FLEXION-REFLEX OF THE LIMB, CROSSED EXTENSION-REFLEX, AND REFLEX STEPPING AND STANDING. BY C. S. SHERRINGTON.

(*From the Physiological Laboratory, University of Liverpool.*)

CONTENTS.

SECTION I. THE FLEXION-REFLEX OF THE LIMB.

(i) IN the spinal cat and dog as in the spinal frog the reflex movement of the limb most readily evoked by stimulation of the skin of the limb or of its afferent nerves is flexion. This reflex may be termed the "flexion-reflex of the limb." In the hind-limb the flexion is of hip, knee, and ankle, in the fore-limb of elbow, shoulder, and wrist[1].

This reflex is obtained from the decerebrate preparation as regularly as from the spinal. By the decerebrate preparation is understood one in which the whole brain in front of the posterior colliculi has been removed. The decerebrate preparation offers in some respects a better field for the examination of the reflex than does the spinal preparation. For that reason the reflex as obtained in the decerebrate preparation will be described first.

(ii) It was sought to ascertain at outset which of the several muscles of the limb are actually employed in the execution of this reflex. The sample reflex taken for examination was excited from one particular afferent nerve only, namely from the cutaneous branch of the musculo-cutaneous division of *n. peroneus*, at a point close above the annular ligament of the ankle (cat, dog). There the nerve was severed, tied, and its central stump faradised or stimulated mechanically by tightening on it a thread previously looped loosely. The experiments showed that, elicited in this way, the reflex brings into contraction certain only of the muscles of the limb. However intense the stimulation the distribution of this reflex effect did not spread in the limb musculature beyond those particular muscles. The muscles which the reflex causes to contract are the following:

TABLE I.

Ilio-psoas.
Pectineus (slight).
Sartorius, (?) the part insected into patella.
Tensor fasciæ femoris (weak).
Rectus femoris.
Gracilis.
Semitendinosus.
Posterior part of biceps femoris.
Tenuissimus.
Tibialis anticus.
Peroneus longus.
Extensor longus digitorum.

The extensor brevis digitorum contracts very slightly if at all.

When the reflex is elicited in the decapitate[2] preparation the same muscles contract and only those. In neither preparation does increase of the stimulus make the reflex contraction spread to limb muscles additional to the above. The threshold of stimulus for the reflex is nearly the same for all the muscles which contract.

---

[1] Sherrington. *Integrative Action of the Nervous System*, p. 28. London and New York, 1906.

[2] Cf. Sherrington. This *Journal*, XXXVIII. p. 375. 1909.

Thus: faradisation of central end of cutaneous branch of musculo-cutaneous division of *n. peroneus*; Berne inductorium, interruptor in primary circuit vibrating 30 p. s. resistance box of 100,000 ohms in secondary circuit.

At 8 Kronecker units contraction just obvious in tibialis anticus.
,, 10 ,, ,, ,, ,, tensor fasc. fem. longus.
,, 10 ,, ,, ,, ,, ,, ,, ,,
,, 10 ,, ,, ,, ,, semitendinosus.
,, 14 ,, ,, ,, ,, psoas magnus.
,, 50 ,, ,, ,, very strong in tibialis anticus and semitendinosus and stronger than before in tensor fasc. fem. and psoas, but no contraction in semimembranosus or gluteus maximus.

At 125 Kronecker units contraction as before.
,, 6000 ,, ,, ,, ,,

Again: stimulation of central end of *n. internus saphenus* half-way up thigh.

At 15 Kronecker units contraction just obvious in gracilis.
,, 18 ,, ,, ,, ,, tensor fasciæ femoris.
,, 20 ,, ,, ,, ,, psoas magnus pectineus, semitendinosus and psoas parvus.

At 50 Kronecker units contraction strong in all the above muscles.
,, 150 ,, ,, ,, very stròng in all the above muscles, but no trace of contraction in semimembranosus, or anterior part of biceps or gluteus maximus.

At 5000 Kronecker units contraction same result as with 150 units.

In these observations the muscles stated as contracting or not contracting are merely those definitely prepared for observation in the particular experiment, the other limb muscles being paralysed by nerve-section or actually excised. The observations do not mean that other muscles than those specifically mentioned would not have been excited had the observations extended to them. The question of spread of reflex was tested in these observations simply on the muscles mentioned as a sample of the musculature. But a number of such experiments were made; those quoted instance the kind of result always reached.

The above list (Table I) embraces all the muscles which contract but the reflex effect is not restricted to contraction. In certain other muscles the reflex result is relaxation of contraction. To detect this it is necessary to observe the muscle at a time when some degree of contraction is already at work for the inhibitory influence to show upon. A background of contraction against which the inhibitory relaxation can show up is generally absent in the decapitated preparation. In my experience the best chance of it is offered during the first forty minutes after decapitation. A background can however easily be produced at any time by faradisation of an afferent nerve of the opposite fellow limb. This evokes reflex contraction in the required muscles and this reflex contraction is readily seen to be inhibited[1] by stimulation of the ipsilateral musculo-cutaneous nerve.

The necessary background of contraction is more conveniently

---

[1] Cf. Fig. 3, *Roy. Soc. Proc.* LXXVI. B, p. 277. 1905.

obtained by simply using the decerebrate preparation not the decapitate. On decerebration there ensues a tonic rigidity[1] of the limb muscles. Each relaxation of them is then easily seen and felt or recorded graphically[2]. Another way, presenting certain advantages is to obtain a rebound contraction (*v. infra,* Sect. II. ii. p. 69) and then to reapply the original stimulus during the rebound contraction; the contraction is then seen to immediately relax under the reflex inhibition. In the flexion-reflex the muscles thus observed to relax are as follows.

TABLE II.

Vastus lateralis.
Vastus medialis.
Crureus.
Gastrocnemius.
Soleus.
Semimembranosus (both parts).
Posterior part of biceps femoris.
Flexor longus digitorum (?).
Quadratus femoris.
Adductor minor.
Adductor magnus (a part).

These muscles are the same as those observed by the other method to relax in the decapitate preparation. The muscles which contract and the muscles which relax are therefore the same in the decerebrate as in the decapitate preparation.

Increase of intensity of the stimulus does not change the inhibitory result; it merely accentuates the sharpness and extent of the relaxation; it does not cause the inhibitory effect to spread to other muscles in the limb than those mentioned above. The limits of the field of inhibition in the musculature of the limb seem as fixed as are those of the field of excitation.

Those limb-muscles which the reflex excites and those which it inhibits if put together are seen not to cover all the items of musculature of the limb. Some of the muscles, the reflex does not so far as I have seen affect at all. Among these are, gluteus medius, gluteus maximus, gluteus quartus, peroneus brevis, peroneus tertius, and tibialis posticus. However intense the stimulus its reflex effect does not appear to reach the moto-neurons of these muscles.

(iii) The reflex as thus elicited from this cutaneous nerve of the dorsum of the foot is typical of the reflex elicitable, by stimuli of like quality, from the limb generally. It can be evoked from the skin as well as from the cutaneous nerve itself, and in the former case has the same features as in the latter.

---

[1] Sherrington. This *Journal*, XXII. p. 319. 1898. Also *Roy. Soc. Proc.* LX. 1906.

[2] Cf. Fig. 1 B, *Roy. Soc. Proc.* LXXVI. B, p. 273.

The term "*receptive field*[1]" may be conveniently applied to designate the total assemblage of receptive points whence by suitable stimuli a particular reflex movement can be evoked. Thus the scratch reflex of the hind-limb of the spinal dog can be evoked from series of points in a saddle-shaped area of skin of the shoulder back and loin[2]. The collective area of distribution of these points constitutes the receptive field of the scratch reflex. For the flexion-reflex of the hind-limb the receptive field includes the skin of the whole limb as far up as the groin in front, the perineum medially and the ischial region behind. The stimuli best effective for the reflex are of mechanical, especially if nocuous, quality and electrical, *e.g.* faradic. In working over the field with mechanical stimuli an impression is received that the reflex is provoked more readily from the foot than elsewhere. Electric stimuli are more easily measurable in intensity and these substantiate the impression given by the mechanical. For electrical stimulation I used a small silver entomological pin as stigmatic electrode inserted about 2 mm. into the skin, the diffuse electrode being a wide copper plate bandaged to the shaven and well-moistened skin of one of the fore-limbs. A resistance box of 100,000 ohms was placed in the secondary circuit to minimise differences in conductivity of the skin, etc. The observations show that from the skin of the distal end of the foot, the digits and the plantar cushion the reflex is provoked by weaker faradisation than from the skin higher up the limb. The surface of the foot on the whole excites the reflex more easily than the limb surface elsewhere.

Illustrative instances from the spinal dog after thoracic transection are the following:

	Intensity of stimulus in units of the Berne coil		
Situation of electrode	Exp. i	Exp. ii	Exp. iii
Outermost toe-pad ...	20	30	25
Innermost ,, ...	25	30	30
Plantar cushion	25	30	70
Between toe-pads and cushion	150	175	275
Outer malleolus	220	300	1000
Close below patella ...	400	600	750
Half-way up front of thigh ...	400	600	1000
Ischial skin	600	800	1000
Calf	1500	1500	1600

The receptive field of the skin for this reflex has so to say its focus at the free apex of the limb. This fact is of assistance in attempting

---

[1] Sherrington. *Integrative Action of the Nervous System*, p. 126. London and New York. 1906.

[2] Sherrington. *Proc. Physiol. Soc.* p. xvii, 1904 (This *Journal*, xxxi.), and xxxiv. p. 1. 1906. Cf. also Graham Brown, *Quart. Journ. of Exp. Physiol.* ii. p. 243. 1909.

to decipher the functional significance of the reflex. In that connection it will be referred to later. (Sect. IV. p. 71.)

From all parts of this receptive field the reflex movement as evoked by the above-mentioned stimuli presents characters so closely similar that the observer at once recognises that it constitutes a single "type-reflex[1]." That is, the individual reflexes produced from the several points of the field are all examples of one reflex which is broadly speaking the same from whatever point of the field it be provoked. This uniformity of the reflex movement excited from the various skin-points of the limb harmonises with the results of observations on the distribution of the reflex effect on the limb musculature when the reflex is elicited from the several cutaneous nerves of the limb. The results of these observations are as follows (Table III).

In this Table the reflex effect of the afferent nerve on any particular muscle is indicated where the abscissa-column belonging to that nerve crosses the ordinate-column belonging to that muscle. The sign + signifies that the muscle contracted; the sign − that the reflex effect was relaxation of the muscle; the sign 0 means that no reaction of the muscle was discovered though searched for; the ease of detecting contraction is greater than that of detecting inhibition, so that 0 may sometimes stand where − should stand. The leaving of the place in the Table blank, *i.e.* without any sign at all, signifies that either no observation was made or the observations made failed to get clear evidence. The sign $\underset{0}{+}$ means that in some experiments contraction was seen and in some none; the sign ± means that sometimes contraction was observed sometimes relaxation.

The results of the observations confirm the inference drawn by inspection from the actual skin-reflexes, namely that whatever the cutaneous nerve-trunk stimulated in the limb the reflex effect is broadly the same in its distribution in the limb musculature. Though broadly the same the Table III also shows that it is not fully the same when nerve by nerve the whole series of afferent trunks are examined; differences in detail appear but are small; the general effect throughout is excitation of the motoneurones of flexors and inhibition of the motoneurones of extensors.

That is the effect as regards the skin and the skin-nerves of the limb proper. But Table III shows that other cutaneous nerves near to but not actually within the limb proper yield reflexes of other type. Where the limb surface abuts on regions inguinal, perineal and gluteal its afferent nerves tend to evoke reflex extension instead of limb-flexion. Nos. 10, 11 and 13 of the Table exemplify this. Their reflexes do not come within the great " flexion-reflex " of the limb.

---

[1] *Integrative Action of the Nervous System*, p. 127.

TABLE III.

Name of muscle	1	2	3	4	5	6	7	8	9	10	11	12	13	
Psoas parvus	...	+	+	+	...	...	...	+	+	...	...	...	...	...
Psoas magnus (iliopsoas)	+	+	+	+	...	+	+	+	+	...	...	...	...	+
Sartorius	...	+	+	+	...	+	...	+	+	...	...	...	...	+
Gluteus maximus anterior	0	0	...	...	...	0	0	0	...	...	0	...	...	0
,, ,, posterior	0	0	0	0	...	0	...	0	0	...	0	...	...	0
Tensor fasciæ femoris ...	+	+	+	+	...	+	+	0	0	...	+	..	...	+
Gluteus medius ...	0	0	0	0	...	0	...	0	0	...	...	...	...	0
Gluteus minimus ...	+	+	+	+	...	+	...	+	+	...	...	...	...	+
Rectus femoris ...	+	+	...	...	...	+	...	...	...	...	...	+	+	+
Vastus lateralis ...	–	–	–	–	...	–	...	...	...	+	±	...	+	+
,, medialis ...	–	–	–	–	...	–	...	...	...	+	±	...	+	+
Crureus	–	–	–	–	...	–	...	...	...	+	±	...	+	+
Pectineus	+	+	+	+	...	+?	...	0	0	...	...	...	+	+
Adductor minor ...	...	0	0	...	...	–	...	–	–	...	...	...	...	+
,, magnus (part) ...	...	0	0	...	...	–	...	–	–	...	...	...	...	...
Gracilis	...	+	+	+	...	+	...	+	+	...	...	...	...	...
Semitendinosus ...	+*	+*	+*	+*	+	+	+	+	+	...	...	...	...	+
Semimembranosus ...	...	–	–	...	0	–	0	0	0	...	...	...	...	+
Biceps femoris anterior ...	...	–	–	...	0	–	0	0	0	...	...	...	...	+
,, ,, posterior...	+*	+*	+*	+*	+	+	+	+	+	...	...	...	...	+
Tenuissimus	0	+*	...	...	...	+	...	...	...	...	...	...	...	...
Quadratus femoris ...	...	...	...	...	...	–	...	...	...	...	...	...	...	...
Tibialis anticus	...	+*	+*	+*	...	+	...	+	+	...	...	...	...	+
Extensor longus digitor ...	...	+	+	...	...	+	...	+	+	...	...	...	...	+
Peroneus longus ...	...	...	...	...	...	+	...	+	+	...	...	...	...	...
,, brevis ...	...	...	...	...	...	0	...	0	0	...	...	...	...	...
,, tertius ...	0	0	...	...	0	0	...	0	...	...	...	...	...	...
Gastrocnemius... ...	–	–	–	–	...	–	...	–	–	...	...	...	+	+
Soleus	–	–	–	–	...	–	...	–	–	...	...	...	+	+
Tibialis posticus ...	0	0	...	...	...	0	0	0	...	...	...	...	...	0
Flexor digitorum perforans	...	...	...	...	...	–	...	...	...	...	...	...	...	+
Extensor brevis digitorum	...	...	...	...	...	...	...	+	+	...	...	...	...	...

Cutaneous Nerves

1 Cutaneus femoris ant. ext. ... ...
2 Saphenus (internal saphenous) ... ...
3 ,, ,, below knee ...
4 ,, ,, br. over adduct.
5 Cutaneus ischiadici (ext. saph.) ... ...
6 Cutaneous of musculo-cutaneous ... ...
7 Cutaneous of anter. tibial. ... ...
8 First digital of plantar ... ...
9 Third digital of plantar ... ...
10 N. to skin of perineum ... ...
11 N. to back of thigh and ham ... ...
12 N. to outer part of back of thigh ... ...
13 Lumbo inguinal (spermat. ext.) ... ...

Skin behind pinna evoking scratch reflex (cat). ...

* The reflex contraction is sometimes weak.

The uniformity of the reflex effect of the various afferents of the limb extends beyond the category of the skin-afferents. It pertains to the deep afferents likewise. The accompanying Table IV summarises observations on the distribution of the reflex effect evoked from the limb's deep afferent nerves severally.

From Table IV it is clear that the reflex effect in its distribution in the limb musculature is broadly the same for all the deep afferents examined. Also that the reflex effect of these afferents is practically the same as that of the skin-afferents and the skin itself. The receptive field of the flexion-reflex of the limb is therefore not merely an area of surface, a skin-field, but is musculo-articular as well and includes the whole thickness of the limb as well as its surface. In this respect the receptive field of the flexion-reflex differs fundamentally from a receptive field such as that of the scratch-reflex which is wholly cutaneous.

It is not surprising therefore to find (Table V) that when the various large afferent nerve-trunks of the limb are themselves examined in regard to the reflex effect they each evoke, the effect found for all of them is flexion, and that the reflex given by each of them is practically the same. In these large nerve-trunks the afferent fibres are of course mixed in origin, cutaneous, fascial, muscular, articular, etc. Yet when the mingled collection of each trunk is thus stimulated the reflex result is regular and harmonious; it is always in fact the flexion-reflex.

(iv) This makes clear how it is that when the afferent spinal roots themselves are stimulated each root of the whole series belonging to the limb evokes in the limb simply the same reflex movement; and how it is that that movement is flexion.

Table VI shows that whichever of the roots is stimulated the movement obtained in the limb is flexion at its larger joints. Flexion of ankle is less marked with the more anterior of the roots of the series and flexion at hip less marked with the most posterior but a general flexion of the limb is the reflex result from each root. The heterogeneity of the afferent fibre constitution of each of these large roots is very great. The uniform result which they regularly produce in their reflex effect becomes however intelligible in light of the flexion-reflex being practically the one reflex obtained by direct stimulation (mechanical and electrical) of each and all the afferent nerves of the limb.

TABLE IV.

