STRETCH RECEPTORS IN THE MUSCLES OF FISHES

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(With Thirteen Text-figures)

INTRODUCTION

The sensory nature of mammalian muscle spindles was established over forty years ago by Sherrington (1894). These structures were formerly thought by some to be pathological, by others to represent developmental stages of muscle fibres; though Kerschner (1893) had, on histological grounds, maintained that they were sense organs, and Ruffini (1893) had brought forward further histological evidence in support of this opinion. Sherrington’s discovery was followed by numerous histological and physiological investigations which have served to establish the important proprioceptive function of muscle spindles in the reflex co-ordination of muscular movement. Muscle spindles exist also in birds (Huber & de Witt, 1898), reptiles (Kulchitsky, 1924) and Amphibia (Huber & de Witt, 1898; Hines, 1930). They have not been found in fishes, cyclostomes or Amphioxus. But muscle spindles are not the only type of sensory nerve ending in muscle: various other, less highly organized, types of end-organ have been described, and it is known that some of these likewise subserve a proprioceptive function. Even in mammals, whose muscles as a rule are richly supplied with spindles, they appear to be entirely absent from some muscles. Cilimbaris (1910) failed to find them in the eye muscles of the cat, dog, horse, fox, rabbit, hare and rat, though he discovered them in the eye muscles of the sheep, goat, ox and deer. But Tozer & Sherrington (1910) showed that in the rabbit, cat and monkey, the cranial nerves supplying the eye muscles, namely the third, fourth, and sixth, are afferent-efferent, “their afferents belonging to the receptive (sensorial) endings with which all the extrinsic eye muscles are richly supplied. The afferent divisions of these cranial nerves are by their distribution exclusively proprioceptive, supplying no other organs either exteroceptive or interoceptive.” Similarly, the absence of spindles from the muscles of fishes certainly cannot be taken to indicate that this group is without muscle proprioceptors. And, in fact, it appears to be tacitly assumed, among physiological workers at any rate (Trendelenburg, 1910; Bauer, 1925; Gray, 1933; ten Cate, 1933; von Holst, 1934), that fishes have proprioceptors, though to the best of our knowledge no single experiment has been performed to demonstrate the existence

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of a myotatic reflex or tendon-jerk in a fish. The recent experiments of Gray (1936b), however, on resistance reflexes in the eel furnish strong evidence for the presence of stretch or tension receptors in this animal.

The histological literature on the subject is remarkably scanty, and the few workers who have concerned themselves with sensory endings in fish muscle do not appear to have had stretch receptors in mind. Baum (1900) could find no spindles in the selachian, Pristius, nor in Petromyzon, nor in the pectoral fins of the teleost, Syngnathus. Giacomini is said to have described "basket-like sensory endings" in the muscles of selachians and teleosts,1 and Wunderer (1908) described and figured "Endkörperchen" in Mustelus, Scylium, Acanthias and Squatina, and "Pinselförmige Endigungen" in Raja. These appear to be free nerve endings, not encapsulated, and were found principally in connective tissue. Wunderer suggested that they might be pressure receptors. He did not find them in teleostean fishes.

It is evident that new histological work on this subject is urgently needed. Meanwhile, it seemed to us profitable to determine whether, when a muscle in a fish is stretched, afferent impulses can be detected in the nerve supplying it.

**PREPARATION AND TECHNIQUE**

The problem was to select a suitable preparation. The musculature of fishes is very compact, and the form and disposition of the muscles renders them mostly unsuitable for nerve-muscle preparations. The bony fishes are, on the whole, worse in this respect than the cartilaginous. Tendons are best developed in the rays, and it was in species of the genus *Raja* that a good preparation was found.

Unlike the integument over the rest of the body, the skin covering the anterior lobe of the pelvic fin of the ray is relatively loose, and can be easily removed so as to expose the underlying radial muscles. The fin is supplied by about sixteen spinal nerves, of which the anterior seven innervate the muscles of the anterior lobe (Fig. 1). These seven nerves run outward anteriorly to the upward-projecting iliac process of the pubic bar. The remaining fin nerves, innervating the posterior lobe, lie behind this process. As described by Müller (1913), the nerves overlap peripherally, and stimulation of the nerves shows that each radial muscle receives motor fibres from two or three spinal nerves. Such stimulation, however, does not give a clear indication of the mechanism of the fin movements because each nerve innervates several groups of antagonistic muscles, which may be thrown into simultaneous contraction by the excitation of an entire nerve trunk. A clearer conception of the innervation of the radial fin musculature is gained when the nerve supply to the pectoral fins is considered.

A ray swims by means of backwardly directed undulations of its enormous pectoral fins, and the two fins undulate in phase. The locomotory undulations therefore occur in the vertical, not, as in the dogfish and ordinary teleosts, in the horizontal plane. This means that the antagonistic locomotory muscles are not, as

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1 This statement is quoted from Kappera, Huber & Crosby's *The Comparative Anatomy of the Nervous System in Vertebrates, including Man*, p. 35. We have been unable to obtain the original paper.
in most fishes, on opposite sides of the body, but are dorsal and ventral with respect to each pectoral fin. It is therefore to be expected that somewhere along their course the motoneurones of a spinal nerve must become segregated into two groups which pursue independent courses to the dorsal and ventral fin muscles respectively. Such a bifurcation is actually found at a point just proximal to the entry of each spinal nerve into the radial musculature, each nerve divides into an anterior ventral and a posterior dorsal branch, and stimulation tests show very clearly that the excitation of the ventral branch causes contraction of the ventral radial muscles, and, therefore, depression of the fin, while excitation of the dorsal branch causes contraction of the dorsal muscles and elevation of the fin.

