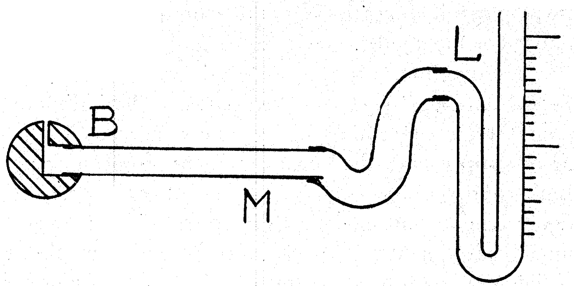

Fig. 2

connected by a bit of rubber tubing to a glass tube *M* which passes axially into a wooden ball *B* into which it is cemented. Connecting the tube *M* with the surface of the ball is a small hole (1 mm diam.) that runs radially in the sphere and at right angles to the axis of *M*. A ball similar to *B* is placed in a vertical water jet fed by the constant head from a large wall pocket. When this has found its level of quasi-equilibrium it is replaced in that position by the ball of Fig. 2, which is clamped rigidly in place. Now we may measure the pressure exerted on the sphere at any point simply by adjusting the ball so that the orifice in its surface is at the required spot. It is necessary to see that the whole tube from the orifice in the surface to the level of the water in the open arm of *L* be continuously full of water—no air bubbles being present that by their surface tension effects might mask the changes of pressure sought. It is also necessary, when one obtains the zero reading of *L*—*i.e.,* the level of the free surface of *L* when no jet strikes the ball—that water be slowly dropped on top of the ball *B* and allowed to run down over the orifice so that the surface of the water at the opening may have the curvature of the ball, as it has when the jet spreads over it. The stopping and starting of the jet would set up disturbances in the flow of the water from the wall reservoir, so it is best to keep the jet running continuously and to intercept it when necessary by a baffle plate between the nozzle and the ball. So after determining the zero reading at *L* one merely removes the baffle plate and observes the excess or defect of the pressure at the orifice from that of the atmosphere without the necessity of waiting for the flow to become steady again. Fig. 3 shows the order of values obtained with a jet of 3 mm diam., impinging on a ball of 2.6 cm diam. (about 7 gm) at a point where it is balanced in the jet (the velocity head being 75 cm). The pressure differences are given in mm of water *less* than atmospheric pressure. The unfeathered arrows indicate the point of impact of the jet. The – 3 at the top of one diagram shows a pressure of 3 mm *greater* than atmospheric caused by water that in this symmetrical case fell back on top of the ball. The feathered arrows in the second case indicate the direction on which most of the water left the sphere. These observations are of value only in indicating the *order* of pressure differences set up. Calculations of pressures to be expected from the change of momentum as the water passes over the curved surface are easily made on the assumption that there is no splash and that the water passes uniformly over the surface of the sphere; but these have little value for comparison with experiment, as neither of these assumptions is even approximately fulfilled in the experimental case.

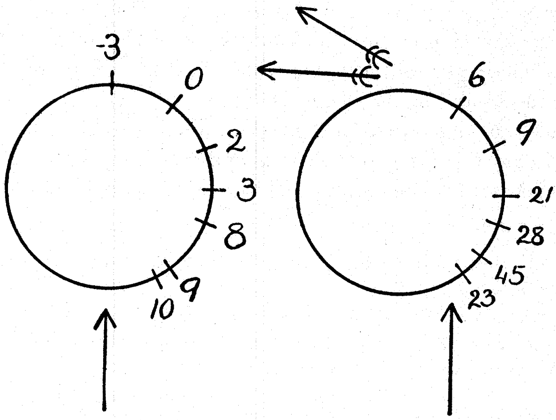

Fig. 3

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SPECIAL ARTICLES

THE BASIS OF REFLEX COORDINATION

In some recent papers Weiss[1, 2] has proposed a new hypothesis for explaining reflex coordination, which invokes the conception of qualitative differences in excitation of nerve fibers. The nature of the reflex coordination involved is best illustrated by the fact that in movements of progression all flexor muscles contract together, while the extensors relax, and *vice versa.* Weiss contends that a single motor neurone, after branching, innervates muscle fibers which are widely distributed and may be components of antagonistic muscle groups. In order to reconcile this contention with the orderly coordination of the muscles, he assumes that the motor neurone may conduct "various specific forms of excitation, to each of which certain particular muscles are attuned, owing to their specific make-up." He suggests something analogous

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[1] Weiss, 1924, Arch. f. mikroscop. Anat. u. Entwicklungsmech., cii, 635.

