COLLISION OF TWO NERVE IMPULSES IN THE NERVE FIBRE

by

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A previous paper (TASAKI AND TAKEUCHI, 1942) indicated that it is possible to lead the action current of a nerve fibre through the myelin sheath. The method consisted in dividing the fluid which surrounds the fibre, by means of two sets of bridge-insulators placed between two neighbouring nodes of RANVIER (see Fig. 1, top), into three independent pools. The electrode dipping in the middle pool of RINGER was led to the grid of the amplifier and those immersed in the two lateral pools were earthed. The fibre was brought into action by means of induction shocks applied to the portion near its proximal or distal stump.

The action current of a single nerve fibre recorded in this manner is of very short duration and has two peaks in its course (Fig. 1, a and b). The time interval between these two peaks is, at room temperature, about 0.1 millisecond, which corresponds to the time required for conduction of the impulse from one node of RANVIER to the next. If the fluid on the distal side (with respect to the stimulating electrodes) of the bridge-insulators is replaced by a narcotizing solution, the second peak alone is extinguished. Introduction of the same narcotizing solution into the middle pool brings about no detectable change in the action current observed.

This method of leading off the action current of a nerve fibre provides us with a very simple means of observing the collision of two nerve impulses at the site of the lead-off electrodes. The purpose of this paper is to present some data obtained by this and another method showing what happens when two impulses, which are made to start at both ends of a nerve fibre, come to the same point from two opposite directions. An outline of this work was included in my Japanese monograph, *Physiology of the nerve fibre*, published in 1944.

METHOD

Motor nerve fibres innervating the sartorius muscle of the toad were used for the experiments. The operation of isolating a single nerve fibre was carried out at a point on the nerve about 25 mm from the muscle. In the first experiment, the width of the middle pool of RINGER was about 0.5 mm (Fig. 1, top), and the gaps between the pools which served to insulate the three pools from one another were about 0.2 mm wide. As the internodal distance of a "rapid" motor nerve fibre of the toad is in favourable cases well over 2 mm, it is easy to mount the fibre in such a manner that the two exposed nodes of RANVIER are situated in the two lateral pools and only the myelinated portion of the fibre is dipped in the middle pool.

In the second experiment, a node of RANVIER was introduced into the middle pool of RINGER as shown in Fig. 2, top. The middle pool was in this case 0.5–1.5 mm wide, and the gaps were about 0.2 mm wide as usual. The non-polarizable electrode dipped in the middle pool was led to the amplifier and those immersed in the two lateral pools were earthed as in the first experiment.

The portions of the nerve on both sides of the operative region were suspended in the air and

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were brought in contact with two pairs of platinum electrodes. Each pair of the platinum electrodes was connected to the secondary coil of an inductorium. The strength of the induction shock was controlled by means of precision resistances in the primary circuits. Break contacts of a HELMHOLTZ pendulum inserted in the primary circuits of these two induction coils served to control the time interval between the two shocks.

The action currents were recorded with a cathode ray oscillograph of which a single sweep was started by the use of another knock-over key of the pendulum. The input resistance of the amplifier was about 0.1 megohm.

RESULTS

In the experimental arrangement shown in Fig. 1, top, an induction shock applied to one end of the nerve fibre set up an action current of the double-peaked configuration (record a in the figure). A stimulus applied to the other end of the fibre caused a similar action current (record b), but the conduction time was in general different, due to a different conduction distance. The time interval from the start of the sweep of the cathode ray to the onset of each of the induction shocks was so adjusted that the figures of the action currents appeared at exactly the same spot on the face of the oscillograph in both cases. Then, without change in the position of all the three break contacts of the pendulum, two induction shocks were applied to the

