motor-impulses directed thither. It is a central instrument which deals with those impulses actively, and adjusts *actively* the contraction-strength of its reflexes; it works on the basis of the "central summation process."^{11 12} Driven and fed by centripetal impulses, it submits them to the summation process. It is in short a "summation-mechanism." It operates on the individual motoneurone by intensity-summation; it exerts a whole scale of grades of excitement on it. It also, it is true, operates partly on the basis of extensity-changes, since it varies the number of motoneurons it engages. But since central impulses in order to excite a motor-unit must be summated, the central mechanism is ultimately wholly a summation apparatus. One secret of its co-ordinative power lies in its ability to summate with almost negligible time-lag shifting fringes and mobile shades of excitation that meet and overlap upon it. These join and disjoin, expand and shrink, as afferent channels leading from various sources come into or drop out of action; and each and every time the central apparatus subjects them to or releases them from its summation. It is an apparatus developing a greater range of intensities both upward and downward than the muscle-fibres which it operates can with their tension follow. If this seem wasteful of central nervous energy, we may remember that additional excitation exerted on a motor-unit, already driven "maximally" for tetanic contraction, is not necessarily wasted. That surplus remains still a contribution to co-ordination, because further excitation offers a further resistance to inhibition;^{11 21} just as an added inhibition in the case of an already quiescent neurone, although in one sense wasted, is a further protection (which

co-ordination may need) against excitation. In times of crisis the dilemma lies between strong actions, and the very strength of the action taken may serve to safeguard it from extrinsic interruption.

CONCEALED REFLEXES

Quantitative adjustment of amount of contraction seems to first thought a function purely quantitative. Yet because strengths of contraction may affect and shift the scope of an act, contraction-strength can acquire a value which is qualitative. The laboratory plan of obtaining reflexes by direct stimulation of bared afferent nerve is for some purposes excellent. But it is an artificiality, and certain reflex artificialities derive from it; among them this, that each large afferent nerve presents a dominant reflex which may conceal other reflexes. This dominance is itself a compromise, although often an overwhelming one, between conflicting reflexes. To display natural reflexes thus submerged we have to turn to localized stimuli natural for them. In this way can be traced the otherwise concealed ipsilateral extension reflex of the limb, and its broad quantitative course can then be followed. It activates the great extensors of the limbs. It enters into that complex of reflexes which works the limb as a tool for standing and locomotion.

[After dealing with this point at some length, the lecturer then proceeded]

REFLEX POSTURE

The importance of posture is alluded to sometimes by saying that it is the starting point and the end point for every movement. But, as Ramsay Hunt remarks, reflex posture "accompanies movement like a shadow."²² Stanley Cobb²³ writes that they "coalesce and often cannot be separated"; illustrating that well is an example of reflex posture familiar in the laboratory. In cat and dog, the brain having been entirely removed, the scratch reflex is easily evoked. A minute localized stimulus, applied for instance behind the ear, provokes scratching from the same hind foot. A stigmatic electrode, in the form of a tiny gilt pin, such as entomologists use, inserted perhaps a millimetre deep into the skin among the hairs, conveys a faradic current barely strong enough to be felt when applied to one's tongue. This stimulus—a make-believe flea—excites the reflex, probably via nerve-endings round the hairs, for after removal of the hairs the reflex is difficult to get. The co-ordination of the reflex, although the preparation is merely spinal, is extensive. The limb is flexed, bringing the foot toward the ear. The digits perform a regularly rhythmic combing movement: there is a similarly rhythmized extension of ankle; the rhythm at ankle involves alternate contraction of extensors and flexors; each beat consists of a short tetanic contraction followed by a pause of quiescence; there is similarly timed but slighter rhythmic flexion of knee. Alongside this, and just as much a part of the reflex, is maintenance of a flexed posture²⁴ of the limb as a whole; moreover, the body is kept steadily incurved to the stimulus side, the neck deviated, and the head partly turned back, so that the foot more readily may reach it. All these latter are quite steady reflex postures. Some of the muscles engaged in the rhythmic movement are engaged in posture as well as in movement, posture and phasic contraction together in the same muscle. The co-ordination instances the way in which posture not merely alternates with movement, but accompanies it "like a shadow."