Name of muscle	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Psoas parvus	...	...	...	...	...	...	...	...	+	...	...	...	...	...	...	...	...	...	...	...	...	...	...	+	+
Psoas magnus	...	...	+	+	+	+	+	...	...	...	...	...	...	...	...	...	...	..	...	...	...	...	+	+	+
Sartorius	...	...	...	...	...	...	+	..	+	+	...	...	...	...	...	...	...	...	...	...	...	...	+	...	+
Gluteus maximus ant. portion	...	...	...	...	...	...	...	...	0	0	...	...	...	...	...	...	...	...	...	...	...	...	0	...	0
Gluteus maximus post. portion	...	...	...	...	...	...	...	...	0	0	...	...	...	...	...	...	...	...	...	...	...	...	0	0	0
Tensor fasc. fem.	...	...	+	+	+	+	...	...	+	+	...	...	...	...	...	...	...	...	...	...	...	...	0	+	+
Gluteus medius	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	0	...	0
Gluteus minimus	...	...	...	...	...	...	...	...	+	+	...	...	...	...	...	...	...	..	...	...	...	...	...	...	+
Rectus femoris	...	...	...	...	...	...	...	...	...	...	...	...	...	...	..	...	...	...	...	...	...	...	...	...	+
Vastus lateralis	–	–	–	...	–	–	–	–	–	...	–	–	–	–	–	–	–	–	–	–	–	–	–	...	–
Vastus medialis	–	–	...	–	–	–	–	–	–	...	–	–	–	–	–	–	–	–	–	–	–	–	–	...	–
Crureus	–	–	–	–	...	...	–	–	–	...	–	–	–	–	–	–	–	–	–	–	–	–	–	...	–
Pectineus	...	...	...	...	...	...	...	...	+?	...	...	...	...	...	...	...	...	...	...	...	...	...	+	...	...
Adductor minor	...	...	...	...	...	...	...	...	–	...	...	...	...	...	...	...	...	...	...	...	...	...	0	–	–
Adductor magnus	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	0	...	part –
Gracilis	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	0	+	...
Semitendinosus	+	+	+	+	+	+	+	...	+	+	+	...	+	...	...	...	+	+	...	...	+	+	...	+	+
Semimembranosus	...	–	–	–	...	...	...	...	–	...	...	...	...	...	...	...	...	–	...	...	...	...	...	–	–
Biceps fem. ant. part	...	–	–	–	...	...	...	...	–	...	...	...	...	...	...	...	...	...	...	...	...	...	...	–	–
,, ,, post. part	+	+	+	+	+	+	...	...	+	...	...	...	+[1]	...	...	...	...	...	...	...	...	...	...	+	+
Tibialis anticus	+	+	+	+	+	+	late +	late +	* +	+	+	+	+	+	+	+	...	+	+	...	+	+	* +	+	+
Extensor longus digitorum	* +	...	+	+	+	...	..	...	...	+	...	...	...	...	...	...	...	+	+	...	+	...	...	...	+
Peroneus longus	...	...	+	+	...	...	...	...	...	...	...	...	...	...	...	...	0	...	...	...	* +	...	...	...	+
,, brevis	...	...	...	...	...	...	...	...	0	...	...	...	...	...	...	...	0	0	...	...	0	...	0	...	...
,, tertius	...	...	...	...	...	...	...	...	0	...	...	...	...	...	...	...	0	0	...	...	0	...	0	...	...
Gastrocnemius	–	–	–	–	–	–	...	...	–	...	...	...	...	–	...	...	–	–	...	–	...	...	–	–	–
Soleus	–	–	–	–	–	–	...	...	–	...	...	...	...	–	...	...	...	...	...	–	...	...	–	–	–
Tibialis posticus	...	...	...	...	...	...	...	...	0	...	...	...	...	...	...	...	...	...	...	...	...	...	0	0	0
Tenuissimus	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	0	+	+
Quadratus femoris	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	–	–

Muscle nerves

1 N. of sartorius medialis ...
2 ,, ,, lateralis ...
3 ,, vastus medialis ...
4 ,, ,, lateralis ...
5 ,, crureus ...
6 ,, rectus femoris ...
7 Superior gluteal ...
8 Inferior gluteal ...
9 N. of gracilis ...
10 ,, adductors ...
11 ,, semimembranosus ...
12 ,, semitendinosus ...
13 ,, biceps femoris ...
14 ,, extensor longus digit ...
15 ,, ,, brevis ,, ...
16 ,, peroneus longus ...
17 ,, gastrocnemius med. ...
18 ,, ,, lat. ...
19 ,, soleus ...
20 ,, tibialis anticus ...
21 ,, flexor perforans ...
22 ,, tibialis posticus ...
23 ,, hamstring muscles ...
24 ,, vastocrureus ...
25 Obturator nerve ...

* means contraction observed was quite weak.

[1] afferent nerve was a twig to anterior biceps femoris.

TABLE V.

Name of muscle	1	2	3	4	5	6	7	8	9
Psoas parvus	+	+	...	...	...	+	+	+	...
Psoas magnus	+	...	+	+	+	+	+	+	...
Sartorius	+	+	+	+	...	+	+	+	...
Gluteus max. ant. part ...	0	0	0	0	...	0	0	0	0
,, ,, post. part ...	0	0	0	0	...	0	0	0	...
Tensor fasciæ femoris long.	+	+	+	+	+	0*	0	+	0
,, ,, ,, brevis	+	+	+	+	...	...	0	+	0
Gluteus medius	0	0	0	0	...	0	0	0	...
Gluteus minimus ...	+	+	+	+	+	+	+	+	...
Rectus femoris	+	...	...	...	...	...	...	+	...
Vastus lateralis	–	–	–	–	–	–	–	...	–
Vastus medialis	-	–	–	–	–	–	–	...	–
Crureus...	–	–	–	–	–	–	–	...	–
Pectineus	+	+?	+	+	...	0	0	...	...
Adductor minor	...	...	–	–	...	–	–	...	...
Adductor magnus ...	...	...	–	–	...	-	...	...	...
Gracilis	+	...	+	+	...	+	+	...	...
Semitendinosus	+	+	+	+	+	+	+	+	...
Semimembranosus ...	–	–	–	...	...	–	...	–	...
Biceps femoris ant. part ...	–	–	–	...	...	–	...	–	...
,, ,, post. part ...	+	+	+	+	+	+	+	+	...
Tibialis anticus	+	+	+	+	+	+	+	...	+
Extensor longus digitor ...	+	+	+	+	+	+	+	...	...
Tenuissimus	+	+	+	...	...	+	...	...	...
Quadratus femoris ...	...	–	–	–	...	...	...	...	...
Peroneus longus	+	+	+	+	+	+	+	...	...
,, brevis	0	0	0	0	0	?	...	...	...
,, tertius	0	0	0	0	0	0	0	...	...
Gastrocnemius	–	–	–	–	–	–	–	...	–
Soleus	–	–	–	–	–	–	–	...	–
Flexor longus digitorum ...	...	...	late +	late +	...	...	...	...	...
Tibialis posticus	...	0	0	0	...	...	...	...	...
Extensor brevis digitorum	...	+	...	0	...	+	+	...	...

Name of nerve-trunk

1 N. femoralis ... ...
2 N. obturatorius ... ...
3 N. peroneus ... ...
4 N. musculo-cutaneus of peroneus
5 N. tibialis anterior ,,
6 N. popliteus ... ...
7 N. plantaris medialis (lateralis gives same result)
8 N. ischiadicus ... ...
9 N. pudicus ... ...

0* means does not contract usually, sometimes does.

Under n. peroneus and n. popliteus are included results obtained from branches of these trunks.

TABLE VI[1].

Cat: bulbar transection; movements of limb provoked by exciting the separate afferent roots.

Right IX post-thoracic root	**Flexion of right knee.**
,, VIII ,, ,,	**,, ,, knee, hip and ankle.**
,, VII ,, ,,	**,, ,, knee, hip and ankle.**
,, VI ,, ,,	**,, ,, knee, hip and ankle.**
,, V ,, ,,	**,, ,, knee and hip.**
,, IV ,, ,,	**,, ,, hip and knee.**
,, III ,, ,,	**,, ,, hip.**
,, II ,, ,,	**,, ,, hip.**

Monkey (*Macacus rhesus*): bulbar transection.

Right IX post-thoracic root	**Flexion of right knee (slight).**
,, VIII ,, ,,	**,, ,, knee.**
,, VII ,, ,,	**,, ,, knee and ankle.**
,, VI ,, ,,	**,, ,, knee, ankle, hip.**
,, V ,, ,,	**,, ,, knee, hip and ankle.**
,, IV ,, ,,	**,, ,, hip, knee and ankle.**
,, III ,, ,,	**,, ,, hip and knee.**
,, II ,, ,,	**,, ,, hip.**
,, I ,, ,,	**,, ,, hip (slight).**

(v) Taken together the results listed in the above Tables can be summarised in the following condensed statements.

1. The afferent nerves of the limb—apart from *n. lumboinguinalis (genitocrural), n. cutaneus clunis* and *n. pudendus inferior*, which are from groin, perineum and buttock rather than from limb proper—all excite a limb reflex of the same type characterised by flexion at hip, knee and ankle. This reflex may be called the *flexion-reflex of the limb*, understanding by that a type-reflex, *i.e.* a group of reflexes of almost identical form which when concurrent combine in harmonious action on the same final common paths[2].

2. Though the individual reflex obtainable from any one of the various afferents of the limb always conforms fully to this type-reflex, and is a "flexion-reflex," it is not of necessity wholly like that produced from some among the other afferents of the limb which also provoke the flexion-reflex. That is the individual reflexes as provoked from nerve to nerve differ one from another to some extent though all conform to the type "flexion-reflex." The differences consist chiefly in

---

[1] **Sherrington, *Phil. Trans. Roy. Soc.* B. 158. As regards monkey and dog cf. also Page May, *Phil. Trans. Roy. Soc.* B. 157.**

[2] **Sherrington. *Integrative Action of the Nervous System*, p. 114.**

the reflex contraction excited by one nerve extending less to certain muscles of the flexor group than it does when excited from some other nerve. The contraction in all cases is limited to the flexor group but each afferent does not in all cases cause contraction of the entire group, and the muscles omitted are not entirely the same for one nerve as for another. Difference in detail of effect are thus detectible between different afferent nerves. Thus, *semitendinosus* contracts more powerfully in reflex response to the cutaneous foot nerves than to branches of external cutaneous or internal saphenous nerves; *tensor fasciae femoris* contracts little or not at all from the plantar nerves but strongly from internal saphenous or external cutaneous. Such differences seem to reach their maximum in the divergence between external cutaneus and hamstring nerve. The former causes reflex contraction in *tensor fasciæ femoris, pectineus, rectus femoris,* and *gluteus minimus* and these muscles the latter nerve does not reflexly reach; and the latter nerve causes contraction in *tenuissimus* and *biceps femoris' posterior part* while the former nerve does not; both however alike cause contraction of *psoas, sartorius, tibialis anticus* and *semitendinosus.* The difference between the segmental origins of *n. cutaneus externus* and hamstring nerve is greater than between almost any other of the limb nerves. Similarly skin-points whose nerve-supplies lie segmentally distant one from another tend to exhibit flexion-reflexes less closely similar than do skin-points segmentally near together. Thus there comes to be some accentuation of movement at this joint or that according as the skin-point stimulated lies in this limb-region or that. Excitation of outer edge of planta (spinal monkey) causes together with the flexion at ankle some eversion of foot; but excitation of inner edge of planta gives some inversion of foot along with the ankle flexion.

3. Apart from these differences in detail the reflex provocable from the limb is the same reflex from whatsoever part of the limb it is produced (by the stimuli mentioned above). The whole limb therefore except for some part of its attached base forms one receptive field whence the reflex provocable is the flexion-reflex, and this field is not merely skin-deep but includes muscles, joints, fasciæ, and other deep structures of the limb.

4. In the flexion-reflex the limb muscles excited to contract are broadly speaking flexors (*v. infr.* p. 45). They are so far as observed: (Fig. 1).

5. In certain of the limb muscles the reflex produces not contraction but relaxation, by central inhibition. These muscles are: (Fig. 1).

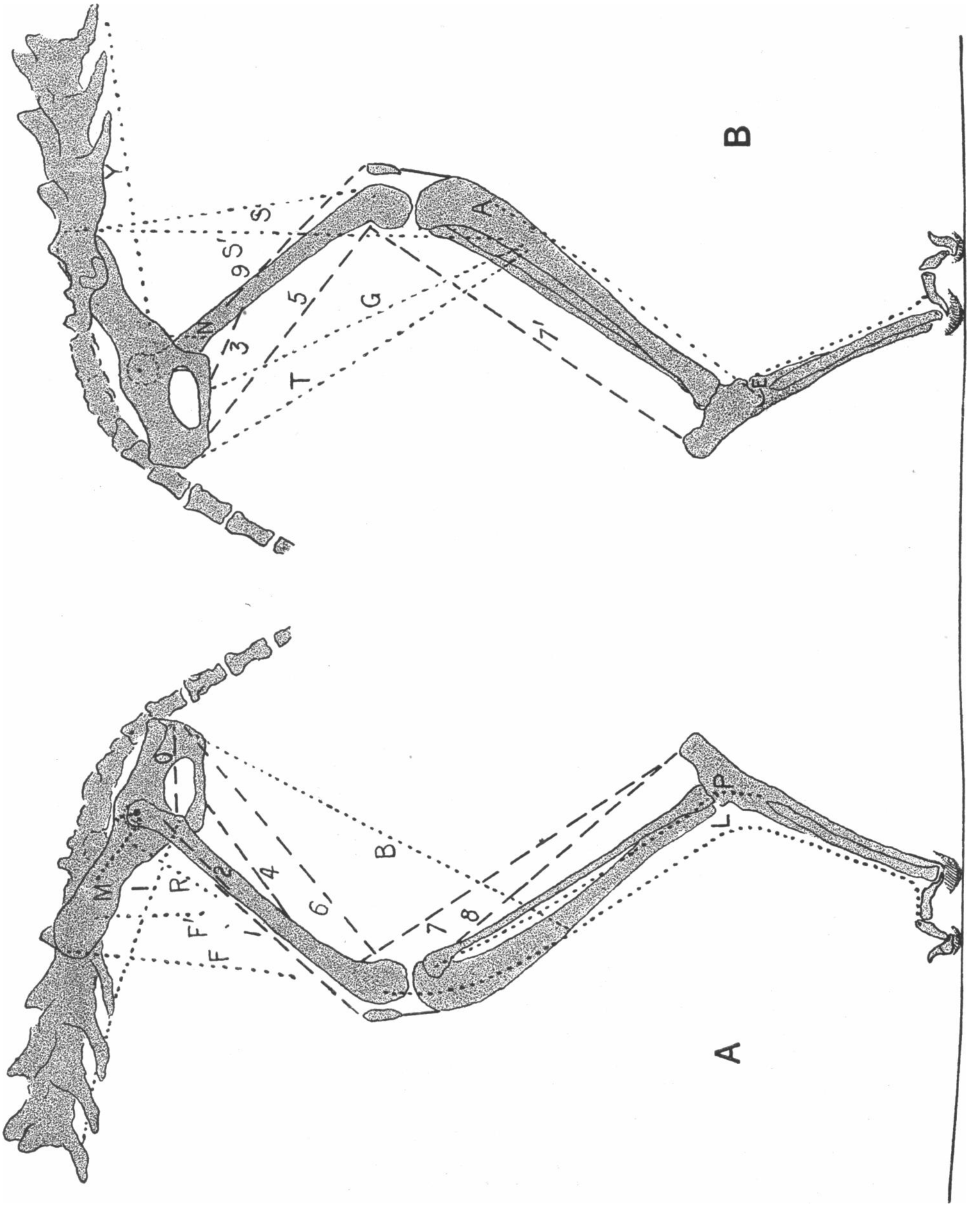

Fig. 1.

Fig. 1. Muscles ascertained by direct analysis to be engaged in the flexion-reflex of hind-limb (cat).

A. Lateral aspect of limb; B. Medial aspect.

Muscles engaged in construction (dotted lines).

A. Tibialis anticus
B. Biceps femoris posterior
E. Extensor brevis digitorum
F. Tensor fasciæ femoris longus, *F′* brevis.
G. Gracilis
I. Psoas magnus
L. Extensor longus digitorum
M. Gluteus minimus (a second dotted line indicates its posterior part).
N. Pectineus
P. Peroneus longus
R. Rectus femoris
S. Sartorius, lateral band, *S′* medial band.
T. Semitendinosus
Y. Psoas parvus

Muscles relaxed by reflex inhibition (interrupted lines).

1. Crureus
2. Vastus lateralis
3. Adductor minor
4. Adductor major (in part)
5. Semimembranosus
6. Biceps femoris anterior
7. Gastrocnemius ext. 7′ int.
8. Soleus
9. Vastus medialis
0. Quadratus femoris

(This figure serves also to illustrate the crossed extension-reflex (p. 56). In that reflex the muscles marked with numerals contract, and *A*, *B*, *S*, *T* of the alphabet-group are relaxed by inhibition—and none of the alphabet group contract.)

TABLE VII.

Psoas parvus.
Iliopsoas (psoas magnus).
Tensor fasciæ femoris longus.
,, ,, ,, brevis.
Sartorius medial band.
lateral band (? distal part).
Rectus femoris.
Gracilis.
Adductor magnus (a small part of).
Pectineus.
Gluteus minimus.
Tenuissimus.
Posterior part of biceps femoris.
Semitendinosus.
Tibialis anticus.
Peroneus longus.
Extensor longus digitorum.
Extensor brevis digitorum.

TABLE VIII.

Semimembranosus (both parts).
Biceps femoris (anterior part).
Vastus medialis.
Crureus.
Vastus lateralis.
Adductor magnus (in part).
Quadratus femoris.
Gastrocnemius and plantaris.
Soleus.
Adductor minor.

The muscles which the reflex relaxes by inhibition are broadly speaking extensors and (*v. infra*, p. 57) therefore antagonistic to those which it excites.

6. It is of interest for study of coordination to note how in this reflex the neural taxis deals with the muscles of the limb. For this some remarks on the action of the muscles at the limb-joints may be prefaced.

To examine their action in the reflex the following plan has been followed. The decerebrate preparation has been supported in the erect posture, *i.e.* spine horizontal and limbs vertical. For this two clamps are fastened one to the spinous process of second sacral vertebra the other to the spinous process of seventh cervical. The muscle to be examined was left intact but all other muscles of both hind-limbs were paralysed by nerve-section. The hind-limb whose movement in result of the muscle's contraction was to be studied was shaved and certain points on it marked with ink or white paint. These points were (1) superior angle of the iliac crest, (2) tuberosity of ischium, (3) great trochanter, (4) the middle of outer condyle of femur, (5) patella, (6) external malleolus. The limb was then placed in the case of muscles contracting in the flexion-reflex either in fairly full extension at hip, knee and ankle; or simply hanging down the plantar surface of its digits just resting on the table. The opposite hind-limb was so placed as to rest with its foot on the table; the fore-limbs also. In this posture the preparation was photographed, a centimeter scale and plumb-line being also included. The reflex was then provoked in various strengths by faradisation of an afferent nerve for 5 sec. Directly the limb assumed a steady pose under the reflex action the preparation was again photographed. The photographs thus obtained were compared. The inclination of the long axis of femur to a line drawn between the points marked in ilium and ischium is used as ilio-ischial femoral angle. The action of the contraction of the muscles which are inhibited in the flexion reflex was included in the examination. To throw these muscles into reflex contraction the crossed extension reflex (*v. infra*, p. 56) was employed.