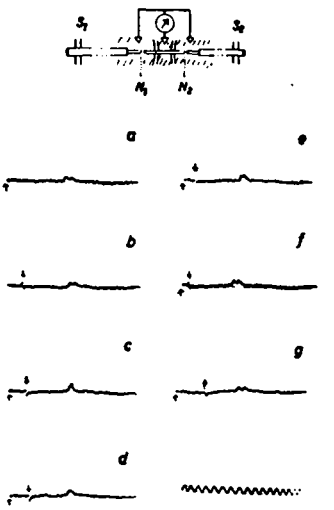

Fig. 1. Collision of two nerve impulses as observed with an amplifier and a cathode ray oscillograph connected t› the myelin covered portion of a single nerve fibre. In a, induction shock S_1 alone was delivered. The arrow indicates the position of the shock artefact. In b, the fibre was excited by shock S_2. In c, both S_1 and S_2 were applied to the fibre in such a manner that the two impulses arrived at the region of the lead-off electrodes simultaneously. In d and g, the impulse from S_1 preceeded that from S_2 by about 0.10 and 0.32 millisecond respectively. In e and f, the impulse from S_1 lagged behind that from S_2 by approximately 0.10 and 0.22 millisecond respectively. A.C. at the bottom 5000 cycles per second. Temperature 21° C.

fibre in succession. By this procedure, the two impulses starting at the two opposite ends of the nerve fibre were made to collide at the region of the bridge-insulators, and this yielded, as may be expected a single-peaked action current record (c in the figure).

A point of interest in this experiment is that a singlepeaked record is obtainable even when two impulses do not reach the middle pool at exactly the same moment. When one impulse lags behind the other by about 0.1 millisecond which corresponds to the internodal conduction time, the peak is much lower than when the two arrive simultaneously, but still the impulses are found to fuse to form a single-peaked action current. When one of the impulses lags behind the other by a still greater period, ordinary records of the double-peaked configuration are obtained. Introduction of a 0.2% cocaine RINGER solution into the middle pool brings about practically no change in the configuration of these action currents.

It is obvious in this experiment that the first peak in the action current record corresponds to the initiation of activity at the proximal node (N_1 in the case when the fibre is excited by S_1) and the second peak to that at the distal node. The variation in the electromotive force at the plasma membrane of the node, namely the "action-e.m.f.", reaches a maximum in a period much shorter than 0.1 millisecond at room temperature

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and then decays almost linearly with time until finally the electromotive force returns to normal about 1 millisecond after the onset of the variation. This action-e.m.f. causes, through the myelin sheath of the fibre, a current which lasts for only about 0.2 millisecond. The myelin sheath is composed of a highly polarizable membrane and the portion of the fibre in the middle pool behaves like a small condenser.

In the experiments in which a node of RANVIER is introduced into the middle pool of RINGER (Fig. 2), the action current recorded is always of a diphasic configuration (record a). When the nerve impulse set up by the induction shock S_1 reaches the node N_0 in the figure, the node N_1 is traversed by a strong outward-directed current. At the moment when this latter node is also thrown into action as the result of stimulation by the outward-directed current, the current through the axis-cylinder between the node N_0 and N_1 ceases at once, for the action-e.m.f. at the latter node tends to cause a current in the opposite direction. But at this moment a strong outward-directed current begins to flow through the node N_2, owing to the start of action-e.m.f. at the middle node N_1 (TASAKI, 1939, Fig. 12). This in turn results in an inward-directed current through the middle node N_1, producing a downward deflection in the action current record.

When the distal node N_2 is finally brought into action, the current through the axis-cylinder between N_1 and N_2 is also terminated, and the current through the middle node N_1 becomes almost zero. In these considerations, the leakage of

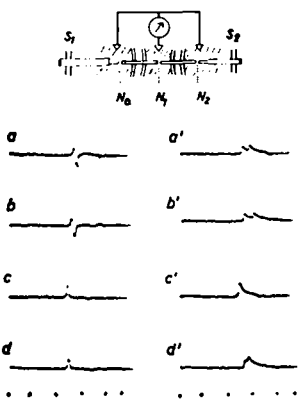

Fig. 2. Records of the currents which traverse a node of RANVIER when an impulse travels along a nerve fibre (a, b, a' and b') and when two impulses collide at the node in the middle pool (c and c'). Records in the right column were obtained after introduction of a 0.3 % cocaine RINGER solution into the middle pool where the node N_1 lay. In d and d', the impulse from S_1 lagged behind that from S_2 by 0.05 and 0.2 millisecond respectively. The time markers 1 millisecond apart. Temp. 21° C.

current through the myelin sheath is disregarded as being too small compared with the current through the node.