In this spinal condition of the reflex its co-ordination presents two defects. The scratching foot, although it may get near to the faradized skin-point, does not actually reach it; it scratches in the air. Further, scratching movement, which is not wanted until the limb has moved to the place, begins first of all.

The field of muscles engaged by the reflex is wide, and

that is characteristic of all tolerably perfect reflexes. When giving isolated consideration to the great extensor muscles of the limbs and following their grades of reaction in the reflexes of standing and running, the concomitant reflexes which contribute likewise to the standing, etc., of the limb are omitted in order to simplify. Similarly, a chart, illustrating a reflexly excited motor centre, pictures the motoneurone pool of a single muscle; whereas even the simplest flexion reflex excites several muscles. Lorente di Nó,²⁵ recording graphically the contractions of the individual eye muscles, shows that every labyrinth-reflex acting on the eyes employs the whole twelve muscles. With the flexion reflex of the limb excited from any afferent nerve of the limb the flexion is plurimuscular from the threshold up. Thus, with a small digital nerve at minimal stimulus the muscular response starts simultaneously in the ankle-flexors and knee-flexors together, and so on. From the point of view of the spinal reflex, motor-units of a muscle have motor-units in another and even distant muscle closer akin reflexly to themselves than are most of the remaining motor-units of their own muscle. The simplest spinal reflex thinks, so to say, in movements, not in muscles.

CENTRAL REFLEX RHYTHM

Hence the tiny stimulated skin spot in the spinal scratch reflex brings into action a whole array of muscles. In the spinal cat—of course, a wholly insentient preparation—they can be freely laid bare and examined naked in their activity. Without exhaustive search we soon reach 36;²⁴ 19 in rhythmic action at five beats a second, 17 in steady, that is postural, action. The rhythmic beating in the rhythmic ones is not a "subtetanus"—that is, not a series of twitches: each beat is a brief tetanus followed by a pause of quiescence, often long enough for complete relaxation from the tetanic contractions. The rhythm is not generated in the skin nerve-ending—the hair-endings—for it occurs on faradizing the afferent nerve itself, and indeed quite easily by electrical stimulation applied to the cut cross-surface of the top of the spinal cord itself.²⁶ Nor is it a rhythm developed, as was suggested above for clonus by a retropulsive effect from the operating muscles themselves; that is clear because the reflex persists after the whole of the scratching limb has been desensitized by severance of its posterior nerve-roots. The rhythm is clearly of central origin, with its seat in the hind-limb region of the cord.

The scratch reflex has of course merely a type interest. It does not stand alone in its unexpected degree of independence of local peripheral reflex guidance. Several of these central lower mechanisms, and even some seemingly higher ones, exhibit a similar feature.

It is surprising to find the movements—for instance, those of arm and hand—evoked by stimulating the motor area of the cerebral cortex not obviously impaired by complete desensitization of the limb itself. For willed movements the upset of them in every respect, except perhaps power, following on complete desensitization of the limb, is extreme. The limb is practically useless, for prehension quite so. The animal quickly treats it as useless, or indeed as worse than useless; it attempts to get rid of it by destroying it. Yet, when the motor cortex is examined by stimulation, not only does it evoke in the de-afferented arm and hand its customary movements as readily as usual, but those movements reveal no obvious departure from their usual co-ordination either as compared with experience of them in normal monkeys or with the movements evoked by corresponding cortical stimulation in the opposite normal fellow limb. It seemed so to Mott and myself²⁷ in our observations now long since. It has seemed so again to Dr. Denny-Brown and myself, applying recent myographic and galvanometric technique to samples of some of the muscles under cortical activa-

tion. Therefore, wild inco-ordination under willed action, and little or none under the action of the directly stimulated motor cortex. One may relate this contrast to the probably very direct play of the pyramidal tract upon the motoneurons.^{28 29} The contrast is at least a caveat against accepting the movement excited electrically from the motor cortex as a close homologue of a willed one. It seems as unimpaired by desensitizing its limb as is the spinal scratch reflex itself.