Returning now to the pelvic fin (Fig. 1), the same arrangement is found to hold, although it is somewhat complicated by the fact that this fin does not, like the pectoral, execute simple undulations in the vertical plane, but performs movements which consist in a forward and downward extension or a backward and upward folding of the fin. The muscles concerned in the former movement are the ventral muscles of the fin, those concerned in the latter movement are the dorsal muscles.
The muscles which have functionally the greatest importance are those which operate upon the relatively massive anterior radial elements of the fin skeleton. Their arrangement is shown in the figure. Along the front margin of the anterior lobe of the fin is a fleshy muscle lying alongside the anterior radial, and attached by tendons to the distal segment of that radial. This muscle is innervated by the ventral branches only of the first three spinal nerves supplying the fin, and when it contracts causes the fin to be extended forwards. We shall name it, provisionally, the anterior extensor. Next to it, and applied to the dorsal side of the anterior radial is a muscle which is attached distally to the same peripheral segment of the anterior radial, close to the insertion of the anterior extensor, but dorso-posterior to it. This muscle is the antagonist of the anterior extensor. It receives motor fibres from the dorsal branches of the third and fourth fin nerves, which fuse, as shown in the figure, to form a single dorsal nerve trunk. We shall call this muscle the anterior flexor. Proceeding backwards, the radial muscles assume again the regular form and disposition of the pectoral fin musculature. The radial skeletal elements are slender, and the muscles are correspondingly small and without conspicuous tendinous attachments. They serve to elevate and depress the fin, always with a backward, i.e. folding displacement.

The anterior flexor muscle was the object of most of our experiments. Its attachment to the distal anterior radial is effected by means of a group of four or five slender tendons. These could be cut and ligatured separately so that tension could be applied to successive thin strips of the muscle. The nerve (fused dorsal branches of the third and fourth fin nerves) was dissected out, ligatured and cut centrally at about the point of fusion. The fin was rigidly fixed to a board, and the muscle and nerve were irrigated at frequent intervals with dilute sea water containing urea (Young, 1933).

The preparation was set up in a screened box. The nerve was laid across electrodes of platinum wire connected to the input of a conventional condenser coupled amplifier, with Matthews oscillograph and loud-speaker. Continuous records were taken, the camera speed, calibrated in 0.2 sec. by means of a Jacquet chronograph, being approximately constant at 59 mm./sec. The sensitivity of the system was of the order of 2 mm. deflexion for 10 μV. across the input.

A preparation set up with the tendons of the anterior flexor muscle intact showed a complex asynchronous discharge of impulses (Fig. 12a). On cutting the tendons this discharge usually ceased, though occasionally a slow simple rhythm persisted. Gentle traction on any one of the freed tendons evoked a rapid discharge of impulses which, as judged by the loud-speaker, was usually composed of two or three, sometimes more, units discharging together at different frequencies. It was often observed that, as the tension was increased, more units would start firing, suggesting a recruitment of end-organs with higher thresholds. However, by a process of careful separation of the tendons and their attached slips of muscle we usually arrived at a preparation which gave a pure single-fibre response. In doing this it was convenient to "feel" for the end-organ by prodding the muscle gently with a fine glass seeker while listening to the response in the loud-speaker. Such
pressure on the end-organ would set up a discharge, and in this way it was possible
to localize the organ with some precision, and direct one's cutting operations
accordingly.

The simplest method of exerting a known tension on the muscle is to lead a
thread from the free tendon over a light pulley, and to allow a weight to hang from
it. We have used this method in most of our experiments. It does not, however,
permit the control of the rate of establishment of tension, which varies with the
weight applied, and in the manner in which the muscle is allowed to take the strain
of the load. On the other hand, the final static tension on the muscle is accurately
known, and this is the most important factor in the behaviour of such slow-adapting
receptors as the ones that we have had to deal with.

Tension can be applied gradually at a known rate of increase by having a weak
spring in series with the muscle. A hard brass spring was attached at one end to the
tendon of a muscle, at the other to the platform of a Palmer screw stand. Since, with
the tension employed, the muscle stretches very little in comparison with the spring,
it was possible to calibrate the extension of the spring in terms of grams of tension.

RESPONSE OF A SINGLE END-ORGAN

The threshold stimulus capable of evoking a regular discharge of impulses from
the pelvic fin muscle preparation is a tension of the order of 1 g., varying between
0.4 and 2 g. for different preparations. With such feeble tensions a regular discharge
may occur at frequencies as low as 2 per sec. The lowest regular frequency recorded
was 1.35 per sec. The upper limit of tension which it was found possible to apply
to our preparation without causing irreversible injury was about 60 g. When the
tension is progressively increased, the discharge of impulses becomes more rapid and
reaches a frequency which, compared with the frequencies observed with the
proprioceptors of other animals, is not very great. An experiment in which traction
was applied to the point of tearing the muscle yielded a maximum frequency of
only 86 per sec. A higher frequency (about 100 per sec.) could be recorded when
a strong tension was suddenly applied to a resting preparation, but such a frequency
was maintained only for a brief interval of time.

When the muscle is slowly extended by means of a spring and Palmer stand as
described in the preceding section, each successive stage of expansion appears to
correspond to a definite tone in the loud-speaker. But examination of the records
shows that the tension-frequency relationship is not so simple as that. The curves
in Fig. 2 are drawn from records of the discharge from a single receptor at pro-
gressively increasing and decreasing degrees of tension, the screw of the stand being
uniformly rotated between each recording and stopped only for the duration of the
exposure. With rising tension the frequency reaches a maximum at about 10 g.,
and, at higher tensions, may even decline somewhat. Moreover, on reducing the
tension again down to zero a different frequency curve is obtained. It follows,
therefore, that the condition of the receptor at any given moment depends not
only on the external conditions existing at that moment, but also on the previous
conditions to which it has been subjected. This serves also to explain the fact that quite different curves are obtained when, instead of ascending progressively from one tension to the next, the muscle is allowed to slacken between the application of each successive tension.

