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Activation of Muscle Spindles in Pinna Reflex.

By

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SHERRINGTON (1917) gave a very complete description of the reflexes obtainable from the cat's pinna, vibrissae and jaw. It used to be one of his class experiments to elicit the pinna reflex by adequate stimulation as well as by electrical stimulation of *n. auricul. magnus* and the easily accessible second cervical ganglion. The skin of the ear has a powerful receptive field, somewhat differentiated with respect to the five reflexes elicitable: retraction reflex, back-folding reflex, head-shake reflex, cover reflex and scratch reflex. Four of these reflexes refer to the ear and the head but the fifth, the scratch reflex, means that there may arise a purposeful movement intended for the removal of the cause of irritation. All leg movements involve postural readjustments.

It will be shown in this paper that twist of the pinna is a very active stimulus for the muscle spindles of the hind leg. The technique used in this experiment was that employed in the study of the effect of stimulation of various parts of the brain on LEKSELL's (1945) gamma efferent fibres of the ventral root and on the muscle spindles (A-type of end-organ, MATTHEWS 1933) activated by them. A feature of this technique is recording from single spindle afferents in the dorsal root, together with myographic control of the muscle to which the spindle belongs. This technique has been described in detail in a more extensive report

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by GRANIT and KAADA (1952) and therefore nothing more need be said about it in this connection. Actually the very first observation made when the technique was tested was that a twist of the cat's pinna greatly accelerated the discharge of the first muscle spindle that was isolated. The pinna reflex was later regularly used as a simple routine test in a large number of experiments, the notion being that, when present, it probably indicated an active preparation. Some illustrations of this effect are given below.

Results.

The effect on the muscle spindles was seen in a large number of animals under Dial or Dial-chloralose (10 mg Dial and 20 mg chloralose per kg) and in a number of decerebrate animals. In the latter the effect proved particularly strong on gastrocnemius-soleus spindles and therefore these were the ones most frequently studied. In the anaesthetised animals some tibialis ant. muscle spindles were also tested and they responded much as did the gastrocnemius spindles. The receptive field proved to be larger in the decerebrate animals. The skin of the entire head was sensitive. Sometimes also pressure below the jaw accelerated the spindle discharge. We did not succeed in eliciting acceleration of hind leg muscle spindles from the vibrissae. In some animals the orbita was exposed in order to gain access to the ventral surface of the frontal lobe. Operation within the orbita nearly always aroused a response — particularly strong when the eye bulb was pulled upon — from the muscle spindles. In some anaesthetised animals twist of the pinna did not activate the muscle spindles and in these cases it likewise proved difficult to influence the spindle discharge by stimulation of various central nervous structures which have been demonstrated to influence the spindles (cf. GRANIT and KAADA 1952).

Two types of effect were seen: (i) during twist of the pinna the discharge rate of the isolated muscle spindle diminished and when the ear was released, or immediately afterwards, great acceleration of the discharge followed; (ii) there was a pure acceleration of the spindles.

(i) *Inhibition followed by acceleration.* Figure 1, record *1*, illustrates that to single shock stimulation of the gastrocnemius nerves the spontaneous discharge of an isolated dorsal root fibre