REFLEX STEPPING

The same thing is met with in the stepping reflex, and to such an extent that Graham Brown³⁰ argues, from his observations, that the stepping is a centrally initiated and executed cyclic reflex essentially independent of—although modifiable by—peripheral stimuli. It certainly often occurs quite in absence of all plantar or foot stimuli—for instance, in the air or with all four feet wholly desensitized. The stepping reflex, like the scratching reflex, can be excited by weak stigmatic unipolar faradization from the cut cross-face of the spinal cord²⁶ at a tiny area in the lateral column, the stepping being, for instance, in the hind limb, and the point stimulated at the top of the cord, the preparation being decapitated. The weak faradic stimulus excites in the hind limb of the same side stepping which from walking becomes running as the stimulus is made less weak. There tends to be the accompaniment of feebler stepping by the opposite hind limb; and this crossed accompaniment agrees in rate with that of the fellow limb, but is oppositely timed so that it alternates in phase with it, as in natural locomotion. By arranging two electric circuits two stigmatic electrodes can be used with separately adjustable strength of stimulation. If then the right and left points are stimulated concurrently on the cut face of the top of the cord a subliminal stimulation of one is found to become effective on applying a subliminal stimulus to the other. Galloping can be obtained by stimulating the two points concurrently with somewhat stronger stimuli. The stepping point lies in the deep dorsal part of the lateral column. If while the stepping is in progress under excitation of this point a weak stigmatic faradization be applied to the ventral part of the ventrolateral column of the same side the stepping at once slows down or stops. Stimulation at this point when the dorsolateral point is not being stimulated will give extension of the same side hind limb. The dorsal point I mentioned as the “stepping” point; the ventral point might be called the “standing” point. As yet I have examined it only at the above-mentioned level. The right and left ventral column points when concurrently stimulated reinforce each other. The observations occur equally well with the stepping limb suspended—that is, with the proprioceptive stimuli in the stepping limbs quite otherwise than when the limb is bearing superincumbent weight, also quite without plantar stimuli, the feet being in the air. This complex cyclic act with the various timings of its sequence, as initiated and maintained by excitation of a slender descending intraspinal channel from above, seems strangely independent of guidance or support from local centripetal factors in the limb itself. Stimulation at the stepping point in the lateral column starts the limb stepping and keeps it going practically at what pace it likes. Stimulation of the antagonistic descending path slows the stepping, and if stronger stops it and changes it into standing. All this just as well with the limb merely hanging in the air. With stepping and standing as incompatible opposites for the limb, this instance, where the reaction deals with the limb on large lines and suppresses one of the incompatible acts to bring in the other, offers analogy to reciprocal innervation. It gives, further, an illustration of a feature

of co-ordination on which I have perhaps with wearisome insistence dealt with elsewhere—namely, that for a muscle or a muscle-group to be contracting does not exclude the being under inhibition. If we glance back, for instance, at our picture of the excited motor centre, and take it a stage further by inserting some inhibition, we see at once that the inhibition, counteracting according to its degree less or more of the excitation, can slacken or stop the firing of some or all of the discharging motoneurons. Only in the extreme grade which stops all the motor-units will the inhibition reveal itself as a complete absence of contraction of the muscle or muscle-group.

CONCLUSION

But I must not detain you longer. The present seems to me a time of unusual promise for neurological investigation both in the clinic and in the laboratory; a time which for that reason calls for close liaison between them. For such liaison to be effectual the two have to lie near at hand one to another. The laboratory, in a word, has to be on the spot. Apropos of this, if I dare think aloud, there is a reflection which is natural on this occasion. Where in all the world could be a more fitting point for such liaison, for such contact, than at the institution which, with its noble tradition of teaching and research, holds with peculiar claim within its portal the bust of the great master to whom our lecture to-day seeks to pay commemorative tribute, Hughlings Jackson?

I have dealt very imperfectly with a small bit of a large problem. I have kept too much within the purely experimental laboratory. The smallness of the piece is disheartening. The problem itself has the interest that large as it is—to speak *more Hibernico*—it is larger still. Hughlings Jackson in his writings turns back and forth between muscular co-ordination and mental experience as if for him they were but aspects of a single theme. It may be that to decipher how nerve manages muscle is to decipher how nerve manages itself. If so, not without significance may be what we have just glimpsed: that there are in the nervous system heights of excitation and depths of inhibition higher and deeper and with grades of adjustment ampler than muscle despite all its subtleties can commensurately express.

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