The analysis of the true tension-frequency relationship demands, therefore, experimental conditions in which the initial state of the muscle before the application of each stimulus is, so far as possible, constant. To achieve this it is necessary first to study the way in which the performance of the organ becomes modified with time, either as a result of functional activity (adaptation), or during rest, or in consequence of the progressive decline of the preparation towards irreversible inexcitability. These are the elementary properties of the receptor, concerning which the curves in Fig. 2 give no information.

![Fig. 2. Effect of increasing, followed by decreasing, tensions on two receptors responding together. It is possible that receptor B was so placed in relation to the tendon to which traction was applied that it received only a fraction of the pull.](image)

Adaptation. The principal characteristic of a sensory discharge evoked by a constant stimulus is the rate at which its frequency diminishes with time. Different categories of receptors can be distinguished according to their rate of adaptation (Adrian, 1928). Proprioceptors are known to be very slow adapting, and those of the ray appear to possess to an unusual degree the power of maintaining a steady discharge for very long periods, if not indefinitely. Nevertheless, their initial adaptation is considerable, as can be seen from the records in Fig. 3, which shows successive portions of the same discharge.

With preparations that have not been injured in any way, nor subjected to excessive tensions, it is possible to obtain adaptation curves of great constancy when the same tension is applied repeatedly, provided that an adequate time is
allowed for recovery between successive stimulations. Typical curves are shown in Fig. 4. These were obtained with a very good preparation which maintained a constancy of behaviour for a long time.

Fig. 3. Adaptation of single end-organ to steady tension. a, 1 g. load applied; b, 5 sec.; c, 10 sec.; d, 20 sec.; e, 30 sec. after loading. Time marker, o-2 sec. All oscillographic records read from left to right.

Fig. 4. Curves showing adaptation of a single end-organ to a load of 2 g. Curve b, three consecutive determinations are plotted (●, x, △). Loadings were continued for 1 min. and were separated by rest intervals of 4 min. duration. Curve a, the same preparation after a longer interval of rest. The stimulation was continued for 1 hour.

The activity of a receptor subjected to a constant tension may be conveniently subdivided into three phases: the phase of establishment of tension, the adaptation phase, and the phase of equilibrium.
During the establishment of tension the discharge rapidly rises to a maximum frequency. The change in frequency from one moment to the next is difficult to interpret, for it depends not only on the excitability of the receptor, but also on the mechanical properties of the muscle-tendon system to which the tension is applied and, of course, on the rapidity with which the tension is established. Our apparatus did not permit an accurate control of this latter factor. When a muscle was loaded directly with a given weight, the rate of stretching would vary with the weight used. According to Matthews (1933) the receptor possesses a greater viscosity than the surrounding tissue. With a rapidly applied tension there would be an effect comparable to a transitory overload, and the high frequency of discharge attained during loading may be ascribed in part to such temporary overloading. Similarly, the initial very rapid decline in frequency cannot be regarded as a pure adaptation phenomenon, for, during this period the effective tension on the end-organ declines from the level of the transitory overload to that of the static tension of the applied weight. The question then arises at what point on the curve true physiological adaptation may be assumed to begin. This point is, of course, the moment when the true tension of the attached weight is established. In the experiments corresponding to Figs. 3 and 4 the receptor was stimulated by attaching a weight directly to the tendon, and the phase of establishment of tension can be roughly estimated as lasting not longer than 0.5 sec. This agrees with results discussed below, relative to the reloading of an already adapted organ after a very brief interval of relaxation (p. 396). It agrees also with several observations we have made on the effect of varying the rate of establishment of tension by means of a spring. When the rate of extension of the spring was signalled on the record, it was found that a tension of 10 g. developed in 0.5 sec. is already a relatively slow stimulus, for the time intervals between the afferent impulses evoked by it attain a maximum much less rapidly than when a weight is applied directly to the tendon. Incidentally, we have observed that a tension rapidly established (10 g. in 0.08 sec.) elicited a burst of several impulses in rapid succession followed by a pause, and then a slower rhythm of discharge. This phenomenon has also been described by Matthews (1931a). We have not paid special attention to it, but, in passing, it may be suggested that such a pause does not differ from the silent period which appears when the tension on a muscle is suddenly reduced to a lower level (see p. 394).

During the second phase, that of true adaptation, the mechanical condition of the receptor is constant, and the variation in the response is determined only by the duration of the stimulus. It is not possible to assign precise limits to this phase; it occupies a period of 20 sec. or so during which the frequency declines steeply to a constant level.

The third phase is characterised by a condition of equilibrium in which the rhythmically active mechanism recovers during each succeeding interval from the exact amount of adaptation which results from the preceding response. Such a state of stable equilibrium certainly exists in the intact animal under normal conditions of rest when the muscles are maintained in a state of slight permanent tension (see Fig. 12a, b). That an organ which is deprived of its circulation and is
slowly declining to a state of inexcitability should exhibit a slow decrease in frequency under constant tension, does not exclude the possibility of a permanent rhythm of activity under normal conditions. We have, for example, recorded a reduction in frequency of only 10 per cent in a preparation subjected to a constant tension for more than an hour. During this period more than 30,000 afferent impulses were discharged! The possibility of a permanent stable equilibrium is supported further by the observation that over considerable intervals of time there may be no systematic reduction in frequency. In one preparation an average frequency of 9·8 per sec. was maintained from the 15th to the 30th minute after loading.