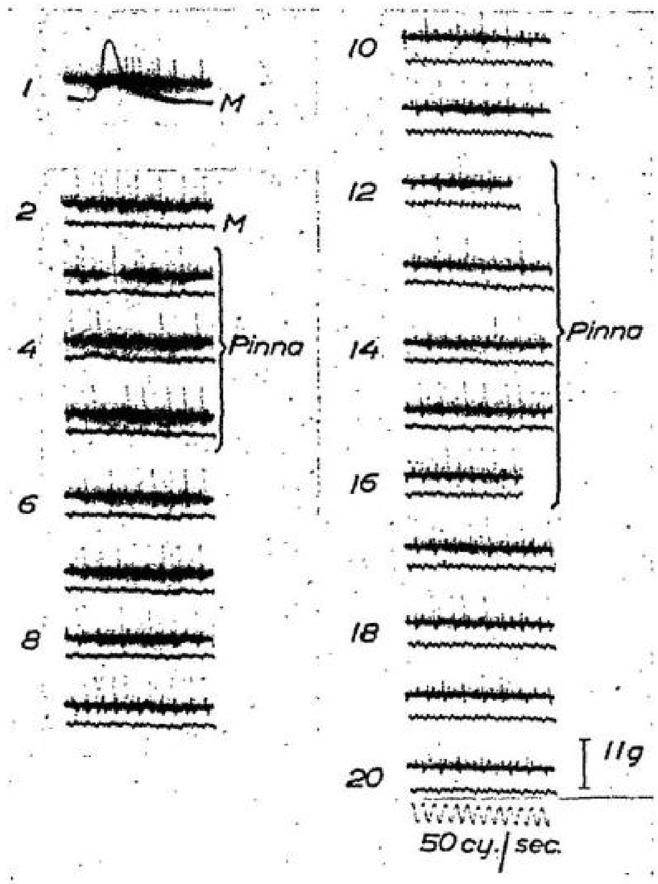

Fig. 1. Effect of twisting ear on firing rate of A-ending in gastrocnemius muscle as recorded from an isolated dorsal root fibre (S_1). Dial-chloralose. Initial tension 86 g. Interval between sweeps 1.5 sec. *1:* contraction of 162 g (low myograph sensitivity) to demonstrate A-character of ending. On the successive records *2—20* maximum myograph sensitivity as shown on record *20*. *2:* baseline discharge. *3—5:* during twisting of ear. *6—9:* after release of grip. *10—20:* same experiment repeated.

has a silent period during the muscle contraction (M). This was the criterion used to establish that the fibre isolated was a muscle spindle afferent. From record *2* onwards the myograph was adjusted to maximum sensitivity (see calibration on record *20*). Record *2* shows the baseline discharge rate. Then follow successive sweeps at 1.5 sec. intervals. Twist of the pinna (records *3—5*) caused a slight contraction of the muscle of 1—2 g. There was, however, considerable deceleration of the rate of firing of the

muscle spindle. Release of the pinna released the activity of the muscle spindle. There was no definite correlation with the myographic changes (cf. records *3*, *8* and *9*). Somewhat later the same experiment was repeated and records *10* and *11* illustrate the new baseline discharge. The pinna was touched during record *12* and the grip released during *16*. The myograph in records *14—16* again reveals a slight tonic contraction but in record *14* there is considerable inhibition of the spindle discharge whereas in 16 there is a great acceleration which gradually decreases towards record *20*.

In another cat, in which inhibition likewise preceded acceleration of the spindle discharge by twist of the pinna, the spontaneous firing of the spindle was decelerated by the simple expedient of pulling on the gastrocnemius muscle and then quickly releasing it. As found by MATTHEWS (1933), this deceleration occurred in pure muscle-nerve preparations and is thus a property of the receptor and elastic forces of the tissue combined. According to HUNT (1951), however, stretch of a muscle also causes inhibition of its own gamma efferents. In our preparations, which possess intact ventral roots, reflex inhibition of gamma efferents has almost certainly been present also. When the pinna reflex was compared before and during suppression of the spontaneous rate of firing succeeding stretch, the effects differed. Thus the characteristic inhibition followed by acceleration before stretch was altered to pure acceleration after stretch.

When inhibition of the muscle spindle discharges was first noted, it was suspected to be due to muscle contraction and that only the acceleration was a genuine effect. The two experiments quoted, however, did not support this view. More decisive evidence against it was provided by an experiment in which records were taken from isolated gamma efferents in the ventral root, the dorsal roots being cut (cf. GRANIT and KAADA 1952). This was an animal which in the beginning of the experiment showed initial spindle inhibition of the type illustrated in Fig. 1. By twist of the pinna the tonic discharge of the later isolated gamma efferents likewise was first inhibited and then accelerated. Both effects, inhibition and acceleration, therefore appear to be genuine in the sense that they represent changes mediated by gamma efferents upon the muscle spindles.