Let us now consider what happens when two impulses collide at the middle node. When the node N_0 and N_2 are brought into action simultaneously, the node N_1 in between begins to be traversed by an outward-directed current much stronger than that in the ordinary transmission. This strong outward-directed current naturally excites the node N_1 very readily, and the latency in excitation is correspondingly shorter than 0.1 millisecond. In other words, when two impulses approach one another, they travel from node to node at a rate much greater than in the ordinary transmission. When the node N_1 is finally brought into action, the strength of the current flowing in- and outside the fibre becomes practically zero. It should be emphasized that, even though there is practically no current along the fibre at this stage, the activity at these nodes is still under way. This activity subsides of itself, by some mechanism inherent to the bioelectric process, in about 1 millisecond from the onset.

In the records of Fig. 2, left, one may notice slight movements of the base line after the prominent deflections have ended. This instability of the base line lasts for about 1 millisecond and is evidently due to slight differences in the magnitudes of the action-e.m.f. at the nodes under investigation.

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Some physiologists seem to believe that, when two impulses collide at one spot on a nerve fibre, the transmission of each of these impulses is blocked by refractoriness left behind by the other impulse. But this is an utterly mistaken idea. We have seen above that, at the moment when the last node of RANVIER in the fibre is involved in action, the current in- and outside the fiber becomes insignificantly small. In other words, there is in this stage no internal stimulus through which the transmission is effected. It is a property of the bioelectric process to subside by itself.

Records in the right column of Fig. 2 were obtained after introduction of a 0.3% cocaine RINGER solution into the middle pool in which the node N_1 was immersed. When the impulse starting at S_1 in the figure reaches the node N_0, the middle node is traversed by an outward-directed current. The first peak in the record a' of Fig. 2 corresponds to the beginning of activity at the node N_0. As the middle node N_1 fails to respond to this outward-directed current, there occurs spread of current along the fibre; and after a latent period much longer than the ordinary internodal conduction time, the distal node N_2 is brought into action by this spreading current (TASAKI, 1939). The second peak in the record a' corresponds to the onset of the action-e.m.f. at the node N_2. In these circumstances, collision of two impulses at this point yields such records as c' and d' in Fig. 2.

SUMMARY

1. Records have been taken of the current that traverses tne myelin sheath and the node of RANVIER as an impulse travels along a nerve fibre.

2. Records of action currents have been obtained from the spot on a nerve fibre at which collision of two impulses has occurred.

3. When two impulses approach one another, the rate of transmission becomes greater.

4. By collision, transmission of impulses is blocked, not on account of the refractoriness left behind by the impulses, but through lack of internal stimulating current by which the normal transmission is effected.

RÉSUMÉ

1. Des enregistrements ont été pris du courant traversant la gaine de myéline et le nœud de RANVIER lorsqu'un influx se propage le long d'une fibre nerveuse.

2. On a obtenu des enregistrements de courants d'action provenant du lieu de rencontre de deux influx dans une fibre nerveuse.

3. Lorsque deux influx se rapprochent l'un de l'autre, la vitesse de leur transmission s'accroît.

4. Lorsqu'il y a collision, la transmission des influx est bloquée, non pas par suite de la période réfractaire qui suit ces influx, mais à cause de l'absence d'un courant d'excitation interne par l'intermédiaire duquel la transmission normale est effectuée.

ZUSAMMENFASSUNG

1. Es sind Aufnahmen gemacht worden von dem Strom welcher die Myelinscheide und den RANVIER-Knoten durchläuft, wenn eine Anregung sich entlang einer Nervenfiber bewegt.

2. Aufnahmen von Wirkungsströmen sind erhalten worden von der Stelle wo der Zusammenstoss von zwei Anregungen stattgefunden hat.

3. Wenn zwei Anregungen sich einander nähern, wächst ihre Fortpflanzungsgeschwindigkeit.

4. Beim Zusammenstoss wird die Fortpflanzung der Anregungen gesperrt, nicht wegen der Unempfänglichkeit welche diese Anregungen zurücklassen, sondern mangels eines internen Erregungsstromes, durch welchen die normale Fortpflanzung bewirkt wird.

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