Such a discharge of constant frequency enables one to examine the regularity of the rhythm. The random variation in frequency for twenty successive impulses is not great. It was found to be 2·5 per cent in one case, 2·1 per cent in another, the frequency for both being 9·8 per sec. Another determination showed a variation of only 1·5 per cent for a frequency of 4·7 per sec.

When the same load is applied repeatedly to a muscle for the same period of time, the adaptation curves derived from the records of the response of the end-organ are closely similar, though slight differences are found. The difference is not always one of a progressive decrease in the response; at times, on the contrary, the excitability of the organ with reference to a given tension is significantly increased as a result of preceding activity. An attempt to determine the influence of the duration of the rest interval on the responses to successive applications of 2 g. tensions for 1 min. periods did not yield results from which simple conclusions could be drawn. The following frequencies were recorded at 45 sec. after each loading:

<table>
<thead>
<tr>
<th>No. of loading</th>
<th>Duration of rest interval preceding the loading, min.</th>
<th>Frequency after 45 sec. loading per sec.</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0·5</td>
<td>12·2</td>
</tr>
<tr>
<td>2</td>
<td>4</td>
<td>Record spoiled</td>
</tr>
<tr>
<td>3</td>
<td>9</td>
<td>13·2</td>
</tr>
<tr>
<td>4</td>
<td>4</td>
<td>12·2</td>
</tr>
<tr>
<td>5</td>
<td>4</td>
<td>12·1</td>
</tr>
<tr>
<td>6</td>
<td>1</td>
<td>13·7</td>
</tr>
<tr>
<td>7</td>
<td>Prolonged</td>
<td>12·1</td>
</tr>
<tr>
<td>8</td>
<td>0·5</td>
<td>14·0</td>
</tr>
</tbody>
</table>

It is difficult to derive a simple rule from these data. The frequency of the response to a given tension-time stimulation appears to be greater both after a short and a long rest period (loadings 7, 3 and 9) than after a period of intermediate duration (loadings 4, 5 and 6). It may well be that the behaviour of the receptor in such a series of treatments depends on the interaction of several factors, which, on account of the small magnitude of their effects, are not easy to disentangle. However, the results do show that when the rest interval is kept constant, as in loadings 4, 5 and 6, the behaviour of the receptor remains practically unchanged through a series of stimulations. Curve b in Fig. 4 is based on values calculated
The agreement is almost complete, except at the beginning of each discharge. Curve a corresponds to the last series obtained with this preparation.

The tension-frequency curve. With a preparation as constant as the one we have just described it was possible to determine the tension-frequency relationship. The experiment consisted of five loadings separated by 4 min. rest intervals. Each loading was maintained for 1 min., so that the total duration of the experiment was 21 min. The order of the weights applied directly to the tendon was 2, 5, 1, 10, 2 g. The last loading, being the same as the first, verified the constancy of the preparation. It was found that this last adaptation curve was identical with the first from the 10th to the 60th second, and the difference in the initial phase was only about 10 per cent.

In general, it may be said that the rate of increase of frequency per unit increase of tension decreases with increasing tensions. This suggests a logarithmic relation, which has already been shown to hold for other sense organs and for proprioceptors (Hartline & Graham, 1932; Matthews, 1931a). But the fact that adaptation occurs renders it meaningless to ascribe a given frequency to a given tension, all that can be done is to select an arbitrary time co-ordinate on the adaptation curves, and to plot a tension-frequency curve from the values
obtained. Such a procedure yields a group of curves as in Fig. 5, corresponding to different time co-ordinates, and it is not possible to attach more importance to one than to another. The adaptation-time values of the six curves given are 0.5, 1, 5, 10, 30, 60 sec. Although there is considerable variation in the initial stage of stimulation, it can be seen that the shape of the curve becomes nearly constant 5–10 sec. after the application of the stimulus. In Fig. 6 the frequencies are plotted against the logarithm of the intensity of the stimulus, and exhibit a linear relation after the fifth second. This confirms Matthews' suggestion that these rhythms obey Fechner's law.

![Curves showing the linear relation between the frequency and the logarithm of the tension at different intervals of time after loading.](image)

**Fig. 6.** Curves showing the linear relation between the frequency and the logarithm of the tension at different intervals of time after loading.

![Record of the effect of a brief loading on a rhythmically active end-organ. Lower line marks the application of 1 g. load. Note the pause after unloading. Time marker, 0.2 sec.](image)

**Fig. 7.** Record of the effect of a brief loading on a rhythmically active end-organ. Lower line marks the application of 1 g. load. Note the pause after unloading. Time marker, 0.2 sec.

**Effect of preceding activity.** The modification which a receptor undergoes in the course of adaptation persists for some time after the discharge has ceased, and is revealed by its effect on the response to a known stimulus applied during the phase of incomplete recovery. In this way the rate of disappearance of the adaptation can be estimated. We have employed two separate procedures, both of which shed light on this problem. In the one an additional transitory stimulus was applied to a receptor which was already in a state of slow rhythmic activity, in the other a constant stimulus was applied at varying intervals of time after the cessation of a preceding stimulation.
Some of our preparations gave a regular spontaneous discharge of impulses which could be temporarily accelerated by attaching a weight to the muscle. In others there was no spontaneous activity, and it was necessary to evoke a slow rhythm by means of a small steady tension (1 g. applied for 1 min.) which provided a constant background of activity upon which the transitory overload could be superimposed. Fig. 7 shows that the immediate result of such an excess of activity is that the primary rhythm is slowed down. The magnitude and duration of this effect are very variable for different preparations and conditions, but in general the longer the duration of the overloading the more marked is the retardation of the primary rhythm.