Psoas parvus: the movement produced in the limb by this muscle is a slight flexion of pelvis on the lumbo-sacral spinal column.

Psoas magnus: produces flexion at hip and marked external rotation of thigh. Initial position: ilio-ischial femoral angle 96°, femoro-tibial 127°, tibio-tarsal 143°; with weak reflex by 40 units Kronecker scale became ilio-ischial femoral angle 85°, femoro-tibial 120°, tibiotarsal, 143°; with strong reflex by 70 units K became ilio-ischial femoral angle 80°, femoro-tibial 115°, tibio-tarsal 143°.

Sartorius: in the dog this muscle consists of two distinct bands often separate throughout their length by a centimeter's space. The lateral band runs along the mid-front of the thigh to the patella, the median lies along the medial aspect. Separate branches of *n. femoralis* pass to each of these divisions. Cat's sartorius has these bands conjoined, but in the cat the median part and the lateral part are likewise supplied by separable nerves, that for median part sometimes coming not from n. femoralis direct but from n. saphenus in thigh. In both cat and dog both parts of sartorius contract in the flexion-reflex but it is questionable whether the lower part of lateral band does, and this part certainly contracts distinctly in the crossed extension reflex. With a fairly strong flexion-reflex sartorius reduced ilio-ischial femoral angle from an angle of 112° to one of 50°, femoral tibial angle from an initial 140° to an angle of 110°. The tibio-tarsal angle it did not obviously alter. The effect of the muscle in the flexion-reflex is therefore to flex hip and knee (cf. Fig. 2).

Tensor fasciæ femoris: this muscle consists both in dog and cat of two portions, an anterior longer (longus) associated with sartorius at its origin; a posterior (brevis) which at its hinder edge abuts on anterior portion of gluteus maximus. This latter part is very amply developed in the rabbit. In a moderately strong reflex the *longus* portion, *brevis* having been detached, lessened ilio-ischial femoral angle to an angle of 70° from an initial posture of 98°. Brevis flexes the hip less and somewhat abducts the thigh.

Semitendinosus: with a fairly strong reflex ilio-ischial femoral angle was seen to be increased from an initial posture of 108° to an angle of 118°, the femoro-tibial from an initial 110° was reduced to an angle of 65°. With a weak reflex the ilio-ischial femoral angle remained not obviously altered from an initial angle of 108°, while the femoro-tibial was contracted from an initial opening of 110° to an angle of 75°. With a still weaker reflex ilio-ischial angle was altered from an initial 108° to an angle of 105°, femoro-tibial angle changing from an initial 110° to an aperture of 70°. The full action may therefore be described as flexion at knee and extension at hip (cf. Fig. 2); and the muscle slightly tilts downward the posterior end of its side of the pelvis.

Biceps femoris: under this name are included two antagonistic muscles. The nerve supply consists of two divisions which accord with the twofold functional action. One division innervates the part of the muscle inserted into tibia; this part of the muscle will be called here biceps femoris posterior; it flexes knee and extends hip (cf. Fig. 2); it is the only part of the muscle which the flexion-reflex causes to contract. The other part of the muscle is inserted higher than bic. fem. posterior; it extends the hip; it is inhibited in the flexion-reflex, but contracts in the crossed extension reflex; it will be called here biceps femoris anterior.

Sartorius, semitendinosus and biceps femoris posterior combined: with a fairly strong reflex an initial position of ilio-ischial femoral angle 108°, femoro-tibial angle 110° becomes altered to a position of ilio-ischial femoral angle 60°, femoro-tibial angle 50°. With a weaker reflex the position assumed was ilio-ischial femoral angle 70°, femoro-tibial angle 65°. Sartorius as a hip-flexor therefore overcame combined actions of semitendinosus and biceps femoris posterior as hip extensors (cf. Fig. 2) both in strong and weak reflexes.

Gracilis: with a weak reflex changed femoro-tibial angle from an initial position of 125° to an angle of 115°; with a strong reflex to an angle of 105°. It produced adduction of thigh as well as flexion at knee.

Tibialis anticus: with weak reflexes this muscle was observed to flex ankle without obvious flexion of knee, for instance initial position being tibio-tarsal angle 115° under the weight of the limb free and 110° when toe-pads rested on table the angle was reduced to 105°. With moderate reflexes the tibio-tarsal angle became 93°, and there was reduction of femoro-tibial angle from an initial 120° (limb free) or 118° (toes on table) to an angle of 112°. The attachments of gastrocnemius and all other muscles were intact and when the ankle is flexed gastrocnemius tends to flex knee. The Fischer effect (cf. *infra*, p. 50) would also be of influence. Tibialis anticus also inverts the foot.

Extensor longus digitorum: a strong reflex with the limb hanging free altered an initial position of ilio-ischial femoral angle 90°, femoro-tibial 132°, tibio-tarsal 125° to a position of ilio-ischial femoral angle 86°, femoro-tibial 110°, tibio-tarsal 76°. The above was with all other muscles intact; with tendo-Achillis cut the flexion at knee is less and there is no obvious flexion at hip. The upper tendon of extensor longus digitorum crosses the knee, and flexion of knee causes slight extension of toes if the ankle be not at the same time much dorso-flexed. If ankle be free to flex the knee flexors by means of extensor longus digitorum dorso-flex ankle but the toes are not extended, or are even flexed by passive pull of flexor longus digitorum. Extensor longus digitorum if ankle be not free to flex extends toes; if ankle be free it can flex ankle and extend toes; it also slightly separates the toes.

Peroneus longus: everts the foot. Its tendon crosses ankle very nearly if not exactly in the axis of rotation of the joint. If ankle be strongly flexed this muscle slightly supports that flexion.

Tibialis anticus, peroneus longus and tensor fasciæ femoris combined: with a moderately strong reflex an initial posture of ilio-ischial femoral angle 110°, femoro-tibial 120°, tibio-tarsal 115° was changed to ilio-ischial femoral 65°, femoro-tibial 110° and tibio-tarsal 95°. There was also slight abduction of thigh, and the marked flexion at ankle was free from inversion or eversion of foot.

Semimembranosus: starting with limb at following angles, ilio-ischial femoral 85°, femoro-tibial 112°, tibio-tarsal 125° a fairly strong reflex changed these to ilio-ischial femoral 132°, femoro-tibial 145°, tibio-tarsal 135°. Some inward rotation of limb accompanied the extension. As felt by the hand the extension of knee and ankle was powerful as well as that of hip. The muscle consists of two parts, both of which so far as I have seen react in the same way in the flexion-reflex.

Biceps femoris anterior (*v. sup.* p. 43): both in moderate and strong reflexes the change in the position of the limb was closely similar to that produced by semimembranosus, but was accompanied by some outward rotation of thigh and limb.

Vasti and crureus taken together: with the limb suspended the whole limb straightens under the reflex action of this group; thus with initial posture of ilio-ischial femoral angle 92°, femoro-tibial 105°, tibio-tarsal 122°, the posture became ilio-ischial femoral angle 102, femoro-tibial 157°, tibio-tarsal 140°. The extension at ankle as well as knee was strong, but that at hip did not overcome resistance so strongly. With the foot resting on the ground under the animal's weight similar extension of knee, ankle and hip occurred lifting the hindquarters forwards and upwards.

Gastrocnemius soleus (*cat*) *and plantaris*: with the limb hanging free of the ground a weak reflex produced extension of ankle without obvious change of posture at knee, a fairly strong reflex produces fuller extension at ankle with distinct flexion at knee; in this latter case the initial posture being ilio-ischial femoral angle 85, femoro-tibial 120° and tibio-tarsal 125° these angles became femoro-tibial 110° and tibio-tarsal 152°, the ilio-ischial femoral not obviously changing. When foot rested on table with the weight of the body on it a weak reflex changed an initial posture of ilio-ischial femoral angle 80°, femoro-tibial 114°, tibio-tarsal 105° to ilio-ischial femoral 78° and tibio-tarsal 120°, femoro-tibial remaining 114°; a strong reflex brought ilio-ischial femoral angle to 70° and tibio-tarsal to 140°, again without change in the femoro-tibial (114°). The ankle as it extended rolled forward over the plantar pads and the knee was pushed upward flexing the hip by raising lower end of femur.

Soleus is wanting in the dog[1]; in the cat it is well developed.

Flexor longus digitorum: powerfully flexes the toes, but appears neither to extend nor flex the ankle. Its tendon passes the ankle-joint very closely to, or exactly in, the line of axis of the joint's rotation.

Rectus femoris and part of vasto-crureus between rectus and knee: the first branch from n. femoralis below nerve of sartorius supplies rectus femoris and also a slip of vasto-crureus passing down from lower end of rectus to knee. When this branch is directly stimulated the limb being suspended freely the effect produced is distinct flexion at hip, with distinct extension at knee. When this branch alone of all the motor nerves in the limb remains intact stimulation of central end of ipsilateral peroneal nerve causes flexion at hip with slighter flexion at knee, while similar stimulation of contralateral peroneal causes extension at knee with slighter extension at hip.

Adductor minor: adducts thigh, and somewhat extends hip especially if hip be in a posture of flexion.

Adductor major, adducts thigh and extends hip.

---

[1] Cf. also H. Fischer (P. Grützner), *Pflüger's Archiv.* 125, p. 541. 1908.

Pectineus, adducts thigh: its relation to flexion of thigh seems to be that it flexes thigh if initial pose of thigh be extension.

Quadratus femoris: extends hip and rotates thigh outward.

Gluteus minimus: abducts thigh and by its anterior and ventral parts flexes hip as well.

Analysis of the muscular effect of the flexion-reflex shows this reaction to exhibit certain features in its coordinate handling of the musculature. Coordination is a wide term and embraces the management of muscles both in their simultaneous and successive employment. The simultaneous coordination of muscles in a reflex effect is conveniently spoken of as the "*reflex-figure*[1]." The form assumed by the reflex figure in the case of the flexion-reflex of the hind limb exhibits the following features.

6. i. The reflex does not in many cases treat as entities muscles regarded as such by anatomical nomenclature. Thus the reflex throws into contraction that part of biceps femoris, *i.e.* posterior part, which is inserted below the knee while it inhibits that part, *i.e.* anterior part, which is inserted above knee. The latter portion is an extensor of hip the former flexes knee. Again, the reflex in dealing with quadriceps extensor causes that part which flexes hip (rectus femoris) to contract while it inhibits that part (vasto-crureus) which extends knee[2]. Similarly in fore-limb, the flexion-reflex inhibits the humeral heads of triceps and at the same time excites to contraction the scapular head: this last is a flexor at shoulder, the former are extensors of elbow. Again, in the sartorius its medial band and the upper part of its lateral band contract in the reflex but the lower part of the lateral band does not appear to contract. This latter part tends to extend knee, the rest of the muscle flexes knee and hip. In regard to quadriceps extensor cruris and triceps brachii the taxis shown in the reflex is similar to that observed by H. Hering and myself[3] under cortical stimulation; we did not particularly examine the other muscles here mentioned.

6. ii. Those muscles which the reflex excites to contract and those which by inhibition it relaxes or restrains from contraction form two functional groups broadly describable as flexor and extensor respectively. Thus, there are excited by the reflex, psoas magnus, sartorius, gluteus mimimus, tensor fasciæ femoris and rectus femoris, flexors at hip; and inhibited are semimembranosus, biceps femoris,

---

[1] *Integrative Action of the Nervous System*, p. 164.

[2] Cf. for independence of rectus from rest of quadriceps in man, Beevor, *Ergebn. d. Physiolog.* Jahrg. 8. 1909.

[3] *Arch. f. d. ges. Physiol.* LXVIII. 1897; *Proc. Roy. Soc.* LXII. 1897.

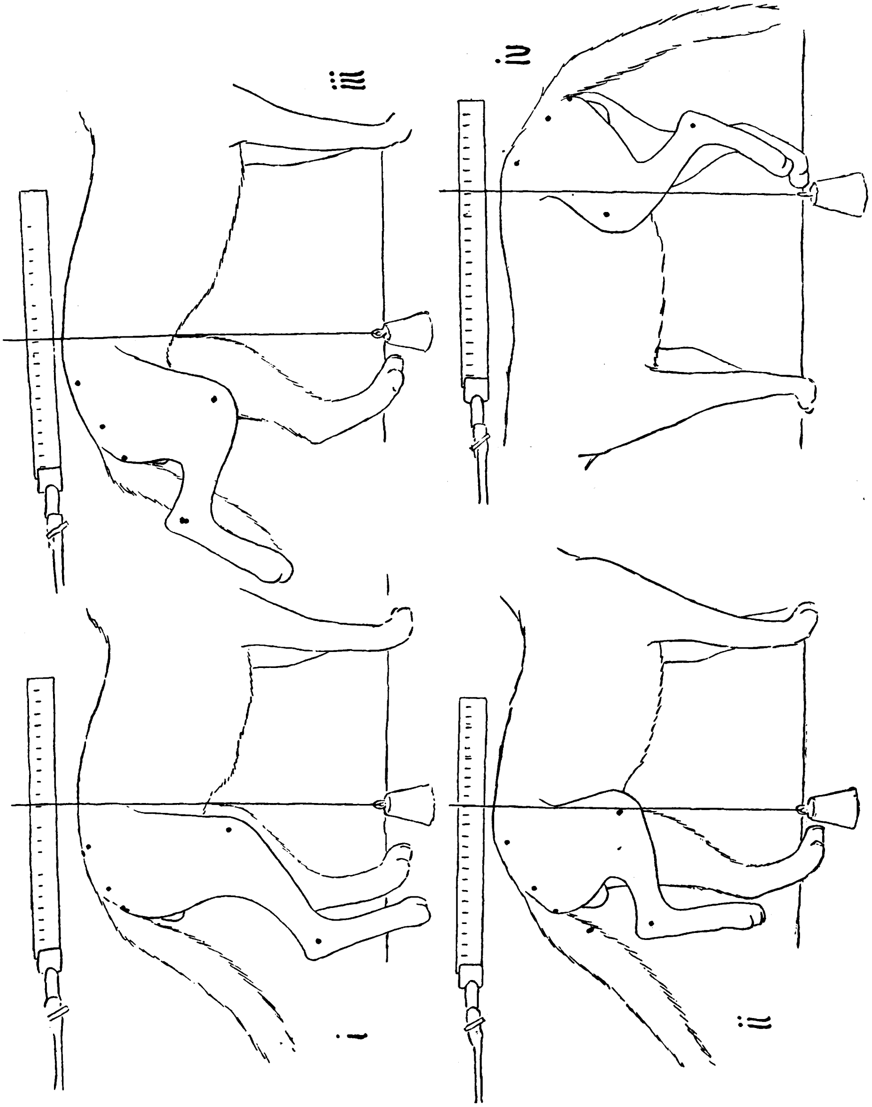

Fig. 2. Pseudoantagonists exhibit identical innervation not reciprocal innervation. Outlines from photographs. The hind limbs shaved.

i. initial pose of limb before reflex; ii. reflex contraction of sartorius, biceps femoris posterior and semitendinosus; iii. of biceps femoris posterior and semitendinosus; iv. of sartorius: all are photographs taken in succession from the same preparation (decerebrate). The five dots on the limb marked tuber ischii, great trochanter, anterior outer angle of ilium, a point selected in outer condyle, and the external malleolus. Centimetre scale and plumb line are included. All nerves in both limbs severed except those of sartorius, biceps femoris posterior and semitendinosus of right side, and of sartorius of left side. Stimulus was faradisation of central end of cut post-tibial of right side for ii. and iii., of left for iv.; induction circuit remained unaltered throughout. Each stimulation lasted 4 secs. and the photographs were taken when the limb moved by the reflex had taken up its reflex posture fully and was steady. Starting from resting posture (i) the reflex contraction of semitendinosus biceps femoris posterior and sartorius combined flexed hip and knee ii.; nerve of right sartorius was then cut, and the reflex repeated (iii), the result being slightly less flexion at knee and at hip extension instead of flexion. For flexion iv. left post-tibial nerve was stimulated and reflex contraction of sartorius gave flexion at hip greater than in ii. and flexion at knee less than in ii. Sartorius evidently by its reflex contraction along with biceps femoris posterior and semitendinosus suppresses their action at hip and enhances their action at knee, *i.e.* these pseudoantagonists under identical innervation act harmoniously and with mutual advantage as flexors although two of them are as judged by their attachments extensors at hip.

adductor minor, and quadratus femoris, extensors of hip. Excited are semitendinosus, biceps femoris posterior, sartorius, and gracilis, flexors at knee; inhibited are vastus medialis, vastus lateralis and crureus, extensors at knee. Excited are tibialis anticus and extensor longus digitorum flexors at ankle; inhibited are gastrocnemius, plantaris and soleus extensors at ankle. It is clear that reciprocal innervation of antagonistic muscles is a principle observed in the nervous taxis of the reflex. The reflex application of the principle seems especially to muscular antagonism such that were both muscles to contract at the same time the main action of one muscle would impede the main action of the other.

6. iii. But among the "flexor" group excited by the reflex to contract, are semitendinosus, biceps femoris posterior, and gracilis, muscles which though flexors of knee are extensors of hip. These are therefore to some extent antagonists of the hip flexors, yet the reflex throws them into contraction along with the hip flexors. Their possible extension-effect at hip is completely prevented during the reflex by the concomitant contraction of the hip flexors. This is a case comparable with the well-known concomitance of contraction of the long flexor of the fingers and the extensors of the wrist. In the execution of the grasp contraction of the extensors of the wrist accompanies contraction of flexor longus digitorum (Duchenne[1], H. E. Hering[2], Beevor[3]). This latter muscle besides flexing fingers flexes wrist; but its action at wrist is prevented by concurrent contraction of extensors of wrist. The action of flexor longus digitorum is less at wrist than fingers; its effect

---

[1] *Physiologie des Mouvements*, p. 154. Paris, 1867.

[2] *Arch. für d. ges. Physiol.* LXX. p. 559. 1898.

[3] Beevor. Croonian Lectures, *Roy. Coll. of Physicians*, p. 11. London, 1904.

therefore which is suppressed by an antagonist is its subsidiary one; and that suppression increases its other and main effect, namely flexion of fingers. So also with semitendinosus, biceps femoris posterior, and gracilis. Their main effect is flexion at knee, their subsidiary extension at hip. The suppression of this latter by the hip-flexors enhances the main effect, flexion at knee. And it was experimentally shown (*v. supra*, p. 43) that in the actual reflex the contraction of merely one of the hip flexors, *i.e.* sartorius, is perfectly able to produce this suppression and thus while flexing hip and knee by its own direct action indirectly reinforces that action on knee by means of its pseudo-antagonists biceps femoris posterior and semitendinosus.