(ii) *Acceleration.* Figure 2, at a somewhat lower myograph sensitivity, shows a case of pure acceleration. Again, record *1* illus-

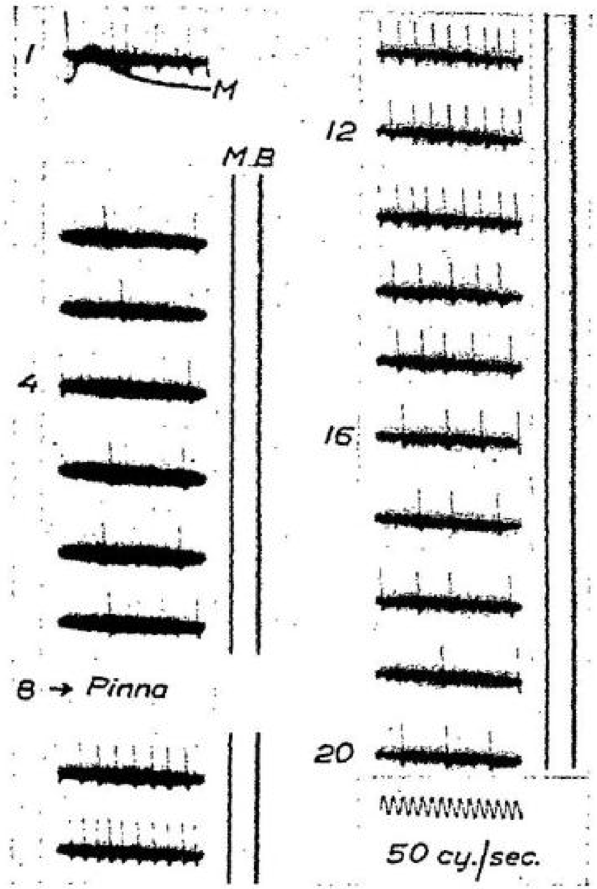

Fig. 2. Effect of twisting ear on A-type of muscle end-organ in gastrocnemius. Dial-chloralose. *Initial tension* 35 g. Myogram (M) in record *1* horizontally; in the successive sweeps *2—20* vertically. Distance between M and baseline (*B*) corresponds to 15 g. Contraction of 118 g in record *1* to demonstrate A-character of ending. *2—7:* control. *8:* twist of ear, marked 'Pinna'. *9—20:* acceleration of spindle discharge in pinna reflex from a baseline discharge of about 7/sec. to about 36/sec. Interval between sweeps 2 sec.

trates the A-character of the muscle end-organ. Then the myograph (M) was shifted alongside the records to another double beam oscillograph, the second beam of which served as a baseline (B). Twist of the pinna, marked by shading one sweep (record *8*), greatly accelerated the slow original rate of firing.

Maximum sensitivity of the myograph was again used in Fig. 3 in which an exceedingly strong effect on the muscle spindle with only slight effect on the myogram is illustrated. Maximum ac-