The following table gives the data for an experiment in which a load of 1 g. was applied for varying periods of time to a muscle exhibiting a spontaneous rhythmic activity. The interval \( \theta \) is the time that elapses between the cessation of the accelerated discharge and the recommencement of the primary rhythm.

<table>
<thead>
<tr>
<th>Period of primary rhythm ( T ) sec.</th>
<th>Duration of overloading ( \text{sec.} )</th>
<th>Duration of the interval ( \theta \text{ sec.} )</th>
<th>( \theta/T )</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.24</td>
<td>0.46</td>
<td>0.53</td>
<td>2.2</td>
</tr>
<tr>
<td>0.24</td>
<td>1.3</td>
<td>0.73</td>
<td>3.0</td>
</tr>
<tr>
<td>0.21</td>
<td>2.2</td>
<td>1.45</td>
<td>6.9</td>
</tr>
<tr>
<td>0.22</td>
<td>5.0</td>
<td>4.82</td>
<td>21.9</td>
</tr>
</tbody>
</table>

Even very brief overloads, evoking no more than two or three accelerated impulses, produce a noticeable silent period. The smallest value of \( \theta/T \) obtained in such cases was 1.5. At the opposite extreme an overload of 6 g. maintained for 60 sec. resulted in a silent period which was about 50 times the period of the primary rhythm, and there can be little doubt that even longer intervals could be obtained.

Fig. 8 shows how the primary frequency is re-established after varying durations of overloading. It should be noted that there is usually a slight acceleration in the initial frequency when the overload is applied for a short interval of time (curves 1 and 2). It is unlikely that this is due to a facilitation at the receptor, for a transient residual effect of the overload may persist after its removal due to the frictional resistance of the system. The same effect would, of course, exist with overloads of longer duration, but here it would have time to disappear during the much longer period of the re-establishment of the initial frequency.

1 The term "silent period" was applied originally to the interval during which action currents cease in a muscle that is executing a myotatic reflex. Denny-Brown (1928) advanced the explanation that this was due to inhibitory impulses set up in muscle spindles. Matthews (1931b), however, suggested that the pause in the discharge from stretch receptors during contraction could account for a reflex pause in the motor discharge to the muscle, but his later work on mammals (1933) led him to modify this conception, and to advance the view that "the silent period appears to be due both to the absence of excitatory impulses from A1 endings, and to the inhibitory impulses set up by B endings". Lindsley's (1934) reflex studies confirm the intervention of inhibition in the causation of the silent period in muscle. Nevertheless, there appears to us to be no danger of confusion if the same term is applied to the pause in activity of muscle fibres during a tendon-jerk, and of stretch receptors after a reduction in tension. Phenomenally, the two events are identical. Bronk & Stella (1935) have already employed the term "silent period" with reference to the receptors of the carotid sinus, and we see no objection to following their example.
It is not easy to explain the silent period. It does not appear to form a continuous series with the succeeding intervals of the discharge, particularly when the stimulus has been of long duration, as in Fig. 8, curve 4. The primary rhythm is always re-established sooner than the length of the silent period would lead one to expect. Is it then to be distinguished as a latent period of the return of the primary rhythmicity? If the intervals between successive impulses are regarded as indicating the rate of disappearance of adaptation, it is perhaps better to make no such distinction, for it is evident that the process of recuperation begins at the moment when the excess of activity ceases. But the successive intervals are probably determined only in part by the process of recuperation. According to Matthews (1933) the viscous elastic properties of the receptor apparatus are also concerned.

In any case it is difficult to obtain results which give more than general indications. The rate of recuperation appears to depend largely on those uncontrolled factors which are embraced by the term "state of the preparation". For example, the following values for $\theta/T$ were obtained with two different preparations, A and B, after varying periods of overloading:

<table>
<thead>
<tr>
<th>Approx. duration of overload sec.</th>
<th>A $\theta/T$</th>
<th>B $\theta/T$</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.4</td>
<td>1.5</td>
<td>2.0</td>
</tr>
<tr>
<td>2.2</td>
<td>2.2</td>
<td>6.8</td>
</tr>
<tr>
<td>5.0</td>
<td>2.8</td>
<td>21.7</td>
</tr>
</tbody>
</table>

Both the absolute and relative values are different, and no comparison is possible. One and the same preparation, subjected to repeated loadings of 6 g. for 10 sec., with adequate periods of rest in between, gave on the first loading $\theta/T = 3.2$, and on the fifth, $\theta/T = 5.2$. 

Fig. 8. Curves showing the effect of increasing durations of overloading on the course of the re-establishment of the primary frequency after the overload is removed. The ordinates are the reciprocals of the period of each successive impulse. On the left, the abscissae are the durations of the four overworkings, and the primary frequency preceding each overloading is marked by a horizontal line. On the right, the abscissae are time in seconds from the moment of removal of the overload.
Such phenomena, which occur when a steady tension on a muscle is suddenly decreased without being abolished can be compared with the adaptation that takes place when the tension is raised to a higher level. With relaxation a kind of "negative adaptation" occurs. Although the two processes are not perfectly symmetrical, it does appear that in both the difference in sensory response to changed conditions is greatest at the instant of change, and tends to become effaced with time. In the reflex control of posture and movement it is the changes in tension, rather than steady states of tension, that demand a maximum accuracy of sensory discrimination.