Again, extensor longus digitorum is by virtue of its femoral tendon a slight extensor of knee as well as a flexor of ankle and extensor of toes. By concurrent contraction of the great knee flexors the reflex prevents extensor longus digitorum from extending knee, and by flexing knee in its despite enhances its action as an ankle-flexor and toe-extensor.

Similarly with the lateral band of sartorius. This band flexes hip but tends to extend knee. The reflex by concurrent contraction of the strong knee flexors prevents the band from extending knee and turns its whole power into flexing hip.

These cases may be summarised thus. A muscle A acts at a joint α and with less ample effect at another joint β; a muscle B opposes A's action at β but by doing so exalts it at α. The co-ordinative relation observed between the two in neural taxis employing both is not reciprocal innervation—the one is not inhibited when the other is excited, but both are excited together or inhibited together. In other words the taxis treats the two muscles not as antagonists but as adjuvants. And this holds whether A's action at the two joints is in similar sense, *e.g.* flexor longus digitorum at fingers and wrist, or in opposite senses, *e.g.* semitendinosus flexing at knee, extending at hip.

6. iv. It is evident that the reflex uses certain muscles as protagonists (*v. inf.* p. 110, Winslow's[1] 'principal movers,' Beevor's[2] 'prime movers') and certain as fixators (Beevor's[3] 'synergics,' H. E. Hering's[4] pseudo-antagonists) and that it commonly employs at one and the same time one and the same muscle in both these capacities. Thus it uses the hip-flexors not only to flex hip but at the

---

[1] Douglas' transl. I. 3. 1756.

[2] Croonian Lectures, *Ibid.* p. 71. 1904.

[3] *Ibid.*

[4] *Zeitschr. f. Heilkunde*, XVI. 1895.

same time to serve as fixation muscles for knee-flexors which would extend hip were the hip not kept from extending. An experimental proof of this was furnished above (p. 43). Similarly the reflex employs semitendinosus, biceps femoris posterior and gracilis as protagonists to flex knee and at the same time also as fixation muscles for certain flexors of hip, namely rectus femoris and lateral band of sartorius, which were the knee not kept flexed would extend it and thereby lose part of their efficiency for flexing hip. In these actions the reflex employs flexors which are prime movers of a joint as fixation muscles at that joint for flexors which act as prime movers at another joint. In the reflex taxis therefore flexors are used as fixators for flexors.

6. v. The concurrent contraction of flexors with flexors so that prime movers serve also as fixators is an extension of a principle well shown by the musculature of the frog's hind-limb and there studied particularly by Lombard and Abbott[1]. Flexors of one joint even when the flexors of other joints of the limb are inactive flex those other joints as well as their own. Thus in Lombard's model the frog's hip flexor when it flexes that joint flexes also knee and ankle. This results from the mere mechanical attachments of the knee and ankle flexors. Similarly in cat and dog contraction of tibialis anticus or extensor longus digitorum not only flexes ankle but flexes knee, in virtue of the attachments of gastrocnemius. By flexing ankle it draws down the heel so that the gastrocnemius even when toneless and paralysed by nerve-section flexes the knee in virtue of its upper insertion at femur.

So again in cat and dog contraction of a hip-flexor produces in consequence of the attachments of semitendinosus and biceps femoris posterior flexion of knee even when these muscles have been paralysed by nerve-section. Now, in the actual reflex these muscles enter into contraction along with the hip-flexors; the taxis of the reflex therefore uses and extends the principle indicated in the mere non-contractile mechanics of the part.

Again, extensor longus digitorum by virtue of its femoral tendon comes to flex ankle when knee flexes. The knee-flexor, *e.g.* semitendinosus, therefore flexes ankle by acting through extensor longus digitorum, even when that muscle is completely passive, paralysed by nerve-section. In the actual reflex however extensor longus digitorum contracts concurrently with knee-flexor; in this way the reflex not only uses but enhances the ability of the knee flexor to flex ankle as well. The non-vital mechanical behaviour of the limb and the nervous taxis

---

[1] *Amer. Journ. of Physiol.* xx. p. 1. 1907.

of its musculature in reflex action thus economically harmonise in their effects and mutually reinforce each other's action.

6. vi. In the above cases the muscles implicated are double-joint muscles, but a muscle which passes across one joint only (a single-joint muscle) may yet effect movements in neighbouring joints, if the point of its origin as well as that of its insertion be free to move. The muscle's contraction acts of course on both these points. This subject has been investigated by Fischer[1] with great care in dead preparations. He has shown that in man brachialis for instance even when the influence of gravity is eliminated not only flexes elbow but flexes shoulder as well. By flexing shoulder I mean movement reducing the angle, already less than 180° between humerus and scapula. Conversely the single-joint part of triceps passing from humerus to ulna not only extends elbow but extends shoulder-joint, *i.e.* opens the angle between humerus and scapula.

This principle is observed and enforced in the nervous taxis of the flexion-reflex. Reflex contraction of tibialis anticus not only flexes ankle but also knee; and in the full reflex with intact and active musculature this knee-flexion is reinforced by active contraction of the knee flexors. So likewise in the fore-limb (cat) the contraction of brachialis in the flexion-reflex of that limb, all other muscles being paralysed by nerve-section and resected from their insertions so as to obviate their passive pull, causes flexion not only of elbow but at shoulder, as Fischer[2] has shown in man. In my observations the limb hung pendent so that gravity was not excluded from the result, as it was in the observations of Fischer; my purpose aiming at application to the flexion-reflex in that pose of the limb in which the reflex occurs naturally. The nervous taxis of the reflex provides that Fischer's principle should take effect and not be opposed in the natural active movement of the limb. It relaxes by reflex inhibition muscles such as humeral heads of triceps and supraspinatus which would oppose it. In addition it reinforces it by throwing into contraction muscles which support it such as scapular head of triceps which is itself a flexor of shoulder.

Here again therefore the non-vital mechanical behaviour of the limb and the nervous taxis of its musculature in reflex action economically harmonise and mutually support each other's effects.

---

[1] *Beiträge zu einer Muskeldynamik*, p. 57, Leipzig. 1895, and *Mechanik d. Lebender Körper*. Leipzig. 1906. Cf. also H. E. Hering, *Pflüger's Arch.* LXV. 627. 1897.

[2] *Loc. cit.*

6. vii. There is a further class of cases in which the flexion-reflex causes concurrent contraction in muscles which partially counteract each other's effect. Thus the reflex concurrently excites biceps femoris posterior and semitendinosus. Both are flexors of knee and their action in that respect is so similar that they form twin flexors of that joint. But arising from practically the same point one descends to the outer side of knee the other to inner side of knee. The former acting by itself rotates the thigh and limb somewhat outward, the latter somewhat inward. When both are excited together by the reflex the knee is seen to be flexed without rotation of the limb. When the two muscles are used by the reflex each counteracts the other's tendency to rotate the limb. Ilio-psoas and tensor fasciæ femoris act harmoniously on hip in the flexion plane, but with antagonistic rotation components one outwards, one inwards. The reflex contracts them both together[1]. Again, tibialis anticus and peroneus longus are both thrown into contraction by the reflex. The former not only flexes ankle but inverts foot. The latter everts foot. When the two muscles, all others being excluded, are thrown into contraction by the reflex, the ankle is flexed but the foot is not, or very slightly, inverted or everted.

The muscles in their lengthwise arrangement along the limb show something of a general arrangement into twin bands, one alongt he medial side the other along the lateral aspect. Thus semitendinosus pairs on the medial aspect with biceps femoris posterior on the outer side, tibialis anticus with peroneus longus, medial band of sartorius with tensor fasciæ femoris, pectineus with gluteus minimus. These muscle pairs are concurrently excited to contract in the reflex action. Again, semimembranosus pairs on the medial aspect of the limb with biceps femoris anterior on the outer aspect, vastus medialis with vastus lateralis, inner division of gastrocnemius with outer division. These muscle pairs are concurrently relaxed by inhibition in the reflex action; and (*v. infra*, Sect. II. p. 56) are concurrently excited to contract in the crossed extension reflex. The main action of the components of these pairs is harmonious, yet each component has a collateral action—a side sag—which is antagonistic to that of the other component. Reciprocal innervation does not appear in the reflex taxis in regard to the mutual co-ordination of the components of a muscle pair of this kind. The reflex taxis does not avoid the exercise of their antagonistic collateral action; on the contrary it employs it. In the case of peroneus longus and tibialis anticus there is little harmonious action between them at

---

[1] Cf. in man, Duchenne, *Physiologie d. Mouvements.*

all, and the former seems used in the flexion-reflex chiefly to correct the side pull of the latter; hence it is perhaps that peroneus contracts in the reflex considerably less than does tibialis.

6. viii. Certain of the muscles which the reflex excites to contraction can in virtue of their attachments act as flexors at one joint and as extensors at another. Thus, the gastrocnemius is potentially a flexor of knee as well as an extensor of ankle. The limb reflex employs its contraction exclusively for extension and not for flexion; it is inhibited in the flexion reflex. Semitendinosus and biceps femoris posterior in virtue of their attachments can extend hip as well as flex knee. The limb reflex employs their contraction exclusively for flexion and not for extension. Rectus femoris is potentially a knee extensor as well as a hip flexor. The limb reflex treats it as though it were simply a hip flexor and uses it for flexion exclusively. In this sense these muscles may all be broadly grouped as flexors, *v. sup.* p. 45.

6. ix. The details of the participation of the adductor group in the flexion-reflex I have found difficult to observe. Pectineus contracts adductor minor undergoes inhibitory relaxation. My observations suggest that those parts of the adductor mass which flex hip as well as adduct contract in the reflex, and those parts which would extend hip as well as adduct do not contract and in part at least are relaxed by inhibition. The circumstance pointed out by Lombard[1] in his study of the frog's hip muscles that some lateral muscles, *e.g.* adductors, abductors, flex when the limb is in one position and extend when it is in another has to be reckoned with and perhaps introduces lack of apparent uniformity in the reflex results.

7. On certain muscles of the limb the reflex exerts so far as my observations go no influence either of excitation or inhibition. These muscles are gluteus maximus, gluteus medius, gluteus quartus, tibialis posticus, peroneus brevis and peroneus tertius.

8. The reflex evoked by the deep afferents of the limb presents no obvious difference from that evoked by the cutaneous. Head, Rivers and Sherren[2] have shown that deep afferents (of forearm) evoke sensations broadly resembling the tactual evoked from the overlying skin. The deep afferents furnish a sort of "deep" touch with qualities differing from and yet entirely harmonious and complemental with the sensations of superjacent skin. Along with this conformity between the surface and deep sensual reactions there coexists a conformity between the surface and deep reflexes. The adequate stimulus for the deep afferents

---

[1] *Loc. cit.*

[2] *Brain,* XXVIII. 1905.

appears to be mechanical in kind; its source lies in movements active and passive of the limb, itself producing changes in shape and tension of muscles, etc. In other words the deep afferents belong to the "proprioceptive" system[1]. The relation in which their stimuli stand to stimuli given by the environment is a secondary one. The secondary character of the relationship argues that the reactions evoked by the deep afferents will be auxiliary and adjuvant to those evoked by the afferents of the surface[2]. Experimental observation supports this argument, and one item of the support is the just mentioned similarity of reflex effect yielded by deep and surface afferents respectively.

9. From observations such as those given above on p. 29 it appears that the difference between a flexion-reflex that is stronger, *e.g.* owing to more intense reflex stimulus, and one that is weaker (its stimulus being weaker) does not lie in the latter's employing few muscles the former many. Both employ approximately, probably exactly, the same muscles, but the contraction of each muscle is in the stronger reflex stronger, in the weaker reflex weaker.

10. Although the afferent nerves from the large area which forms almost the whole surface of the limb yield as their reflex effect pure flexion of the limb, a few afferents belonging to the attached base of the limb excite, instead of flexion, extension of the knee. Among these afferents are *n. lumbo inguinalis* (spermaticus externus), *n. cutaneus femoris posterior*, a small branch from 3rd lumbar to skin of groin, and certain perineal nerve-branches.

(i) *N. lumbo inguinalis* (spermaticus externus, genito-crural). From this nerve the reflex obtainable as regards contralateral knee is always contraction of the extensors; on the ipsilateral knee the effect is sometimes contraction, sometimes relaxation. Examination of the reflex in fourteen individuals yielded contraction of the ipsilateral knee-extensor in all, but complicated in two individuals by occasional replacement of the contraction by distinct inhibitory relaxation. The inhibitory relaxation seemed favoured by faradic stimulation instead of mechanical. Among the afferent fibres of the nerve some therefore excite reflex extension of ipsilateral knee and others excite flexion of it. This holds of both the inguinal and the spermatic branches of the nerve. The field of distribution of the nerve includes the inguinal mamma and a pad of fat covering the medial part of the groin. Manipulation of the groin of the spinal dog not unfre-

---

[1] Sherrington. *Integrative Action of the Nervous System*, p. 129. 1906; *Brain*, XXIX. 1906. *Ergebn. d. Physiol. Biophysik.* 1905.

[2] *Ibid.*

quently evokes reflex extension of the ipsilateral knee. The extension which the nerve provokes may be movement unflexing the limb to allow the young better access to the inguinal mammilla, as in suckling. The reflex effect of the nerve is however in my experience the same in the male as in the female. The sense of the movement is compatible with a sexual significance. Beck and Bikeles[1] have recently reported a somewhat similar reflex movement elicitable in the spinal dog by stimulation of the skin of the scrotum.

(ii) The small branch from the 3rd lumbar nerve to the skin of the groin enters that region between the external cutaneus and the spermaticus externus. It causes reflex contraction of the ipsilateral vastocrureus muscle extending the knee.

(iii) *Ischial and perineal nerves.* From the skin over tuber ischii and from that of the perineum broad touches excite extension of the ipsilateral knee as well as of the contralateral. The vasti and crurei of both limbs are seen to contract. The crossed reflex is the more powerful and the root of the tail is deflected toward the crossed side. N. cutaneus femoris posterior bared, severed, and proximally stimulated mechanically by ligation yields usually a similar reflex result; so also do the afferent nerves of the perineal skin. Yet this result is not regular in regard to the contraction of ipsilateral knee-extensor, sometimes the contraction is replaced by inhibitory relaxation. Similarly the ischial and perineal skin sometimes yields flexion instead of extension of ipsilateral knee. Flexion is the result when the skin is pinched or pricked: extension when merely touched or stroked. Ischial skin therefore resembles plantar in so far that it yields reflex extension of ipsilateral limb when stimulated by harmless pressure, but yields flexion in response to stimuli whose character is hurtful. The irregularity of result from the ischial nerve-trunks may mean that it contains afferents some of which excite ipsilateral extension others ipsilateral flexion. Faradisation seems more effective for the latter, mechanical stimuli for the former.

Apart from the usual but not invariable extension elicited by these afferents of perineal skin, buttock and groin, and apart from the extensor thrust elicited by broad pressure on the planta, the reflex elicited from the limb is uniformly flexion—the flexion-reflex. It has to be remembered however in thus summarising the above observations that in them the excitation of the deep afferents was unavoidably very artificial in character, namely by faradism or gross mechanical stimuli. The

---

[1] *Arch. f. d. ges. Physiol.* cxxix. p. 416. 1909.

observations therefore although they show the existence in all these nerves of afferent fibres which evoke ipsilateral flexion hardly excludes the possibility of the coexistence in some of the nerves of fibres which can evoke ipsilateral extension. In the plastic tonus of decerebrate rigidity we have evidence that in the nerves of the extensor muscles there coexist along with afferents which reflexly relax those muscles other afferents which reflexly excite their contraction especially in tonic form.

SECTION II. REFLEX MOVEMENTS ACCESSORY TO THE FLEXION-REFLEX.

1. The stimulus which evokes the flexion-reflex in the stimulated limb commonly evokes at the same time certain reflex movements elsewhere. In the fellow limb of the crossed side the movement is almost invariably extension. In the other pair of limbs it usually provokes extension and retraction of the homonymous limb and flexion with protraction of the crossed limb. Thus, when the seat of stimulation is a hind-limb the reflex effect is extension at knee, hip and ankle of the crossed hind-limb; extension at elbow, shoulder and wrist of the ipsilateral fore-limb with retraction; flexion at elbow, shoulder and wrist of the crossed fore-limb with protraction. When the stimulus is applied to a fore-limb the flexion-reflex results in that limb itself and in the other limbs extension of elbow, shoulder and wrist of the crossed fore-limb, extension at hip, elbow and ankle in the ipsilateral hind-limb and flexion at knee, hip and ankle in the crossed hind-limb.

These reflexes are accessory to the flexion-reflex rather than parts with it of one integral reflex. Though often linked with it they are separable from it. The flexion-reflex of the stimulated limb itself is of such constancy that given the stimulus the ensuing flexion is a matter of practical certainty. But the reflex results extending to the other limbs are not so. The most constant of them is the crossed extension in the contralateral fellow limb. The least constant is in my experience the flexion of the limb diagonal to the limb stimulated. Here the effect is usually flexion but is not rarely extension. The effect does not oscillate from one form to the other in the course of any one experiment; but in some experiments it is flexion in others extension. Occasionally in the course of the same experiment it suddenly changes from flexion to extension, but I have not seen it then change back again. When reflex extension replaces the more usual flexion the total result of the reflex is extension of all the limbs outside the stimulated limb itself. This variability of the accessory reflexes separates them from the reflex of the stimulated limb itself. Even the crossed extension-reflex of the twin limb has a variability which indicates that it is adjunct to rather than part and parcel of the reflex of the stimulated limb itself. The threshold stimulus for the crossed extension-reflex may differ considerably from that of the ipsilateral flexion-reflex itself; often it is practically the same for both, but often that of the crossed reflex is markedly the higher. In some instances the crossed reflex is unobtainable though the ipsilateral is obtained readily. The crossed reflex is clearly separable from though usually adjunct to the ipsilateral flexion-reflex. Ether and chloroform narcosis also commonly dissociates these reflexes by suppressing crossed extension-reflex earlier and longer than ipsilateral flexion-reflex. So also does spinal shock (*v. inf.* Sect. III. p. 67).

2. *Crossed extension-reflex.*

(i) So commonly is the crossed extension-reflex an accompaniment of the ipsilateral flexion that serial analysis of its muscular composition does not involve great expenditure of material. The limb muscles which contract in it are found to be the following (Fig. 1 shows these muscles by the broken lines and numerals):

vastus medialis,
vastus lateralis,
crureus,
adductor minor,
adductor major (a part),
sartorius (part inserted into patella),
quadratus femoris,
gastrocnemius,
soleus,
semimembranosus,
anterior biceps femoris,
flexor longus digitorum (late).