[2] Weiss, 1926, *Jour. Comp. Neurol.,* xl, 241.

to resonance and insists that the distribution of orderly motor effects must be based on "the specific accord between the end-organ and the excitation form."

This conception of tuning of muscles to a specific form of excitation involves such a radical and fundamental departure from the doctrines now held as to the functional properties of nerve and muscle, and if substantiated would revolutionize the entire physiology of the nervous system so profoundly that it should be subjected to the most careful scrutiny. Detwiler[3] has raised objections to the proposed hypothesis, but Weiss was not convinced of their validity, for he has insisted with increased emphasis upon the necessity of his view.[2]

The basis of Weiss's theory seems to be his conviction that the branching of motor axons involves their distribution to antagonistic muscle fibers. Both he and Detwiler have shown the remarkable fact that in amphibians a supernumerary limb transplanted close to a normal limb will receive an innervation which coordinates its muscular action with that of the adjacent normal limb. Weiss denies the possibility of specificity "involved in the control of the direction of the nerve-fiber branches in their outgrowth toward the periphery" and concludes that their distribution among the muscles is altogether a matter of chance; thus he is forced to the conclusion that coordination can only be explained by "tuning" of the muscle.

It is indeed difficult to conceive of any explanation of coordination other than the two following interpretations contrasted by Weiss. (a) If coordination depends on the central distribution of nerve impulses, then the functionally indivisible conducting path (presumably the motor neurone) must innervate only those muscle fibers which are to work together. (b) If a single motor neurone, through branching, innervates antagonistic muscle fibers which do not contract together(as Weiss contends), then the muscle must have some power to select a special component in excitation, in order to account for the observed coordination, unless, as seems improbable, the functional unit is not the neurone, but the neurofibril.

Weiss furnishes neither proof nor evidence for his assertion that a single motor neurone may innervate antagonistic muscle fibers. The only reason for that conclusion appears to be the fact that when a supernumerary limb is added, an increased number of muscle fibers is innervated from the same number of ganglion cells that normally innervated but a single limb. This implies increased branching of neurones. It is well known that a single motor neurone normally innervates several muscle fibers, and if there is an increase in the number of muscle fibers without a corresponding increase in motor neurones, this condition must be intensified. But it does not follow that "every ganglion cell is connected with several different muscles," as Weiss maintains. The individual spinal root, containing many axons, may so branch as to supply both the normal and the supernumerary limb, but the individual axon may (and probably does) remain unbranched till it approaches the muscle and there distributes itself only to adjacent fibers, which are necessarily synergic. If a single neurone branched in such a way that it innervated both limbs, an amazingly high degree of specificity would be required to direct the growing axons to homologous muscle groups in each. But the proof that there is any such remote distribution of branches does not exist. There is no need, therefore, of accepting that assumption.

Let us consider the physiological demands of the theory proposed by Weiss. The ability of muscle fibers to respond selectively to certain components in the "excitation" broadcast over a branching neurone would require either the power of nerve to conduct qualitatively different impulses or a property of resonance in muscle to a special frequency —a resonance so selective that higher or lower frequencies would fail to excite it.

Let us examine the possibility of varying the quality of a nerve impulse. Experiments have shown that whatever form of stimulus is applied to a motor nerve—electrical, mechanical or reflex—the response appears to be identical in character, as far as objective criteria can reveal it.[4] Furthermore, not only the character, but the size of the nerve impulse in the conducting unit, has been shown to be independent of the strength of stimulus.[5, 6, 7] It is well established that the energy of the impulse comes from the nerve fiber and not from the stimulus; the latter releases energy from an unstable system, and the response is thus analogous to an explosion. This fact puts the impulse in the class (dynamically) with a fuse or train of gunpowder; and just as it is impossible to alter the manner in which a fuse burns by changing the character of the flame which first ignites it, so it is impossible to vary the character of the nerve impulse by any variation in the stimulus. The same statement applies to the functional response of muscle, which is fundamentally of the same nature as the nerve impulse.

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[3] Detwiler, 1925, *Jour. Comp. Neurol.*, xxxviii, 461.

[4] Forbes and Gregg, 1915, *Am. Jour. Physiol.*, xxxvii, 118, and xxxix, 172.

[5] Adrian, 1914, *Jour. Physiol.*, xlvii, 460.

[6] Kato, 1924, "The Theory of Decrementless Conduction in Narcotised Region of Nerve." Tokyo.