![Diagram showing adaptation curves](image)

*Fig. 9. Curves showing the effect on the adaptation curve of reloading the muscle after brief intervals of rest. Curve a is the normal adaptation curve from the 20th to the 30th second after loading, and curve e shows its beginning during the first 10 sec. after loading. Curves b, c and d show the behaviour of the end-organ when the load, having been maintained for 20 sec., is removed and applied again after varying brief intervals of rest.*

Our second approach to the problem of the rate of disappearance of adaptation was to investigate the effect of a preceding activity upon the response to a new stimulus applied before recovery is complete. Fig. 9 shows three adaptation curves to a test stimulus of 1 g. maintained for 20 sec. The stimulus was applied three times in groups of two, and 4 min. periods of rest were interposed between the groups. A 30 sec. stimulation given at the beginning and end of the experiment showed that the preparation had remained constant. The two stimulations of the first group were separated by an interval of 0.44 sec., the second group by 1.15 sec., and the third by 3.38 sec. The curves given show the response to the second stimulation of each group.
The most striking feature of these curves is that after a brief interval of relaxation the afferent discharge descends abruptly from a short rapid burst of a few impulses to a slow rhythm almost without adaptation. This can be readily explained. The high frequency of the initial impulses is determined by the temporary overload of the establishment of tension, and is co-extensive with it in time. The absence of a period of transition from rapid to slow rhythm is due to the fact that the receptor is already adapted to the particular tension applied. But the interpretation of certain details is less obvious. One finds a considerable irregularity in the length of the first few periods of the slow rhythm, and in curve $b$ the frequency drops even below the level of normal adaptation. This may be due to an excess of adaptation resulting from the brief initial burst of rapid discharge, an excess which the slight recuperation of the short rest interval may not be adequate to compensate.

We have occasionally observed effects which, although abnormal in the sense that they occur when a preparation is not in good condition, are nevertheless of some interest. They usually appear as a consequence of an excess of activity induced by stimulation that is relatively too intense, or of too long duration, and they are associated with an irreversible alteration in the state of the receptor which in most cases becomes inexcitable soon after.

We have, in the preceding pages, emphasized the slow adaptation of the tension receptor of the ray, and we have inclined to the possibility of a state of permanently equilibrated activity. Actually, it is not rare to find that a constant stimulus evokes a discharge which stops after several minutes or even seconds (Fig. 10). It is possible that not all the muscle receptors are identical in their power of adaptation, but it seems more probable that in such cases we are dealing with preparations which are in some way imperfect, for they soon become completely inexcitable. Such preparations, moreover, tend to give irregular discharges of a type that also appear when a good preparation is subjected to a strong tension for a long time. The discharge slows down rapidly and the intervals between successive impulses become irregular.

In some cases the apparent irregularity is found to be due to the dropping out of one or two impulses from a perfectly regular series. An example of this is redrawn on a convenient time scale in Fig. 11, and the following table leaves no doubt that the rhythm is fundamentally regular. The distances of twelve successive impulses on the record from an arbitrarily selected impulse are given, and are to be compared with simple multiples of the distance 12.27 mm., which is the true period of the series.

\[
\begin{align*}
\text{Distance} & \quad \text{Multiple} \\
12.27 & \quad 1 \\
12.27 & \quad 2 \\
12.27 & \quad 3 \\
12.27 & \quad 4 \\
12.27 & \quad 5 \\
12.27 & \quad 6 \\
12.27 & \quad 7 \\
12.27 & \quad 8 \\
12.27 & \quad 9 \\
12.27 & \quad 10 \\
12.27 & \quad 11 \
\end{align*}
\]
The greatest deviation from the theoretical values is in impulse No. 9 which is 0.59 mm. out. The camera speed was 59 mm. per sec., therefore, during a period of 4-5 sec. this irregular discharge did not depart from a fundamental regularity by more than 0.01 sec. The conclusion that is to be drawn from this is that during the interval of time under consideration the receptor did actually generate a regular train of twenty-two impulses, but that ten of them were blocked at irregular intervals of time at some region central to the receptor, and failed to pass along the nerve fibre.

A similar block probably occurs when, as in Fig. 10, a constant stimulus evokes a discharge which stops abruptly soon after its commencement. This effect always appears just before a receptor ceases permanently to function. The interesting feature of this type of behaviour is that it is not a rapid adaptation. On the contrary, adaptation has hardly begun before the discharge is suddenly interrupted. The block, in this case, is permanently maintained throughout the period of stimulation.

There appears to be a locus in the receptor or in the nerve close to it which is more unstable than the region where the train of impulses originates. It may well be that the weak link is that portion of the nerve fibre which lacks a myelin sheath, and which, therefore, is likely to be especially sensitive to deformation, and also to K+ ions which are liberated from muscle fibres which may be injured by excessive tensions.