On the other hand certain muscles relax in it. Amongst these are:

semitendinosus,
biceps femoris posterior,
tibialis anticus,
sartorius medial band,
" lateral band in proximal part.

Probably the other flexors relax also, but only those observed by actual isolation are entered on this list. In the fore-limb the reflex excites contraction in supra-spinatus and humeral heads of triceps; and relaxes by inhibition brachialis anticus. Other muscles as well are excited and inhibited in fore-limb, but those actually observed by isolation are the above.

(ii) In its handling of the limb musculature this reflex exhibits the same principles of simultaneous coordination noted above in the flexion reflex (*v. sup.* p. 95). It illustrates them further. Muscles regarded as units by anatomical nomenclature, *e.g.* biceps femoris, triceps brachii, quadriceps extensor, are not so treated by the reflex. The reflex handles each of these as compounded of antagonistic parts; in each it inhibits and restrains the contraction of one part while it excites that of the other.

As in the flexion-reflex so in this extension-reflex muscles which are antagonistic, in the sense that one as a prime mover would oppose the other as a prime mover, are dealt with by reciprocal innervation. But in this reflex all of the muscles which are excited to contract are muscles which in the flexion-reflex are inhibited and restrained from contraction. Conversely in this extension-reflex the muscles inhibited are those which in the flexion-reflex contract. Reciprocal innervation though exercised in this reflex equally with the flexion-reflex is exercised in exactly the reverse direction.

This reflex like the flexion-reflex employs at one and the same joint one and the same muscle both as prime mover of the joint and fixator of the joint for muscles which are prime movers at other joints. Thus, it employs vastocrureus to extend knee and gastrocnemius to extend ankle: but gastrocnemius of itself would flex knee as well as extend ankle; its former action is prevented by the concurrent contraction of vastocrureus and this the reflex provides. And by prevention of the knee flexion the action of gastrocnemius as an extensor of ankle is enhanced. Again lateral band of sartorius at its distal end contracts in this reflex. It is an extensor of knee but also a flexor of hip. Experiment shows that when all other muscles of hip and knee are paralysed including medial band of sartorius itself the lateral band as excited by the crossed extension reflex does actually flex hip as well as extend knee. But in the crossed reflex when the other hip muscles are intact concurrent contractions of the extensors of hip prevent the hip flexion and the whole power of the lateral sartorius so far as excited in the reflex is devoted to extending knee. In the flexion-reflex flexors at one joint act as fixators for flexors at the next joint. In the extension reflex extensors at one joint act as fixators for extensors at the next joint. In the extension reflex, as in the flexion-reflex, where muscle A acts at joints α and β, and muscle B opposes A's action at β but by so doing exalts it at α, the neural taxis does not treat A and B by reciprocal innervation: it excites them together or inhibits them together; it treats them not as antagonistic but as adjuvant each to the other.

Again, as in the flexion-reflex, the mechanism (Lombard and Abbott[1]) whereby an extensor of one joint in virtue of the transarticular attachments of other muscles indirectly extends other joints as well as its own is not only employed but is by the distribution of contraction in the musculature greatly reinforced. Thus semimembranosus is primarily an extensor of hip, but it extends knee and ankle as well (*v. supra*, p. 44). This effect on knee it owes mainly to quadriceps extensor and lateral band of sartorius, and through the extension of knee thus obtained it by means of gastrocnemius extends ankle also. Again the vastocrureus is primarily an extensor of knee but it extends ankle as well, in virtue mainly of the transgenual attachments of gastrocnemius[2]. All these indirect effects are in fact used and greatly reinforced in the reflex action of the limb; the adjuvant muscles instead of being allowed to remain at their passive length are actually reduced in length by concurrent contraction.

Again, as in the flexion-reflex, Fischer's[3] mechanical effect in virtue of which vastocrureus tends to extend hip as well as knee is not disregarded by the reflex taxis but is favoured and reinforced; when vastocrureus contracts so also do semimembranosus, biceps femoris anterior and quadratus femoris, the main extensors of hip.

The neural taxis of the extension-reflex as of the flexion-reflex far from disregarding the subsidiary non-vital mechanical effects (Fischer, Lombard, Strasser[4] and others) inherent in the levers and muscular ties of the limb, so to say adopts them and reinforces them in its use of the limb.

(iii) The afferent nerves which evoke crossed extension include all those which evoke ipsilateral flexion, and in addition those of groin, ischial and perineal regions which evoke ipsilateral extension at knee. The receptive field of the crossed reflex is therefore wider than that of the ipsilateral flexion-reflex.

The reflex extension of the crossed limb is often less pronounced at hip than at knee and ankle. In the decerebrate preparation the extension usually persists during the continued application of the stimulus, but is sometimes followed by active flexion on withdrawal of the stimulus. Occasionally in the decerebrate preparation and usually in the decapitate the reflex during the continuance of the stimulus is

---

[1] *Loc. cit.*

[2] Joh. Müller, *Handb. d. Physiol.* Vol. II. 971. 1834.

[3] *Loc. cit.*

[4] *Muskel. u. Gelenkmechanik*, I. 1908.

an alternating one of extension and flexion. But the reflex movement opens with extension.

It might appear from the above that a crossed reflex from one hind-limb to the other always takes the form of extension at least as its primary movement. In this connection the nature of the stimulus has to be remembered; the stimulus in the above observations has been unavoidably of limited and artificial kind. With more natural stimuli and especially such as are more suited to the proprioceptors crossed flexion is not unfrequently seen. In the spinal dog passive extension of one knee not unfrequently produces flexion of crossed knee[1]. Similarly passive extension of one hip not unfrequently produces immediately active flexion at the opposite hip[2]. Dorsal flexion of ankle sometimes results on stimulation of an afferent nerve of the crossed foot.

Initial posture of the joint at which the reflex effect occurs is also of influence in determining the direction of the reflex movement there (Magnus *v. inf.* Sect. IV. p. 92).

3. *Rebound extension following on reflex flexion.* In the decerebrate preparation the flexion-reflex of the limb is commonly diphasic[3]. After withdrawal of the stimulus which excites the reflex flexion there ensues a well-marked extension of the limb. This is more than a mere return to passive extension. It is an extensor contraction more powerful and ample than that of the tonus previously present[4]. It is a rebound contraction of those muscles inhibited during the flexion phase. I have examined it particularly in vasto-crureus and gastrocnemius in hind-limb, supra-spinatus and humeral part of triceps in fore-limb. The flexion phase of the reflex after withdrawal of the stimulus followed by a rebound phase of extension.

SECTION III. THE FLEXION-REFLEX AND ITS ACCESSORY REACTIONS IN THE DECEREBRATE AND THE SPINAL PREPARATION RESPECTIVELY.

The flexion-reflex with its accessory reactions (*v. supra*, Sect. II.) can be studied very completely in the decerebrate preparation. In spinal preparations also it is the readiest reflex to obtain and shows characters very similar to those it exhibits in the decerebrate preparation. The same muscles contract and relax or are unaffected in the one preparation

---

[1] Sherrington. *Quart. Journ. of Expt. Physiol.* II. p. 109. 1909.

[2] Sherrington. *Loc. cit.*; Magnus. *Arch. f. d. ges. Physiol.* CXXX. p. 219. 1909.

[3] Sherrington. This *Journal*, XXXVI. p. 185. 1907.

[4] Sherrington. *Roy. Soc. Proc* 80, B. 53. 1908.

as in the other. Perhaps no one feature of the reflex by its absolute default or intrusion succinctly differentiates the reaction of one preparation from that of the other. Yet differences do exist between them and are significant though mainly quantitative.

The spinal preparations employed have been (1) the decapitated preparation[1] (cat) observed within eight hours after decapitation; (2) the late spinal preparation (dog, cat) observed at various periods, often long, *e.g.* four years after thoracic spinal transection. The observations on the decapitated preparation are as regards time strictly comparable with those of the decerebrate preparation. In the decapitated preparation the transection lies usually 2—6 mm. behind the point of the *calamus scriptorius.*

One difference between the reflex reactions of the spinal and decerebrate preparations lies in the duration of the after contraction. Myograms from the late spinal preparation show that the reflex contraction for a short period outlasts the duration of the stimulus. The discharge from the reflex centre does not subside absolutely at once. This after-discharge[2] is best marked in reflexes which are strong and follow on stimuli intense and rather brief (Fig. 3). The reflex contraction may attain even its greatest height just after the brief stimulus has ceased. Even so the after-contraction soon runs down, with a rapid and usually tremulous decline[3]. At longest it lasts a few seconds. With weak and moderate reflexes there may be hardly a trace of it at all. It occurs with the reflex contractions both of flexor and extensor muscles.

In the decerebrate preparation the reflex movements exhibit great sluggishness not of onset but of subsidence[4]. Each position into which a stimulus moves the limb is retained and persists as a slowly subsiding posture. Each reflex becomes in this way an attitude struck and retained so as to recall the condition of a cataleptoid state. On examination with the myograph[5] each reflex contraction is seen (Fig. 4) to persist long after cessation of the stimulus; a persistent tonic after-effect follows it. Analysis detects that not all the muscles of the limb exhibit this protracted after-contraction. It is met with regularly in *semimembranosus, biceps femoris anterior, vasti* (Fig. 3), *crureus, gastro-*

---

[1] This *Journal,* XXXVIII. p. 375. 1909.

[2] *Integrative Action of the Nervous System,* p. 26.

[3] *Ibid.*

[4] Sherrington. *Roy. Soc. Proc.* LX. 411. 1896, and this *Journal,* XXII. 319. 1898.

[5] *Roy. Soc. Proc.* LXXIX. B, p. 338, Fig. 1. 1907: LXXX. B, p. 554, Fig. 2A. 1908.

cnemius, *soleus*, *supra-spinatus* and humeral part of *triceps*. It is absent from sartorius (medial band), psoas, tensor fasciæ femoris (Fig. 5),

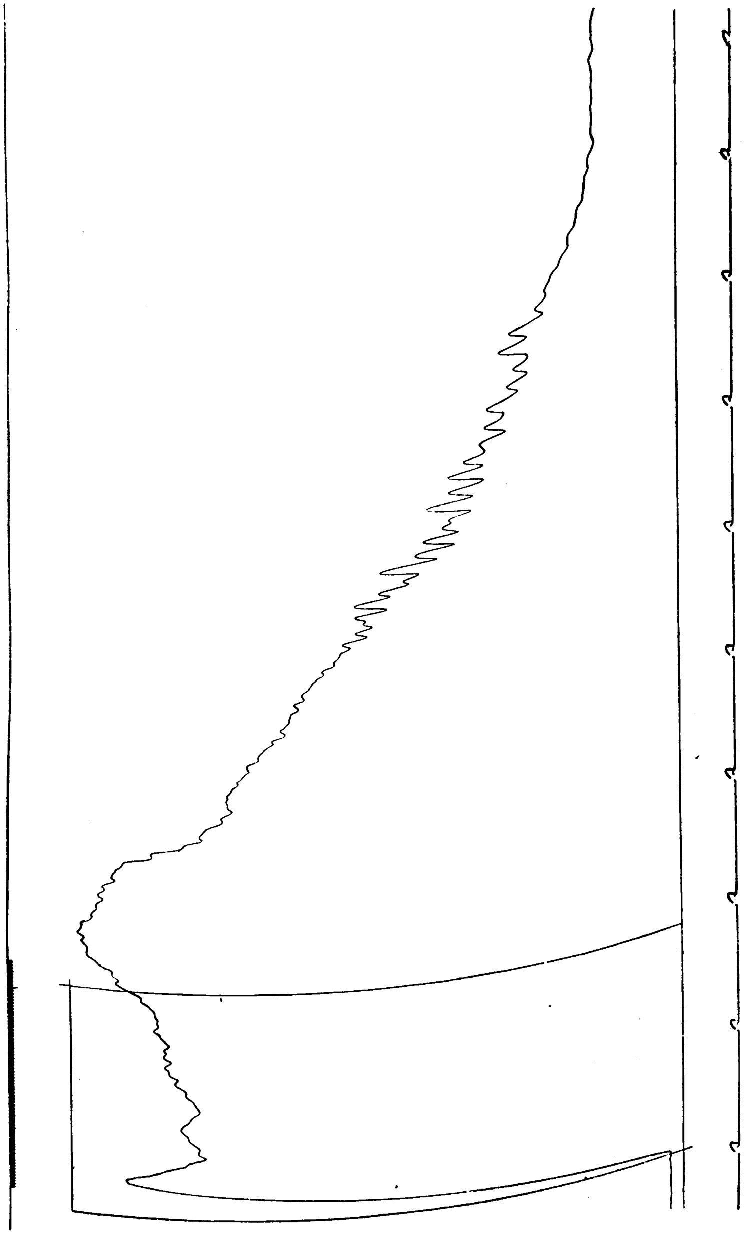

Fig. 3. Reflex contraction of sartorius (spinal dog, after period of shock has passed). Faradic stimulation of skin of digit of ipsilateral hind-foot. Stimulus marked above. Time in seconds.

semitendinosus, tibialis anticus, brachialis anticus and biceps. In these latter the reflex contraction exhibits hardly even the short-lived after-discharge such as the spinal preparation exhibits. That is, the tonic after-prolongation of contraction characteristic of the decerebrate preparation is restricted to the extensor muscles. It constitutes in the decerebrate preparation a difference between the reflex contractions of extensors and flexors. There is the question whether the difference is between extensors and flexors or between crossed reflexes and ipsilateral reflexes. The readiest way of obtaining a reflex contraction of extensors of the limb is to employ a crossed reflex and for the flexors an ipsilateral reflex. The contraction of the extensor is however found still to exhibit the peculiar tonic after-prolongation when excited by one of the uncrossed extension reflexes obtainable from inguinal ischial or perineal nerves (*v. supra*, Sect. I. p. 54).

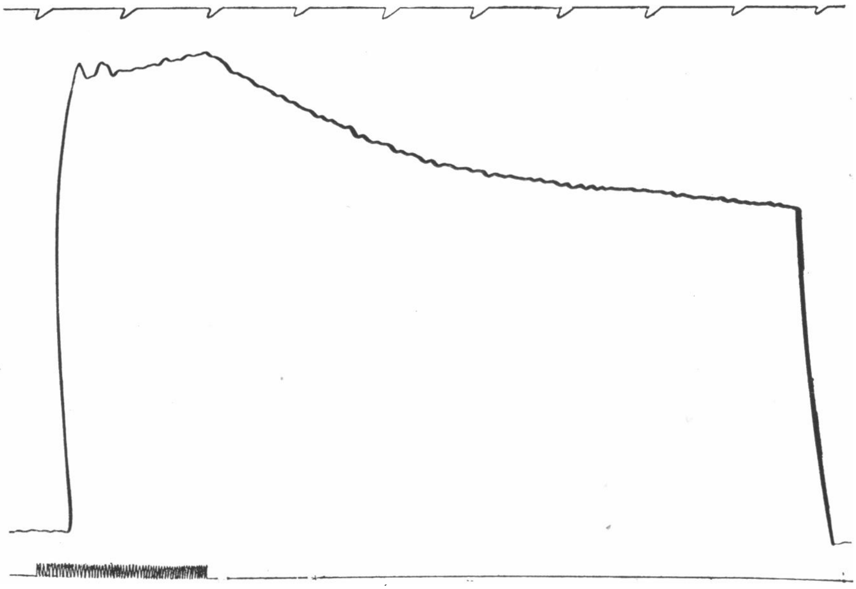

Fig. 4. Reflex contraction of vastocrureus in decerebrate cat. Faradic stimulation of central end of musculocutaneous branch of peroneal of contralateral limb. Stimulus marked below. Time in 2 sec. periods marked above. At end of the 18th second the contraction was cut short by forcibly stretching the muscle by hand to test the "plasticity" of the after-contraction. The plasticity is seen to be very complete; the muscle continues at the length thus passively given it.

The after-prolongation of the reflex contraction of the extensor muscles in the decerebrate preparation is of tonic character. It often endures for many minutes. It is not tremulous. It is with weak reflexes proportionately as marked as with strong. It is due to a tonic reflex which appends itself[1] to the reflex contraction excited by the external stimulus. Severance of the afferent nerve of the extensor muscle itself at once abolishes it; reflex contractions of the extensor then remain easily elicitable but exhibit no tonic after-prolongation[2]. The tonic reflex appending itself to the reflex of external origin has been shown to be autogenic.

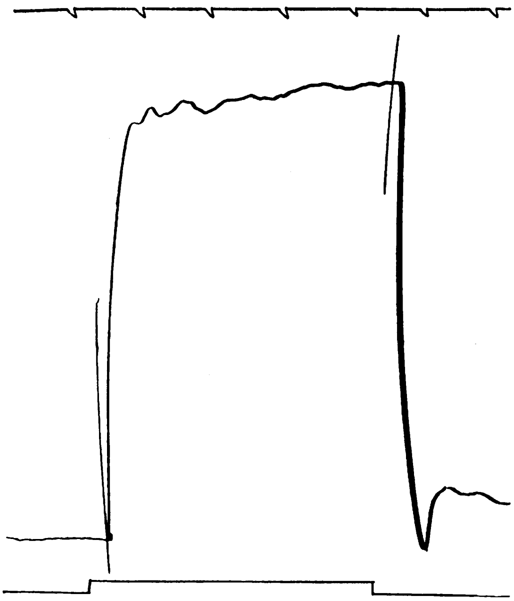

Fig. 5. **Reflex contraction of combined psoas and tensor fasciæ femoris in decerebrate cat. Faradisation of central end of ipsilateral peroneal nerve. Stimulus marked below. Time in 1″ periods above.**

Certain other muscles of the decerebrate preparation show an after-prolongation of contraction the same as do the extensors of the limbs. Among these are the dorsal muscles of the neck, the extensors of the tail and the elevators of the lower jaw. These therefore form a functional group with the extensors and in speaking of extensors in what follows I include them.