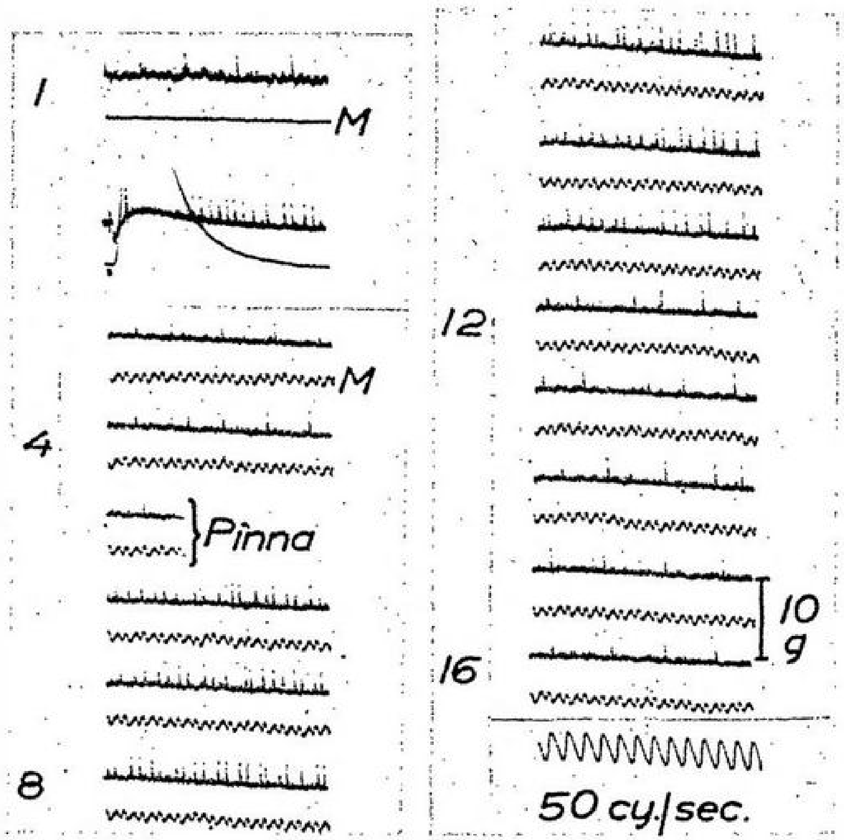

Fig. 3. Effect of twisting ear on the firing rate of an A-end-organ. Dial-chloralose. Gastrocnemius. Initial tension 120 g. *1:* control. *2:* contraction at lower sensitivity of myograph (M) to demonstrate A-character of ending. *3—16:* myograph at maximum sensitivity as shown on record *15*. Successive sweeps at interval of 1.1 sec. at 'Pinna' as marked by shading of the cathode ray. The frequency of discharge rose from about 20/sec. to maximally 80/sec. without significant effect on myogram (cf. text).

celeration is seen to have occurred in record *8* with no significant influence on the myogram. Actually there were greater myographic changes in the control records *3* and *4* and in records *12* and *14* than during maximum acceleration. This spindle also responded very actively to pull on the dura mater, the scalp musculature and the eye bulb.

In some active cats the pinna reflex consisted of a long series of rhythmic retractions of the ear. In these cases it was noted that the spindle acceleration also occurred in rhythmic bursts. Again there was no correlation with the myographic changes.

No effect was ever noted on the B-type of end-organs (Golgi tendon organs).

Comments.

HUNT (1951) has described a number of reflexes from hind limb afferents on the gamma efferent system of LEKSELL (1945). It is interesting to note that also the pinna reflex contains a gamma component strong enough to influence muscles as distant as those of the hind limb. Considering that irritation of the pinna ultimately may lead to a scratch reflex (SHERRINGTON 1917), spindle excitation and inhibition mediated by gamma efferents probably represent the initiation of the postural adjustments necessary for the execution of this movement.

In the experiments of GRANIT and KAADA (1952) it was found that electrical stimulation of various central nervous structures, known to influence motor activity, generally started with changes of the gamma discharges in advance of those of motor alpha activity. These authors used anaesthesia most generally, which may have altered the relative sensitivity of inhibitory and excitatory influences to electrical stimulation. It is therefore of some significance to adduce an example of primary activation and inhibition of gamma efferents in response to adequate stimulation of sense organs.

Summary.

The pinna reflex in decerebrate and Dial-chloralose cats either accelerates or initially depresses and then accelerates hind leg muscle spindles. It has similar effects on the gamma efferents in the ventral roots. These effects may occur in the absence of contraction of the muscles tested.

Acknowledgments.

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