**COMPARISON WITH STRETCH RECEPTORS OF OTHER VERTEBRATES**

The stretch receptors of the ray are similar in their physiological properties to those of other vertebrates, so far as they have been investigated. A uniform tension-frequency relationship, a slow adaptation, a brief burst of rapid discharge during the establishment of tension, and a silent period following a decrease of tension are features which the end-organs in the pelvic fin muscles of the ray have in common.
with the receptors of the frog's sterno-cutaneous (Adrian & Zotterman, 1926), the frog's toe muscle (Matthews, 1931 a), the muscles of the cat (Matthews, 1933), and the carotid sinus of the rabbit (Bronk & Stella, 1932, 1935). That there should be such close resemblance to the receptors concerned in mammalian cardio-vascular reflexes is indeed an unexpected conclusion. There exist, of course, quantitative differences. The range of frequency of discharge appears to be considerably lower in the fish than in Amphibia and mammals. The highest frequency that we were able to obtain was about 100 per sec. In the frog frequencies of 200–250 have been recorded, and in the cat Matthews reached a maximum of 500 per sec. The high frequency of the response of mammalian receptors is, of course, due to the high body tempeature at which they work. But the highest frequency obtained from the receptors of the carotid sinus was only 70 per sec. Similarly, the slowest regular rhythm in the ray was less than 1.5 per sec.; in the frog's toe muscle Matthews found that the rhythm became irregular below 20 per sec., although in the cat a rhythm of 5 per sec. was recorded. Moreover, the remarkable performance of one of our preparations, which maintained a regular discharge at about 10 per sec. for over an hour (Fig. 4, curve a) establishes, we believe, a new record for sustained activity in a sense organ. Matthews found that under constant stimulation the discharge from the frog's toe muscle continues for some minutes, but in the cat he noted a resting discharge from a muscle before its tendons were divided, which indicates that, as in the ray, there is no limit to the duration of a discharge from a muscle under slight tension in the intact animal. Again, the silent period in the ray appears to be relatively of longer duration than in the frog and mammal, although the data on this are meagre. But in the carotid sinus Bronk & Stella recorded a silent period of 18 sec., which compares with periods of 10 sec. that we have obtained with our preparation.

In general it is interesting to note that the stretch receptors of the ray are slower in their action than those of frogs and mammals. They attain a lower maximum frequency under comparable loads, they adapt even more slowly, they continue to function with a slow regular rhythm for a longer time, and they take longer to recover from the effect of a period of activity. This is in keeping with the sedentary and sluggish habits of the animal, which can be seen lying motionless on the bottom of an aquarium tank for hours at a time, and which does not execute any movement which is comparable in suddenness and vigour with the jump of a frog. The muscular activity of small mammals is, of course, of an altogether different order. The carotid sinus, on the other hand, is an organ which is not called upon to execute rapid and violent movements. Its activity is rhythmical, like the locomotory fin movements of the ray, and the frequency of its rhythm is of a similar order. In keeping with this parallelism, the stretch receptors of the carotid sinus bear a closer resemblance to those of the ray than to those of the somatic musculature of frogs and mammals.

We have examined several different muscles in the ray and in the dogfish, Scyllium canicula, and have always found this type of stretch receptor present. A few tests with teleostean fishes (plaice and gurnard) have so far yielded negative results.
This may well be due to the fact that a really satisfactory teleostean nerve-muscle preparation has not yet been found.

THE ROLE OF MUSCLE RECEPTORS IN THE SWIMMING RHYTHM

From the point of view of reflex control of movement the silent period following a decrease of tension is perhaps the most interesting aspect of the behaviour of a stretch receptor. It is a phenomenon which is closely linked to the property of slow adaptation, for an organ whose response to constant stimulus rapidly declines to zero could not exhibit it. We have pointed out elsewhere that the silent period and the impulses that succeed it can be regarded as a kind of negative adaptation. Like the initial brief discharge at high frequency accompanying the establishment of tension, the silent period which follows a decrease of tension serves to exaggerate the sensory effect of change. In other words, the difference in frequencies corresponding to any two tensions is greatest during the moments following a change of tension. The curves of Fig. 5 illustrate this very clearly. The advantage of this arrangement becomes clear when we consider the behaviour of a receptor in a muscle engaged in the undulatory activity of swimming. The distribution of the nerves innervating the locomotory musculature in the ray was described in a preceding section (p. 385). Their separation into dorsal and ventral branches supplying the antagonistic muscles of the pectoral fin makes it possible to examine with certainty the behaviour of stretch receptors in these muscles during the act of swimming. To do this it is necessary to expose a spinal nerve, and to skin the fin completely so as to exclude the possibility of afferent impulses in the nerve coming from tactile endings in the skin. A spinal nerve so prepared, when laid across the

Fig. 12. Top records, resting discharge from radial muscles of a, pelvic fin; b, pectoral fin of Raja, when fish lies flat and muscle attachments are intact; c, record from dorsal branch of pectoral fin nerve; d, record from ventral branch of pectoral fin nerve. In both c and d the fin was initially drooping down, and the signal marks the raising and lowering of the fin.
electrodes, shows a steady stream of asynchronous centripetal impulses while the fin is lying flat on a board in the normal attitude of rest. A similar resting discharge is found in the nerve of the pelvic fin muscle before the tendons have been severed. Records of these two discharges are shown in Fig. 12a and b.

If the fin is supported in such a way that it can be both raised and lowered, it is found that in both cases the frequency of the discharge is increased. The reason for this becomes apparent when, instead of recording from the whole nerve, the dorsal and ventral branches are taken separately and their activity during elevation and lowering of the fin examined. The records obtained in such an experiment are shown in Fig. 12c and d. In the drooping position of the fin the dorsal muscles are stretched, and the dorsal branch of the fin nerve carries a train of asynchronous centripetal impulses from the stretch receptors (record c). When the fin is raised the tension on the dorsal muscles is slackened, and the silent interval intervenes, abruptly abolishing the discharge. On lowering the fin again, the discharge instantly reappears. The receptors of the ventral muscles (record d) behave in the same way, but in the opposite sense.