---

[1] Sherrington. *Proc. Roy. Soc.* LXXX. B, p. 562. 1908.
[2] *Ibid.*

In the decapitated[1] preparation the tonic after-prolongation of contraction is absent (Fig. 6) just as after severance of the extensors own afferent nerve. It is absent from strong reflex contractions as it is from weak (Fig. 6). Spinal transection, or bulbar transection, anywhere behind the pons, sets it aside in all extensors posterior to the

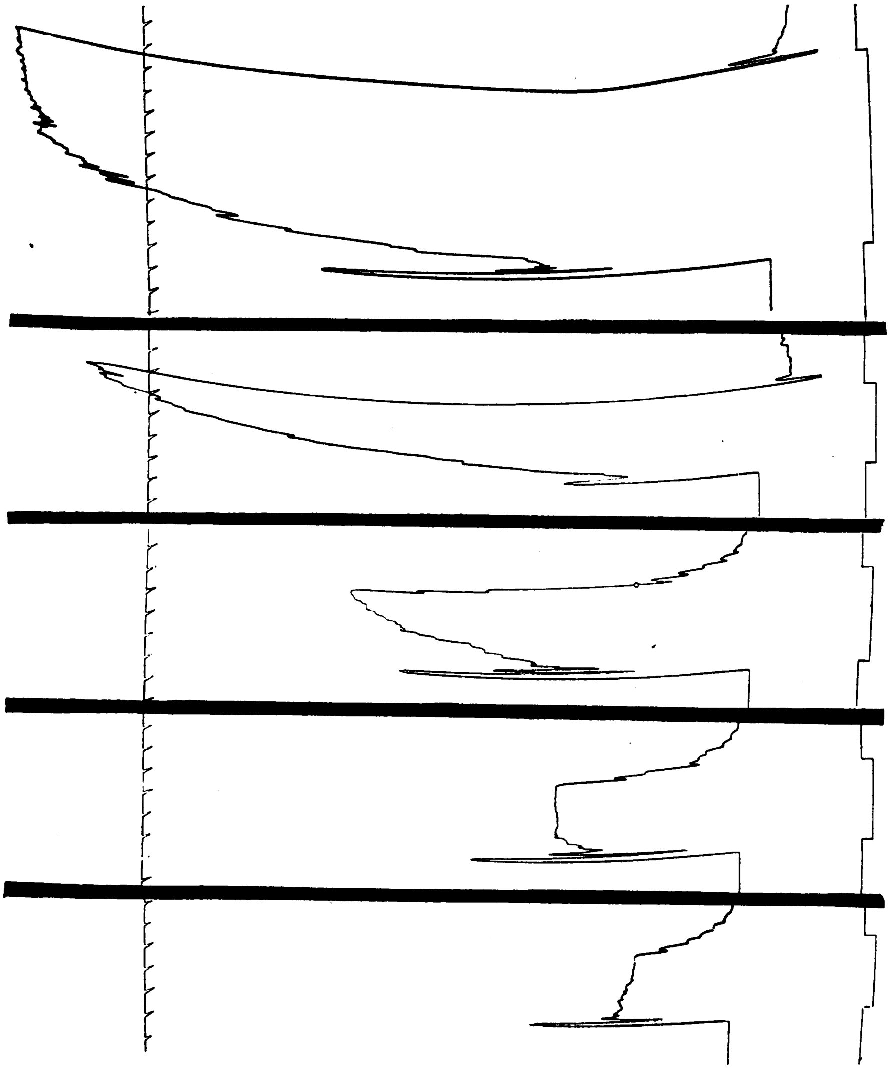

Fig. 6. Reflex contraction of vastocrureus in decapitate cat. Faradisation of central end of crossed popliteal nerve, with increasing strengths of stimulation. Stimulations marked below. Time in 1″ periods above.

---

[1] Cf. this *Journal*, xxviii. p. 375. 1909.

lesion[1]. Whether this abolition is permanent or only a temporary or "shock" phenomenon, is a further question. In the few hours during which observations on the decapitated preparation can be continued the abolition remains. Where the observations can be carried over longer periods, as after thoracic spinal transection, there is no return of the tonic after-prolongation at least for several weeks. My material has further included preparations where intervals of nine weeks, eight months and thirty-one months were allowed after thoracic spinal section. In these cases mechanical and faradic stimuli to the central stump of the peroneal nerve elicited fair reflex contractions of contralateral vastocrureus. In no instance did these contractions exhibit the tonic after-prolongation characterising the decerebrate preparation, although at the time of the observation the extensors of the fore-limbs, the animal being decerebrate, were actually exhibiting the characteristic prolongation. There was however a difficulty in deciding whether all trace of the after-prolongation was absent. By recourse to successive induction[2] reflex contractions of vastocrureus could be evoked which outlived the stimulus—a brief one—for 10—12 seconds. This is of course a very short after-effect as compared with the after-prolongation enduring for whole minutes in a decerebrate preparation. The difficulty is to distinguish between a small amount of true tonic after-prolongation and an ample after-discharge of ordinary kind. The tremulous character of the after-contraction in these spinal preparations argues against the former. Not that vastocrureus was toneless, for the knee-jerk, if that is evidence, was brisk. But to a certain degree the evidence from the observations is clear. Despite allowance of ample time for complete recovery from "shock" in the ordinary meaning of that term the spinal preparation did not show a tonic after-prolongation such as characterises the reflex contractions of the extensors in the decerebrate preparation. When in certain instances some tonic after-prolongation was present it was very brief as compared with that of the decerebrate preparation and less steady. The tonic after-prolongation characterising the reflex extensor contractions in decerebrate rigidity requires some reflex mechanism having its peripheral afferent path in the nerve of the extensor muscle and central apparatus pre-spinal as well as spinal. The pre-spinal apparatus involves some neural field between the levels of anterior colliculus and hind edge of

---

[1] Cf. **F. H. Thiele.** This *Journal*, xxxii. 358. 1905.

[2] *Integrative Action of the Nervous System*, p. 206; *Roy. Soc. Proc.* lxxvii. B, p. 478. 1906.

pons. Reflex excitation and reflex contraction and even passive movement of extensor muscles excite this mechanism. On the contrary by reflex excitation and reflex contraction of the flexors it is usually inhibited though subsequently rendered more active (successive induction).

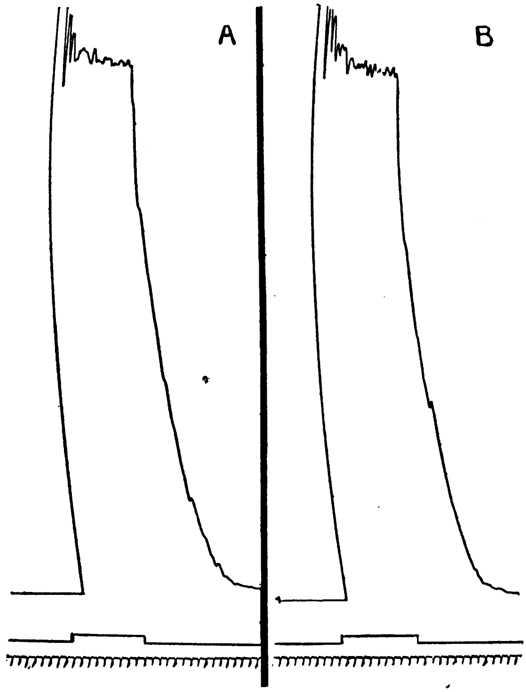

Fig. 7. See text.

To a certain extent spinal transection affects the reflex condition of the extensor musculature in the same way as does severance of the afferent nerves of the extensor muscles[1]. The latter's effect is however local, the former's covers the whole field posterior to the transection. This resemblance harmonises partly with an inference drawn by C. Brooks[2] to the effect that severance of the afferent spinal roots produces the same shock effects on spinal reflexes of the limb as does transection of the cord itself.

The reflex contraction of the flexors as obtained in a decerebrate preparation is little modified by subsequent spinal transection[3]. Fig. 7

---

[1] *Roy. Soc. Proc.* LXXX. B, 552. 1908.

[2] *Amer. Jnl. of Physiol.* 1909.

[3] Cf. F. H. Pike, *Amer. Jnl. of Physiol.* XXIV. 124. 1909.

A shows the reflex contraction of psoas and tensor fasciæ femoris (flexors of hip) in a decerebrate preparation two hours after decerebration and prior to spinal transection in the thoracic region. Fig. 7 B shows their reflex contraction elicited by a similar stimulus in the same preparation ten minutes later eight minutes after spinal transection at the ninth thoracic segment.

With the extensors the case is different. Fig. 8, 1 shows reflex contractions excited in vastocrureus (extensor E) and semitendinosus (flexor F) in a decerebrate preparation and Fig. 8, 2 shows their contractions elicited by the same stimulus twenty minutes later, fifteen minutes after the preparation had been made spinal by decapitation. The reflex contraction of the flexor is little altered by the transection. In each case the stimulus was the tying of a ligature on n. peroneus, ipsilateral for the flexor, contralateral for the extensor. The reflex of the extensor is much reduced in amplitude and deprived altogether of tonic after-effect. The threshold stimulus for the reflex contraction had in the decerebrate preparation been practically the same for both muscles and stood between 5 and 10 units on the Kronecker scale. Ten minutes after decapitation 10 units evoked no obvious contraction in either muscle but 15 units evoked a small contraction in the flexor none in the extensor, and 50 units evoked a strong contraction in flexor and none in extensor. An hour later 10 units evoked a slight contraction in flexor and 30 units a slight tremulous contraction in the extensor. 80 units evoked a strong

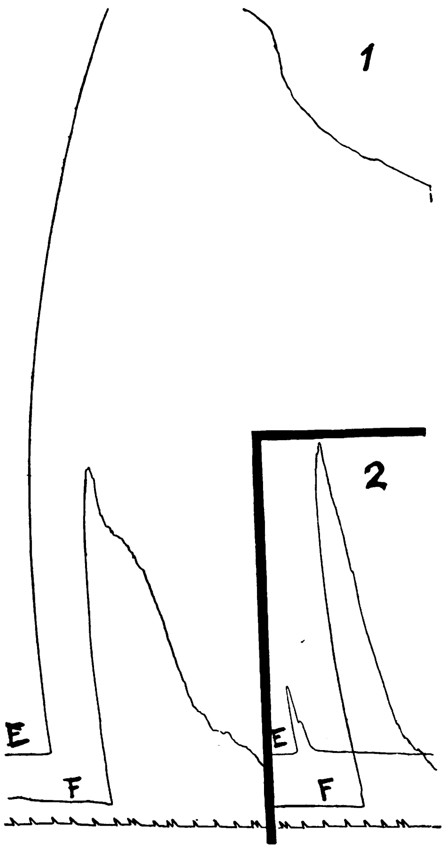

Fig. 8. See text.

contraction in flexor very similar to that which the same number of units had evoked prior to decapitation. From the extensor it elicited a contraction of sluggish onset and quite unlike the contraction it had elicited from that muscle prior to decapitation, for then the contraction had been succeeded after cessation of the stimulus by the usual prolonged tonic after-contraction, whereas now the contraction subsided immediately on withdrawal of the stimulus.

In my experience the threshold value of stimulus for reflex contraction of the flexor often becomes a little lower when the decerebrate preparation is made spinal but that of the extensor always becomes higher. In the decapitated preparation it is often difficult to elicit reflex contractions of the extensors of more than minimal degree; sometimes they can hardly be obtained at all; occasionally however they can be elicited in considerable amplitude though never maintained beyond the withdrawal of the stimulus. Sometimes the contraction lapses even during the continuance of the stimulus, and then returns and lapses again and in this way the extension assumes a rhythmic form. A certain degree of asphyxia tends to augment the extensor reflexes more than the flexor. In the decapitated preparation the short after-discharge of a flexor reflex seems usually rather more marked than in the decerebrate preparation.

The reflex contraction of the extensors has usually been elicited by a crossed reflex, that of the flexors by an ipsilateral. The heavier depression of the extensor's reaction than of the flexor's by the spinal transection might be a difference less between extensors and flexors than between crossed reflexes and uncrossed. But the same depression of the extensor's reaction is evident when the reflex is excited by genitocrural or perineal afferents which evoke it ipsilaterally. Moreover in cases where the crossed extension reflex fails in the decapitate preparation to elicit any contraction of the extensor muscles of the crossed limb it nevertheless exerts its usual influence on the flexors of that limb. This influence is inhibitory and can be detected by provoking a slight ipsilateral reflex contraction in the flexors and then stimulating a crossed afferent; this is often seen to suppress the flexor contraction by inhibition, although it fails to cause contraction of the extensors. The same effect can be more easily observed when there is, as frequently is the case, a more or less persistent slight contraction of the flexors of knee and hip in the decapitate preparation.

The depressant effect of spinal transection therefore falls unequally on the flexors and extensors of the limb. In agreement with this the direct extension reflex elicitable from the planta (extensor thrust) emerges from the condition of spinal shock much later than does the flexion-reflex. How far the depression of the extensor reflexes is a permanent effect or a temporary or shock phenomenon can be gauged from spinal preparations kept under observation for long periods after spinal transection. In these the crossed extension reflex accessory to the ipsilateral flexion-reflex, the extensor thrust, and the crossed extension of knee on flexion of the ipsilateral are all obtainable and often with considerable facility. The heavy depression of the extensor reflexes by spinal transection is therefore largely a shock effect. On rare occasions I have found the extensor thrust elicitable in the cat even within five hours after decapitation.

Spread of the reflex effect from the hind-limbs to the fore-limbs is in the decapitated preparation less facile than in the decerebrate. The reflexes of the fore-limb are more depressed in the former preparation than in the latter. A strong stimulus to a fore-limb though it evokes a reflex movement in the ipsilateral hind-limb may evoke hardly any in the fore-limbs themselves.

A further difference between the decerebrate preparation and the spinal concerns the rebound of extension which so usually in the decerebrate preparation ensues after withdrawal of the stimulus exciting the flexion-reflex. This rebound in my experience is often absent from the decapitated preparation, and when obtained soon tires out under a succession of trials. It is however met with. In the spinal preparation when some weeks have elapsed subsequent to spinal transection it becomes obvious enough when the limb is intact and not subjected to the procedures necessary for isolating individual muscles. It is however never prolonged and tonic as in the decerebrate preparation. In the dog as early as 16 days after thoracic spinal transection the flexion-reflex elicited by a pinch on the foot may be followed by an active though feeble extension of the limb. But in the decerebrate preparation the rebound may be great even within an hour of decerebration and is elicitable in each individually isolated extensor muscle, and after such severe procedure as severance in both limbs of all other afferents than that of the isolated extensor muscle itself. In the spinal preparation even after long periods of many months have elapsed the rebound never approaches this degree of resistance and protracted course. A phenomenon allied to it however is commonly seen in the increased facility and intensity with which reflex extension can be provoked shortly after a strong flexion-reflex (successive spinal induction).

A significant difference between the limb-reflexes in the decapitate and decerebrate preparations respectively is the following. Alternating movement characterises[1] spinal reflexes. The crossed extension reflex in the decapitate preparation is generally rhythmic whereas in the decerebrate preparation it is unbroken and steadily maintained. A similar difference is traceable in the ipsilateral flexion-reflex. A small clip when applied to a digit in the decerebrate preparation provokes a maintained flexion-reflex. In the decapitate preparation it causes a flexion-reflex broken commonly by a few brisk active extensions which after a few repetitions of extension die out leaving a more or less pronounced flexion persistent under the continuous stimulus. Similarly the clip applied to a fore-limb digit in the decerebrate preparation usually evokes a maintained extension of ipsilateral hind-limb. In the decapitate preparation it usually evokes in ipsilateral hind-limb an extension which is rhythmic. Applied to perineum or scrotum the clip evokes in the decerebrate preparation a steadily maintained extension of both hind-limbs; in the decapitate preparation it evokes rhythmic alternating extension and flexion of opposite phase in the two hind-limbs. Again, the rhythmic reflex of alternating flexion-extension which constitutes the scratch-reflex is more readily elicitable in the decapitate or spinal preparation than in the decerebrate. So also, in the dog, is the 'shake-reflex' resembling the action of a dog coming out of water.

In short the limb reflexes of the decapitated preparation tend more than those of the decerebrate to exhibit rhythmic character with alternation of flexion and extension during the continuance of the stimulus. The decerebrate preparation may be described as exhibiting less tendency to develope refractory phase under the continuance of a stimulus. The tendency is especially marked when as happens in the great majority of cases the decerebrate preparation presents its characteristic extensor rigidity. In describing the rhythmic reflexes of the decapitate preparation as due to development of recurrent refractory phase under a continuous stimulus it must be remembered that refractory phase does not express the entire case because not only does for instance extension temporarily lapse in face of the stimulus but flexion temporarily replaces the extension.

In respect of proneness of the hind-limb reflexes to exhibit a rhythmic alternating form the spinal preparations which have passed beyond the period of "shock" resemble the decapitated preparation.

---

[1] **Sherrington**, *Textb. of Physiol.* Art. *Spinal Cord.* Vol. II. pp. 820, 831. 1900.

SECTION IV.

I. THE NOCICEPTIVE FLEXION-REFLEX.

The flexion-reflex is elicitable from the skin of the limb and with especial facility from the skin of the foot (*v. supra,* Sect. I). The stimuli especially effective are of nocuous quality. The flexion-movement provoked lifts and withdraws the foot. If the stimulus be continued the reflex holds the limb even for minutes at a time flexed under the body as though out of harm's way. If the stimulus be strong and the reflex condition brisk the first flexion which results may be quickly followed by a brief active extension as if to shake off the irritation[1]. This secondary extension is always short and followed by immediate return to flexion, this latter occasionally to be broken by a brief extension and the manœuvre repeated a few times before unbroken flexion ensues. This result occurs even when a small spring clip affixed to the foot is used as stimulus, and when therefore the mechanical stimulus is constant. It is of interest as showing the reflex in the form of alternating flexion and extension although the alternation is irregular, repeated only a few times and then subsides into steady flexion. The more usual form of the reflex is maintained flexion unbroken by active extension even from the first. The description given is for the hind-limb (cat) but applies to the fore-limb also; there also not unfrequently the flexion is broken at first by a few brief irregular extensions especially at elbow.

Under these stimuli and in these forms the flexion-reflex is evidently protective. It is often accompanied by stepping of the crossed hind-limb and, though less commonly, of the other limbs as well, but not of the limb itself stimulated. The irritated foot is withdrawn from harm and the other legs run away. The protective reflex is associated with a flight-reflex. The dog kept under observation by Goltz subsequent to ablation almost entire of both cerebral hemispheres was noted after incidental injury to one hind foot to keep the injured foot off the ground and run on three legs. Goltz's interpretation of that "behaviour" as largely reflex is borne out by the above mentioned less complete yet broadly analogous reaction in the decapitate preparation (cat). The decerebrate rabbit shows a similar reaction, except that in the rabbit while the stimulated limb is kept flexed the other three legs show the hopping movement more usual to the natural

---

[1] Cf. in the donkey, Chauveau, *Brain,* XIV. 173. 1891.

progression of that animal. In the decerebrate preparation (cat) the reaction shows in addition to the limb movements, a turning sideways and backward of the head, an opening of the mouth, retraction of the lips, and occasionally vocalisation. The significance of this pseudo-affective reflex is clearly related to the nocuous quality of the stimulus. There is a reflex combination of movements of protection signifying both flight and preparation for defence.