[7] Davis, Forbes, Brunswick and Hopkins, 1926, *Am. Jour. Physiol.*, lxxvi, 448.

Since we can rule out qualitative differences in the nerve impulses as a basis for the proposed selective power of muscle, we must consider the question of frequency. It is possible to design an electrical apparatus in which a current flowing through a single wire traverses several resonant devices tuned to different frequencies. It is then possible to send through the wire a complex alternating current in which any desired combination of frequencies is present and thus make any desired combination of the resonators respond. But if we try to liken the neuromuscular mechanism to such a system, we encounter at the outset the difficulty that the nerve fiber is not a passive conductor like the wire, in which alternating currents of an unlimited number of frequencies can be transmitted simultaneously; it is more like a machine gun which can only be discharged with one frequency at a time, and a definitely limited frequency at that. The refractory phase in nerve, during which there must be recovery from one response before another can occur, is a well-known property of the nerve impulse, which Adrian[5] has shown to be inseparably associated with its all-or-none character. This refractory period sets a definite limit to the frequency of nerve impulses—in the case of mammalian motor nerves, about six hundred per second. It is obvious that in view of the all-or-none character of the response, it would be impossible to superimpose a second impulse frequency upon a nerve already responding with a frequency near its limit, and thus to obtain two simultaneous frequencies, as is done with alternating currents in a wire.

As to resonance in muscle, the same general principles apply. Underlying a sustained muscular contraction there are separate functional responses, which can be revealed by recording the electrical action currents. The frequency of these responses is limited in muscle, as in nerve, by the refractory period, which varies with temperature. Normally in mammalian muscles the upper limit is about four hundred per second or less. If time enough between stimuli is allowed for recovery from the refractory phase, it is as easy to stimulate a muscle with one frequency as another. Therefore a muscle can have no more tendency to respond at a particular frequency, like a resonant body, than a magazine rifle. The muscle can not respond with a frequency above the limit imposed by the refractory period. Below that limit it responds to the stimuli as they come, provided they are strong enough.

It is clear then that muscle response belongs to a class of phenomena to which the principle of resonance does not apply and in which there can be no such tuning to a special frequency, as Weiss's hypothesis requires. We are, therefore, forced to accept Detwiler's conclusion that coordination depends on the central distribution of nerve impulses, as has been generally supposed, and not on peripheral selection.

Weiss, in his answer to Detwiler, states that "the all-or-none law holds good only in electrophysiology," and does not apply in normal reflex nervous activity. In support of this proposition he cites Sherrington's emphasis on the differences in the results of artificial and natural stimuli. Sherrington, in dealing with this subject, has described differences which are explicable on the basis of anatomical distribution and sequence in time of the individual impulses in the conducting units; but he has brought out no facts which are incompatible with the view that the underlying unit response is always the same in kind and obeys the all-or-none law. Indeed, Sherrington has recognized the validity of this law in the following words: "All or nothing as a principle of nerve-fiber response seems to me, as to you, established. It must appear as a new datum for whatever schemata we offer of central mechanisms."[8] Thus the statement that the all-or-none law only applies to electrophysiology is altogether unwarranted and is in no way supported by Sherrington's writings. Indeed the "all-or-none" law is explicitly recognized and woven into the fabric of his more recent discussions.[9]

Since the nature of the functional response of nerve and muscle renders Weiss's theory of muscle tuning untenable, we must seek another explanation for the striking fact that almost as soon as the muscles are innervated, the normal and supernumerary limbs exhibit "homologous function"; that is, corresponding muscles in both limbs contract in unison. The explanation may perhaps be found in the proprioceptive impulses. Sherrington has shown the important rôle played by the nerves of muscle sense in coordinating limb reflexes.[10, 11] Detwiler and Weiss have both shown that homologous function only appears when the transplanted limb is innervated from the proper level of the spinal cord. Apparently only those motor neurones which lie at this level can acquire the capacity for this coordination. Given this capacity in the neurones, it is altogether conceivable that the proprioceptive impulses, set up when the muscles begin to contract, initiate the necessary organization of the spinal centers whereby the motor neurones are soon enabled to coordinate the limb movements in the remarkable manner that has been experimentally observed.

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[8] Extract from letter; see SCIENCE, 1916, xliv, 809.

[9] Sherrington, 1925, Proc. Roy. Soc., xcvii, 519.

[10] Sherrington, 1915, *Brain*, xxxviii, 203.

[11] Liddell and Sherrington, 1924, Proc. Roy. Soc., xcvi, 212; 1925, *ibid.*, xcvii, 267.