It has to be admitted that these observations were made on a fin that was passively raised and lowered, and the question at once arises whether the same sequence of events can be assumed to occur in a fin that is executing an active undulatory movement. We have not examined in detail the behaviour of the muscle receptors of the ray during active muscular contraction, though a preliminary experiment showed that no very conspicuous discharge from the end-organ occurs when the muscle is stimulated. The muscle spindle of a frog, as Matthews (1931b) has shown, behaves in exactly the same way during active contraction and relaxation as it does during passive slackening and stretch, a rhythmic discharge from a loaded muscle stops during the rising phase of contraction, and is set up again during relaxation. That is to say that, so far as this receptor is concerned, it is the shortening of the muscle that is significant, whether it results from active contraction, or from the passive removal of a stretching force. The A1 receptors in mammalian muscle, which Matthews (1933) believes to be flower-spray endings in muscle spindles, behave in the same way: relaxation after active contraction is equivalent to passive stretching in exciting the end-organ. On the other hand the A2 endings (the annulo-spiral endings, according to Matthews), although they respond to passive stretch in the usual way, are excited also by supramaximal stimulation of the muscle. The existence of receptors in mammalian muscle which respond to active contraction is confirmed by the work of Cooper & Creed (1927a, b), who, following up the original observation of Sherrington (1893), showed that active contraction of a muscle can cause reflex inhibition of an antagonist, and reflex excitation of a synergic muscle.

It is possible that “contraction receptors” of this type exist also in fishes, though, since they have been found hitherto only in mammals, and since muscle spindles are believed to be absent from fish muscle, it is safe to assume provisionally that they do not. On this assumption the sequence of events in the proprioceptive fibres of a spinal nerve during a swimming wave may be schematically represented as in
Fig. 13. Owing to the intervention of the silent period the discharge from the ventral receptors will cease abruptly at the peak of the wave, and similarly the discharge from the dorsals will cease at the trough. The stretching of the dorsals on the downward slope of the wave will evoke a rapid discharge (establishment of tension), similarly with the ventrals on the upward slope. The net result is that the sensory discharge does not follow the approximately sinusoidal course in time of the fin movement, but an almost instantaneous switch-over occurs at the two turning points of the undulation, and through the greater part of the rhythm of contraction and relaxation the sensory discharges from the dorsal and ventral muscles are maintained alternatively at zero and high frequency. It is evident that this mechanism must provide an accurate central control for the timing of the undulatory rhythm.

![Diagram](image)

Fig. 13. Scheme to illustrate fluctuations in the sensory discharge from the dorsal muscles (dotted line) and ventral muscles (broken line) during a single undulation of the pectoral fin (continuous line). The ordinates (frequency) apply only to the dotted and broken lines. The continuous line furnishes the time co-ordinate in terms of the period of the undulatory rhythm. In normal swimming a complete undulatory wave is accomplished in 1-1.5 sec. At a much slower rate of movement this scheme would not hold.

It should be noted, however, that Fig. 13 can be assumed to describe the proprioceptive response during swimming only when the rhythm is fairly rapid. With a very slow rhythm the response of the receptors would tend to resemble the type shown in Fig. 2, and, in the limit, the frequency of discharge would follow the sinusoidal course of an infinitely slow undulation. But, although we have not analysed in detail the relation of the rate of stretching and relaxation to the character of the response, it is highly probable that at normal rates of swimming (about 30-60 undulatory waves per minute), the response of the receptors agrees fairly closely with Fig. 13.

The presence of a resting discharge from the muscle receptors when the fin is in the normal flat position of rest, and the fact that the discharge from any individual receptor is increased when the fin is bent one way, and abolished when it is bent the
other way, suggest a close similarity to the mode of action of the horizontal ampulla of the dogfish as described by Löwenstein & Sand (1936). Their records, showing the response of the two horizontal ampullae to left and right swaying of the head, are comparable to our records c and d in Fig. 12. The labyrinthine and muscular proprioceptors, in fishes at any rate, have this in common, that they are called upon to respond to equal and opposite deviations from the normal resting position. To meet this contingency it would seem that their “setting” is so adjusted that they are maintained in a moderate state of excitation during muscular inactivity, and are in a position to signal to the centre the occurrence of either a negative or positive phase of movement by a decrease or increase in frequency of discharge.

The exact nature of the contribution of the muscle receptors to the co-ordinated mechanism of swimming must remain for the present undecided. In the eel (Gray, 1936a) and in the dogfish (Gray & Sand, 1936a, b) it has been shown that the locomotory rhythm is determined by the intrinsic activity of the spinal cord. This statement holds for the basic phasic activity of the motor centres, it does not necessarily apply to the modification in frequency and intensity that occur as a result of exteroceptive stimulation in the accurately orientated movements of the intact animal. The same distinction has arisen in connexion with the mechanism of progression (stepping) in mammals, and the words of Creed et al. (1932) on this question would appear to hold with equal force for fishes: “The phasing of these alternating reflexes can be affected by the proprioceptive and other stimuli which they generate... but their phasing is not caused by peripheral stimuli. The self-generated proprioceptive stimuli of the muscles which take part in progression can regulate the act but are not essential to its rhythm.”

**SUMMARY**

1. The presence of stretch receptors in the muscles of *Raja* and *Scyllium* has been physiologically demonstrated. Their morphology is unknown.

2. The behaviour of a single end-organ in the radial muscles of the pelvic fin of *Raja clavata* has been examined in detail.

3. The adaptation curve and the tension-frequency relationship have been determined.

4. Under constant tension a single end-organ has continued to function rhythmically for over 1 hour.

5. When tension is suddenly reduced, there follows a silent period before the frequency of discharge corresponding to the reduced tension appears.

6. The quantitative aspects of the behaviour of the stretch receptor of *Raja* bear a closer resemblance to those of the receptors of the carotid sinus than to those of mammalian and amphibian limb muscles.

7. The response of muscle receptors during a passive undulatory movement of the pectoral fin has been recorded, and their role in the swimming rhythm is discussed.
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