This reflex is elicitable from all points of a large area of the limb surface and also though less easily from the deep structures as well (*v. supra*, Sect. I p. 35). But from the deep structures of the limb certain stimuli which are not nocuous can evoke reflex flexion. This latter reflex flexion is not a movement of withdrawal of the limb out of harm's way but is the flexion phase of the alternating reflex act of stepping. The above described maintained flexion-reflex excited by nocuous stimuli applied to the limb itself is therefore not the only form of flexion-reflex exhibited by the limb. And its sub-variety mentioned above as showing some brief and irregular discontinuity in the flexion is of interest as indicating a transitional form toward the rhythmic flexion-reflex of the step. But the nociceptive flexion-reflex of the limb and the rhythmic locomotor flexion-reflex of the limb are, as is obvious from their significance to the individual reactions, mutually incompatible. Hence the nociceptive flexion-reflex can interfere with, break through and interrupt the rhythmic locomotor flexion-reflex (Fig. 9). The peculiar character, in fact the "adequacy," of its stimulus lies in intensity[1]. It is prepotent when pitted against the

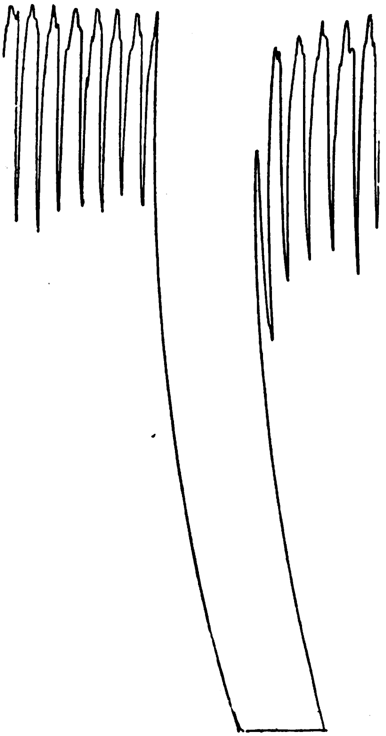

Fig. 9. Reflex stepping of hind-limb interrupted by a nociceptive stimulus to skin of foot evoking a nociceptive flexion-reflex. Decapitate preparation (cat); descent of lever = flexion.

---

[1] *Integrative Action of Nervous System*, p. 231.

locomotor reflex: and this is a further mark of its nociceptive character, since nociceptive reflexes like painful sensations are habitually "dominant" in competition against others.

II. SPINAL STEPPING.

1. From the decapitated preparation (cat) reflex stepping of the limb can be readily evoked. As to the reflex being really that of stepping there is no doubt, and other facts known of stepping as a reflex act make it not surprising that the decapitate preparation should exhibit it. After spinal transection in the thoracic region when the period of shock is passed the hind-limbs of the dog execute stepping movements strikingly complete. Photographic kinetoscope analysis of the outward character of these movements establishes the fidelity of their resemblance to those of the natural step (Philippson)[1]. Usually the spinal stepping is that of walk or trot, sometimes it is that of the gallop (Philippson)[2]. Occasionally the decapitate cat also shows the gallop; the decapitate rabbit does so more frequently.

The ordinary stepping movement of hind-limb may be briefly described as exhibiting two phases. In one the limb suspended from pelvis is brought forward above the ground to a new point of support in front of that which it last used. In this phase the limb carries its own weight only, and even for that, conditions non-vital, *e.g.* atmospheric pressure on hip-joint (Weber), largely obviate the strain from falling upon muscle. Then follows a phase in which, while the foot presses on the ground, the limb is extended, carrying its own weight and a share of the superincumbent body weight, and finally aids the advance of the body by a propulsive thrust from the ground. Thus the stepping in each limb is a rhythmic movement of alternating flexion and extension. The salient features of this movement in the walk and trot (cat, dog) may be summarised thus[3].

i. Flexion phase, during which the anterior angle between thigh and ilio-ischial[4] line continually decreases owing to flexion at hip. During the earlier two-thirds of this phase flexion at knee and ankle proceeds along with the hip-flexion. In the latest third the angles at

---

[1] *Travaux du Lab. de Physiol., Instituts Solvay. Bruxelles*, VII. 2. 5. 1905.

[2] *Ibid.*

[3] Cf. the kinematograms from Prof. Marey's Station physiologique, Paris, published in Philippson's paper, *op. cit.* 1905.

[4] Defined above, Sect. I, p. 42.

knee and ankle begin to open. During part of this phase the toes are somewhat spread and extended (dorsal flexion) on metatarsus. During the whole of this phase the foot is off the ground.

ii. Extension phase, during which the anterior angle between thigh and ilio-ischial line gradually opens, and the angles at knee and ankle also open (except for a transient yield under the weight of the body[1] in the earliest third of the phase). During this phase, except at its extreme end, the foot is on the ground; at the extreme end of the phase, after the foot leaves the ground, the toes are adducted together and plantar-flexed on metatarsus.

iii. At end of flexion phase there is an anterior turning point when hip flexing changes to hip extending. At end of extension phase there is a posterior turning point when extension of limb changes to flexion.

iv. Synchronism of extension phase in one limb with flexion phase in opposite fellow limb; in other words, synchronism of anterior turning point of one limb with posterior turning point of the other.

These main features of the normal step of the hind-limb characterise also the reflex stepping of the limb in the spinal preparation. They are main items calling for examination in the analysis of the neural taxis of the reflex step.

2. *Stimuli for stepping-reflex.*

Remote. Among the stimulations which excite stepping movement of the limb in the decapitate preparation are certain of cutaneous application and nociceptive character. The most effective *loci* for these are as follows: perineum especially at scrotum or near vulva; a foot not that of the limb itself exhibiting the stepping movement; neck or back, tail, and pinna when this has been preserved in performing the decapitation. The stimulus may be simply rubbing or squeezing the skin, or the affixing to it of a small clip, or the faradisation or ligation of an exposed nerve. Although cutaneous stimulation of that limb which itself exhibits the stepping is not provocative of the reflex in that limb during the stimulation, on the cessation of the stimulus reflex stepping of that limb may follow. And occasionally stimulation of the skin of the limb near its base excites stepping in it. The stepping evoked by stimulation of perineum or of pubic skin just in front of vulva is always bipedal. It might be thought that this stepping is bipedal because stimuli applied to the mid line of

[1] Philippson. *Op. cit.* p. 17.

body may excite both right and left nerve-afferents together at their overlap in mid-ventral line. But the reflex is still bipedal when the stimulus is shifted well to one side of the mid line, and also when the afferent nerves of one side have been severed. Under these latter circumstances the reflex stepping begins with flexion in ipsilateral limb and with extension in contralateral. In all cases the stepping of the two limbs is synchronous in tempo and of opposite phase in right and left limbs.

But stimuli to the skin of the limb itself elsewhere than at its extreme base excite unipedal stepping of the crossed limb and in the stimulated limb itself the maintained flexion reflex, and when the limb is already stepping a stimulus to its own skin actually stops the stepping replacing it by maintained flexion (the nociceptive reflex) (Fig. 9). The cutaneous nociceptive stimuli which excite stepping are as regards their seat of application "remote," *i.e.* situate outside the limb itself. And in their case the significance of the reflex stepping is clearly protective, the protective act being flight.

Intrinsic. But other stimuli which are non-nocuous and have their seat in the limb itself can evoke reflex stepping of the limb. And in fact in using the spinal limb itself for starting and controlling its stepping the observer has recourse not to skin stimuli but to passive movements. A sure way of eliciting the reflex stepping of the spinal hind-limbs (dog, "late spinal" preparation) is the lifting of the animal from the ground with spine vertical and hind-limbs pendent. The reflex stepping immediately sets in and continues for long periods at a time. This manœuvre evokes the reflex even so soon as a couple of weeks after thoracic spinal transection. Later when the reflex is better developed it occurs with spine horizontal as well as with spine vertical. Extension at both hips is a condition favouring the reflex and the passive hip-extension is greater with spine vertical. With spine vertical when one limb, *e.g.* right, hangs freely under its own weight and the other, left, is supported by the observer's finger with hip semiflexed, both limbs usually remain quiet and there is no stepping. On then removing the support and allowing the left thigh to drop into passive extension a transient active extension seems to ensue with the falling of the limb and on the limb's reaching its fuller extension there follows an active flexion at hip, knee and ankle. This is succeeded by extension partially active, to be followed again by active flexion, and so on. Thus the stepping-reflex commences and proceeds. But it is at once arrested by passively supporting one thigh in semiflexion.

The reflex-stepping thus proprioceptively excited is bilateral. At the first dropping of the limb (left) reflex flexion sets in in the opposite hip; and this occurs so immediately that the left limb has not nearly reached its full extension when active flexion is obvious at the right hip. And when the left limb after its extension flexes, right limb having completed its flexion extends. The reflex is therefore bilateral with opposite phase in the opposite limbs.

In this experiment the passive extension of hip and knee under the limb's own weight evidently provides the stimulus. Passive extension of ankle or knee alone or together but without hip does not suffice to start the stepping, although frequently exciting extension of contralateral knee without hip. Passive full extension of one hip alone, knee and ankle being even flexed, evokes reflex extension of opposite hip and limb. Stretching psoas muscle in the decerebrate preparation sometimes evokes extension of crossed knee. The inference is that in starting the reflex stepping by allowing one limb to drop under its own weight the stimulus is mainly due to extension of hip.

Evidently passive movements of the limb can excite from it its reflex step or at least can initiate that reflex. And the reflex when once started either by a passive movement or by one of the remote skin stimuli above mentioned shows like the scratch-reflex a tendency to continue, as if the movement of the stepping or scratching limb constituted to some extent an intrinsic stimulus in the limb itself further promoting and maintaining the reflex. Reinforcements of action in this way is not uncommon in complex reflex acts. Thus in the scratch-reflex the neck stimulus not only causes a flexion of ipsilateral hip but a turning of neck to ipsilateral side, and this turning of neck itself excites reflex-flexion of ipsilateral hip. Local proprioceptive stimulation as a factor in the reflex is further shown by the prompt arrest of the reflex by gentle restraint applied to the moving limb itself.

What are the receptors in the limb which movements of the limb excite? The limb receptors belong to the two categories exteroceptive and proprioceptive. The former are broadly speaking those of the skin, the latter belong broadly speaking to musculo-articular and deep fascial structures.

It might have been supposed that the main stimulus for the reflex step would arise in the planta from contact with the ground. Facts argue, however, against this somewhat natural suggestion.

A light harmless stimulus, a touch, on the planta does it is true evoke in the spinal hind-limb a lifting and slight spreading of the toes and slight dorso-flexion of ankle. But this movement of the toes and ankle is often a conspicuous feature of the reflex step when the dog is supported free from the ground and the reflex stepping of the spinal hind-limbs taking place in the air. Moreover in the intact animal (cat, dog) severance of all the nerve-trunks directly distributed to all four of the feet up to and above the wrists and ankles impairs walking so little as to make it highly unlikely that the loss of receptivity of the feet destroys any large factor in the reflex basis of these acts.

For the denervation of the feet the following nerves have been severed, in hind-limb the anterior and posterior tibials, musculo-cutaneous and external saphenous about 5 cm. above ankle and internal saphenous above knee. In the fore-limb the severed nerves have been musculo-cutaneous, radial, median and dorsal and palmar divisions of ulnar about 4 cm. above wrist. It makes no obvious difference to the result whether these sections are made all at one time or seriatim. The section of anterior and posterior tibial, and of median and ulnar paralyses of course the intrinsic muscles of the feet. Yet in some cases hardly any noticeable disturbance follows. More often however the following defect appears in one or more of the feet. The animal is apt to stand with the toes of one or more of the feet doubled up underneath the planta. And although it may not do this in standing, on taking a few steps the toes of one or other foot are apt to double under in that manner. The way in which this occurs is that in the advance movement of the step the toes instead of just clearing the ground brush against it and are passively turned under the foot and when the foot is set down at the anterior turning point of the step the toes lies under it, and no correction of the malposition is made, the animal seeming unaware of it.

It might be thought that this defect was due to motor paralysis of the short extensor of the toes which of necessity follows severance of anterior tibial nerve. But section of that nerve alone does not produce the underturning. Moreover a similar defect appears in fore-foot where there is no short extensor of the toes. In some cases this disturbance is transient. Slight increase of the lift of the foot in the advance phase of the step would obviate it. Hence it occurs less when the walk is quick than when it is slow. The desensitised foot later in some cases shows an abnormally high lift in stepping.

Apart from this defect in the management of the toes the natural standing and walking of the animal appears little affected by this denervation of the feet. In regarding the feet as denervated by the above nerve-sections it must be remembered that long tendons which enter the foot proceed from a number of leg muscles situate far above the ankle, and the fleshy parts and musculo-tendinous regions of these muscles contain many deep receptors, whose afferent nerves enter high up and never approach the foot directly and are therefore not severed in the above experiments. But the fact remains that in so far as contribution to the reflex taxis of the step is made by receptors from the foot the contribution concerns merely the posture and movements of the digits of the foot. With the actual reflex execution of the step by the rest of the limb these receptors seem to have little or nothing to do. Reflex stepping excited by any of the stimuli mentioned above as competent in the decapitate or spinal preparations is evoked as easily and perfectly from the limbs with denervated feet as from the limbs with foot-nerves intact. Moreover in those preparations the reflex stepping starts and continues well when the preparation is laid on its side the feet not touching the floor or when, as mentioned above, the preparation is supported freely above the ground so that the feet hang merely in the air.

Nor is the reflex stepping annulled or even obviously impaired by section of all the various cutaneous nerves of the limb. When in addition to the foot-nerves the external cutaneous, ilioinguinal, internal saphenous, small gluteal, and postero-external cutaneous in both hind-limbs are severed no obvious impairment results in the reflex stepping.

A prominent skin-fold (dog) extends along the outer edge of the groin. Stroking the anterior part of this fold or the skin in front of it often evokes reflex stepping of the spinal hind-limbs, and this is accentuated if the skin right and left be stroked alternately. This stepping opens with flexion of ipsilateral knee and hip and ankle. It seemed that stretching of this skin might occur when the limb extends fully as at end of the extension phase of the step. Yet stretching of the skin with the fingers fails to give the limb reflex. Also cocainisation of this skin region makes no obvious difference to the reflex stepping.

There is one reflex from the planta which appears in several ways suited to play a part in the reflex step. Broad innocuous pressure on the planta spreading the digital pads and cushion excites a vigorous brief extension of the whole limb. This is the "extensor thrust[1]." It is practically annulled by severance of the two plantar nerves. The movement amounts to a vigorous thrust of the foot downward and backward. Were the foot on the ground this extensor thrust would propel the body forward and upward. The mode of its elicitation suggests that the weight of the animal applied through the foot against the ground probably excites it in the natural course of the step. When first describing[2] the reflex I regarded it as likely to supply the looked for stimulus of direct extension of the stepping limb. Philippson[3] has allotted this rôle to the reflex in his description of the reflex mechanism of the trot.

Further acquaintance with this reflex leads me to doubt whether it plays an important part in the stepping of the walk and trot. Section of the nerves of the foot annuls this reflex, but does not seriously impair reflex stepping. The ipsilateral extension which the reflex gives is

---

[1] *Integrative Action of the Nervous System,* p. 67.

[2] This *Journal,* xxix. p. 58. 1903.

[3] *Op. cit.* p. 32.

usually synchronously accompanied by crossed extension, the form of extension of the crossed limb being a brisk vigorous thrust backward like that of the ipsilateral limb itself. The stimulus evokes, in fact, a bilateral thrust backward symmetrically executed by both hind-limbs. Such a movement is incompatible with walk or trot. It is however perfectly accordant with the movement of the gallop. This latter significance for the reflex is strengthened by a further observation. In a dog, in which spinal transection had been carried out between 6th and 7th cervical nerves and the animal kept under examination 132 days subsequently, the "extensor thrust" was easily obtained from either hind-foot. The elicitation of the thrust in either hind-foot was accompanied by a synchronous sharp extension not only of the fellow hind-limb, but of both fore-limbs as well. Elbows and wrists were extended and thrown forward at the same time that hind-limbs were extended and thrust back. The movement obviously resembled a phase of the gallop. The observation supports Philippson's[1] view of the reflex as contributory to the gallop. If however it plays any part in the walk or trot it can only do so in some weakened form in which it is unaccompanied by its collateral effects on crossed hind-limb and ipsilateral fore-limb. Moreover, reflex stepping, even in the shape of the gallop, goes forward in spinal dog, as Philippson[2] has shown, when the animal is supported in the air and therefore in absence of all pressure stimuli to the feet. The extensor thrust cannot therefore be an indispensable factor in the reflex step. The possibility however remains that, under conditions appropriate to it, it is a contributory factor, though not an indispensable one.

Extension of the limb can also be obtained as a reflex result of stimulation of certain superficial afferents of the inguinal, ischial and perineal regions. Grounds were adduced above (Sect. I, p. 54) for regarding these reflexes as not concerned with progression, but as more probably sexual, etc. The extension they evoke in their own limb is accompanied by synchronous extension of the crossed fellow limb, a movement incompatible with walk or trot.

The intrinsic stimuli for reflex stepping of the limb do not therefore appear referable to any part of the skin of the limb. Movement of the limb as an excitant of stepping in it appears to act in virtue of deep receptors of the limb. Supporting this latter possibility are the following data. (i) Artificial stimuli, both mechanical and electrical, applied to the afferent nerves of the limb muscles uniformly evoke (*v. supra,*

---

[1] *Op. cit.* p. 36.

[2] *Op. cit.* p. 29.

Sect. I, II, pp. 35 and 55) reflex flexion of their own limb and reflex extension of the fellow limb. (ii) Passive stretch of the knee extensor excites reflex relaxation of that muscle[1] and reflex contraction of the crossed fellow muscle[2]; and this reflex is excited through the afferent nerve of the extensor muscle itself[3]. (iii) Passive, and also active, shortening of the knee extensor excites contraction of that muscle and sometimes, though not regularly, reflex relaxation of the crossed fellow muscle[4]; and here again the afferent nerve is that of the knee extensor itself. (iv) A gentle brief passive extension of the limb in the decapitate preparation is often immediately followed by active flexion of the limb. Of the muscles engaged in spinal stepping, one of the most active is the sartorius. With this muscle the following observation can usually be obtained in the decapitate preparation (cat). The peroneal, popliteal, small sciatic and obturator nerves are severed, also internal saphenous at groin and the nerve of quadriceps extensor. Sartorius in that limb is rapidly resected from its insertions and separated from all lateral and deep connections, so that it lies free and retracted on the front of the thigh, retaining however its nerve and blood supply. The knee is then lightly held with one hand and somewhat quickly extended by means of the foot held in the other hand. As this is done the sartorius is seen to contract, especially when the extension of knee reaches completion. This reflex contraction of sartorius occurs chiefly in the medial band (*v. supra*, p. 45) of the muscle. That band is pre-eminently a flexor of knee. This reflex can be obtained many times in fairly rapid succession. Conversely on passively flexing the knee a reflex contraction usually occurs also in sartorius, but pre-eminently in the lateral band of the muscle. This band is especially in its distal part an extensor of knee. Adduction and abduction of thigh under these circumstances and also when obturator nerve has been left unsevered does not in my experience cause contraction in sartorius. Extension of hip does do so occasionally and then the contraction is chiefly of the proximal part of lateral band; that part is a flexor of hip.

Similar observations can be obtained from semitendinosus, biceps femoris posterior, tenuissimus and gracilis. Passive extension of knee and ankle or of either of these joints alone excites contraction in

---

[1] Sherrington. *Q. J. of Expt. Physiol.* II. 1909.

[2] Philippson. *Op. cit.* p. 31.

[3] Sherrington. *Q. J. of Expt. Physiol., loc. cit.*

[4] Sherrington. *Ibid.*

those muscles when they have been completely detached from their insertions at knee. The passive extension still excites the reflex when internal and external saphenous nerves, and musculocutaneous of peroneal and posterior tibial close above ankle have been severed and the foot thus far deafferented is used for manipulating the limb in the movement. The reflex contraction is a brief one, the stimulus seeming to consist therefore in the movement of extension and not in the extended posture when once assumed.

(v) An important stimulus in the reflex step lies at the attached base of the limb and is produced by extension of hip (*v. supra*, p. 76). Exteroceptive stimuli having been excluded (*v. supra*, p. 78) it seems natural to relate that stimulus to changes in form and tension of muscles and fasciæ. The muscular sense-perceptions of the limb are finer for its proximal joints than for its distal (Goldscheider)[1]. Magnus[2] has shown that in regard to the influence of initial posture upon the direction of the reflex movement of the limb, the influence of hip is greater than knee and of knee than ankle. The flexion-reflex, as an exteroceptive reaction, is most potently excited from the free apex of the limb (*v. supra*, Sect. I, p. 32). The stepping reflex, as regards deep stimuli situate in the limb itself, seems most excitable by stimuli at its attached base. This is as would be expected if the latter reflex is as regards its afferent source in the limb itself a proprioceptive reaction.

3. *Flexion-phase of the spinal step.*

The flexion movement evinced in the reflex step differs in several particulars from that seen in the scratch-reflex. But with the flexion movement of the nociceptive flexion-reflex it agrees singularly closely. The main difference is that in the flexion phase of the step the flexion is not maintained and flexion at knee and ankle ceases somewhat earlier than does the flexion at hip, whereas in the nociceptive reflex flexion at all three joints is maintained. But when the reflex step is not vigorous in the spinal preparation the flexion at all three joints tends to cease at the same time. The stepping reflex then has the character to which its earliest observer, Freusberg[3], probably alluded when he termed it the "mark-time" reflex, for it then fails to properly advance the limb over

---

[1] *Arch. f. Physiol.* Leipzig, 1889.

[2] *Pflüger's Archiv*, CXXX. p. 219. 1909.

[3] *Ibid.*, IX, 1874.

the ground. The other differences between the flexion of nociceptive flexion-reflex and that of the reflex step are that in the former the flexion is greater, and is succeeded by extension only after the stimulus is withdrawn, whereas in the step-reflex it is succeeded by extension during the continuance of the stimulus.

Under analysis of the musculature at work in the two reflexes the similarity between the flexion of the flexion-reflex and that of the flexion phase of the step is again significantly close. By appropriate isolation of the muscles of the limb and by then exciting the stepping-reflex it is possible from a series of experiments to draw up a list of the muscles which contract and relax in the flexion phase of the spinal step. The list can hardly hope to be complete, since the procedure for isolating the individual muscles is necessarily severe and heightens the reflex threshold. The interference with the reflex which the requisite severance of a number of muscular nerves in the limb causes is greater than in the case of the nociceptive flexion-reflex. This is of itself suggestive of the proprioceptive nature of the former reflex. Often when the necessary isolation of a particular muscle has been completed the reflex, although previously regular and vigorous, is obtainable no longer.

In the series of experiments performed the muscles actually observed to contract in the flexion phase of the reflex step have been as follows:

Psoas magnus
Sartorius median band
Sartorius lateral band, upper part

Rectus femoris
Gracilis
Biceps femoris, posterior part
Semitendinosus
Tibialis anticus
Extensor longus digitorum
Tensor fasciæ femoris brevis
Peroneus longus
Gluteus minimus
Tenuissimus.
Extensor brevis digitorum.

These are all of them muscles which contract in the flexion of the nociceptive flexion-reflex. In the latter certain other muscles (psoas parvus, pectineus, tensor fasciæ femoris longus) were ascertained to contract also. In the flexion phase of the spinal step I have not been able to assure myself that they do, but it would be hazardous to say that they do not when the step is well developed.

In addition to the above which contract the experiments show that certain other muscles relax in the flexion phase of the reflex step. These are:

Semimembranosus
Vastus lateralis
Vastus medialis
Crureus
Adductor minor
Gastrocnemius
Soleus
Biceps femoris anterior.

These also are all of them muscles which relax in the flexion of the nociceptive flexion-reflex. In the latter there were also ascertained to relax part of adductor major, and distal part of lateral band of sartorius. These may relax also in the flexion phase of the reflex step but I have not been able to assure myself that they do.

4. *Extension phase of the spinal step.*

Just as flexion phase of the reflex step resembles the flexion-reflex in its play on the musculature of the limb, so the step's extension phase resembles similarly the crossed extension reflex of the limb. Observations by the same method show that in the extension phase of the step muscles which contract are:

Quadratus femoris
Vastus lateralis
Crureus
Sartorius (part of lateral band)
Vastus medialis
Adductor minor

Biceps femoris, anterior part
Gastrocnemius

Soleus
Flexor longus digitorum.

The muscles observed to relax are:

Psoas magnus
Sartorius, medial band
Rectus femoris
Gracilis
Semitendinosus.

Biceps femoris, posterior part
Gluteus minimus
Tibialis anticus
Extensor longus digitorum

The muscles which contract are muscles which contract in the crossed extension reflex and those which relax are muscles which relax in that reflex. Flexor longus digitorum in the crossed extension reflex certainly contracts late; its contraction appears to come late also in extension phase of step.

5. *The "simultaneous coordination" exhibited.*

Analysis of the behaviour of the individual muscles confirms therefore the similarity between flexion phase of step and the flexion-reflex of the limb and between extension phase of step and the crossed extension reflex of the limb. The principles (Sect. I, p. 45, and II. p. 56) of neural taxis and coordinative handling of the muscles exemplified in the nociceptive flexion-reflex and the crossed extension reflex therefore apply also to the reflex step.

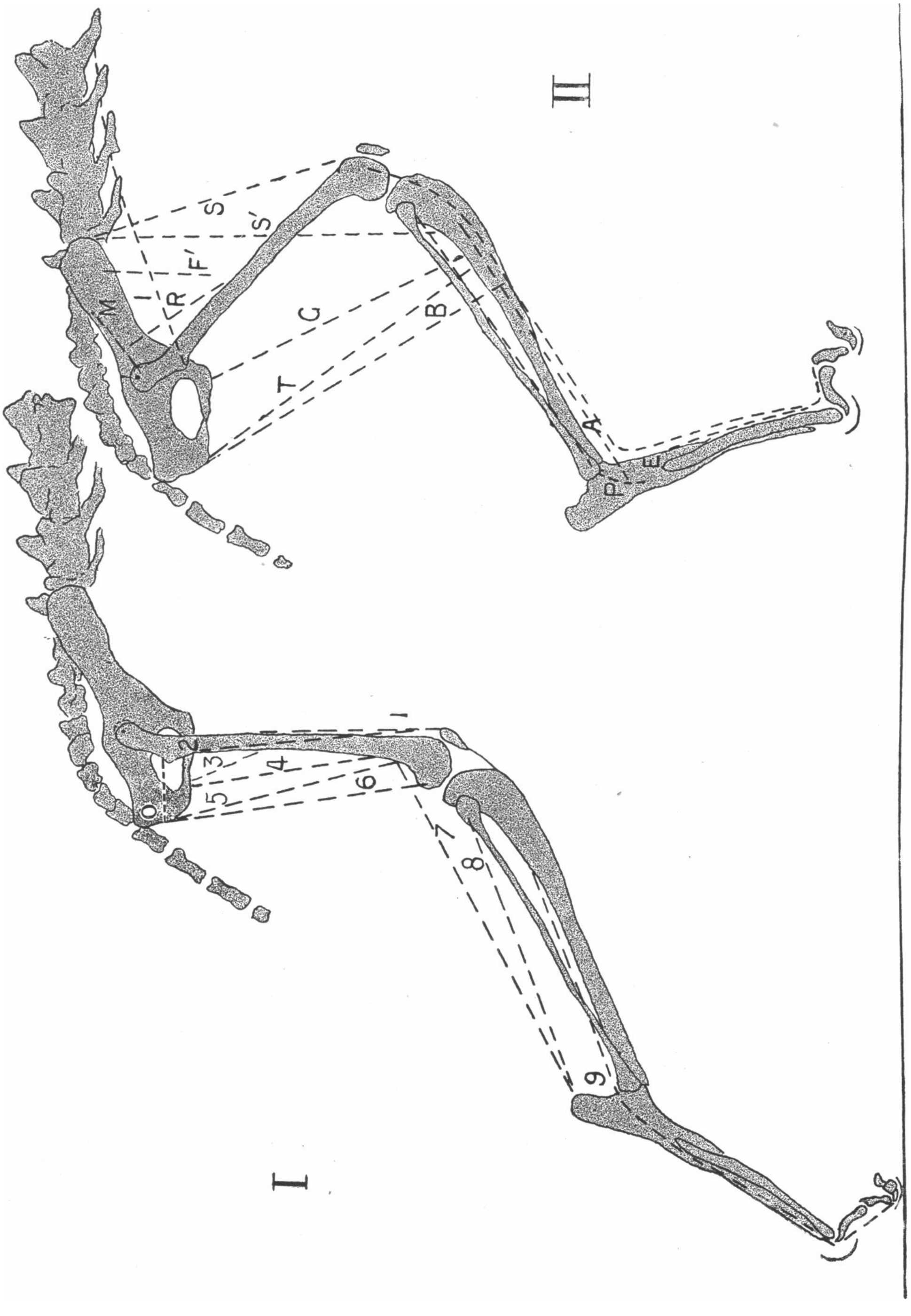
II
S
S'
F'
R
M
C
B
T
A
P
E
I
1
2
3
4
5
6
O
7
8
9

Fig. 10. Muscles observed by direct analysis to contract in the spinal step (cat, dog) I, in the extension phase, II, in the flexion phase.

1. Crureus and vastus medialis
2. Vastus lateralis
3. Adductor minor
4. Adductor major in part
5. Semimembranosus
6. Biceps femoris anterior
7. Gastrocnemius
8. Soleus
9. Flexor longus digitorum (really passes internal to ankle)
0. Quadratus femoris

A. Tibialis anticus and extens. long. digit.
B. Biceps femoris posterior
E. Extensor brevis digitorum
F′. Tensor fasciæ femoris brevis
G. Gracilis
I. Psoas magnus
M. Gluteus minimus
P. Peroneus longus
R. Rectus femoris
S. Sartorius lateral band, S′ medial band
T. Semitendinosus.

Just as the nociceptive flexion-reflex does not exhibit fully the same form when excited from widely different small afferent nerves of the limb (Sect. I) so in the decapitate preparation the step-reflex varies somewhat in character as excited from this or that afferent source. When elicited in the decapitate preparation from perineal region or tail the stepping movement includes less flexion at hip than when elicited from a fore-limb or from the neck. In the dog the stepping when it first emerges after spinal transection in the thoracic region is often almost exclusively a rhythmic flexion at hips. The most usual imperfection in the step executed as a purely spinal reflex is in regard to the extension and flexion of the digits. The digits may even slightly passively flex when the ankle dorso-flexes, indicating that extensor brevis digitorum is not acting and that extensor longus digitorum is not acting strongly. Movement of the digits is often practically absent when the spinal stepping is feeble, though strikingly present in the vigorous reflex stepping of the spinal preparation after full recovery from shock[1]. These variations in form and completeness of the spinal step suggest that as regards any source which it has in the afferents of the limb itself that source is multiple, and though predominantly connected with the hip has also contributory channels from other regions of the limb. The remote source is often single, but the intrinsic source is probably commonly multiple.

6. "*Successive coordination*" *in spinal stepping.*

i. Salient features in the problem of the successive coordination of the reflex step are the anterior and posterior turning points of the movement. The reflex consists of an alternation of two antagonistic reflex movements, of flexion and extension respectively. It might have

---

[1] H. Munk. *Sitzungsber. d. Berlin Akad. d. Wissensch.* 1909.

been thought that for this two rhythmically repeated external stimuli were necessary. But experiment shows that it can be excited in its entirety by various single stimuli and these not rhythmic but continuous in character. I include here among continuous stimuli faradic since although intermittent their rhythm (30—100 p. sec.) obviously bears no relation to the rhythm (about 2 p. sec.) of the reflex. In the decapitated preparation it is excited and maintained in a hind-limb by continuous pressure of a clip affixed to a remote point of skin (*v. supra*, p. 74); by faradisation of one or other of certain points in the cross section of the bulb or of the cord in the 1st and 2nd cervical segments; or by faradisation of an appropriate afferent nerve.

For direct stimulation of the cut surface of the bulb or cord this faradisation has been carried out as follows. A diffuse electrode consisting of a large copper plate covered with cotton wool soaked in warm strong NaCl solution is applied to the shaved surface of the upper arm. A single-wire electrode of the pattern described in a previous paper[1] is applied to the fresh cross-section of bulb at calamus scriptorius after removal of the head. Weak faradisation, *e.g.* 40 units of the Kronecker scale when applied in the region of funiculus gracilis evokes reflex stepping in the ipsilateral hind-limb; this stepping commences with flexion of the limb including hip-flexion. If the stimulus be weak the stepping may be confined to the ipsilateral hind-limb; if stronger, stepping of the contralateral hind-limb commencing with extension, occurs also. Occasionally a similar result has been obtained from an area ventral to the caput cornu posterioris. These localisations in the cross-section are mentioned but the uncertainty in restricting the effect of the currents to minute spots makes them mere approximations.

Elicitation of the reflex by these continuous stimuli must mean that the stimulus having produced its opening effect, *e.g.* flexion becomes after a ¼ sec. or so inoperative for that reflex, and on the other hand apparently operative for the opposite reflex, viz. extension for which it was not at first effective; and then ¼ sec. later becomes again operative for flexion and not for extension, and so on. In other words there occurs rhythmically a refractory phase for flexion accompanied by removal of a refractory phase for extension, and then a refractory phase for extension accompanied by removal of a refractory phase for flexion. In the stepping reflex we have as in the scratch reflex a reaction with a rhythmically recurrent refractory phase which seems to alternately block one and then the other of two opposed simpler reflexes. The seat of the rhythm is obviously not peripheral. It is not in the muscles or their motor nerves for they do not when thrown into activity in other ways show any trace of rhythm of this frequency. Nor can it lie in the receptive organs of the skin or their afferent nerve trunks for

---

[1] A. Fröhlich and Sherrington. This *Journal*, XXVIII. 14. 1901.

direct stimulation of the cross section of the spinal axis itself provokes the rhythmic reply. The rhythm is therefore central in its seat.

Remembering that proprioceptive stimuli aroused in the limb itself can excite the reflex the possibility naturally suggests itself that the reflex movement of the limb initiated by a distant stimulus will arouse in the limb stimuli capable of modifying the influence there of the original stimulus. To take for instance the step-reflex of the hind-limb as evoked by stimulation of the ipsilateral fore-foot. The opening phase of the step-reflex is then usually extension. But as shown (*v. supra*, p. 75) extension of the limb produced by letting the limb drop under its own weight provokes when the extension has reached its full an ensuent active flexion of the limb, accompanied by extension of the opposite hind-limb. Extension of the limb appears therefore to evoke in the limb a stimulus exciting flexion of its own limb, accompanied as usual by crossed extension of fellow limb. Applying this to the step-reflex produced by fore-limb stimulation, the stimulation of fore-limb by extending hind-limb tends to evoke secondarily in hind-limb a stimulus for flexion of this latter. Now, stimuli exciting the flexors of the limb concurrently inhibit the extensors. There would therefore ensue from the primary, the distant, stimulus A, a secondary stimulus in the limb itself, a proprioceptive stimulus, B tending to cut short the influence of A and replace A's reflex by the opposite reflex, namely flexion. But the mere execution of the flexion removes the stimulus B which caused it, and allows the influence of the continuous primary stimulus A to exert itself again. Thus the proprioceptive stimuli aroused secondarily in the limb tend to give the continuous influence of A a rhythmic intermittent effect[1].

The experimental results point therefore to a mechanism comparable with that of the *Selbsteuerung* of the inspiratory movement first noted by Hering and Breuer[2]. There contraction of the diaphragm in inspiration is in due course cut short by a reflex inhibition traceable to a stimulus generated by the mechanical action of the diaphragm itself. In this respiratory mechanism the stimulus so generated arises mainly in the lungs and the vagus is therefore the main afferent nerve. Baglioni[3] has moreover shown a contributory source in the diaphragm

---

[1] Cf. H. Winterstein, *Pflüger's Archiv*, CXXVII. 527. 1909.

[2] *Sitzungsb. d. k. k. Akad. d. Wissensch. Wien.* LVIII. 909. 1868.

[3] *Centralbl. f. Physiol.* 23. 1903; also Mislawski, *Centralbl. f. Physiol.* 1901. Cf. also for the chest wall as a whole, R. du Bois Reymond and Katzenstein, *Arch. f. Physiol.* p. 513. 1901.

itself, the centripetal impulses ascending afferent fibres in the phrenic. In these reactions there is evident analogy between the rhythmic reflex inspiration and the rhythmic reflex of the step; for in each the movement is arrested and reversed by a secondary reflex generated mechanically by the primary movement itself and antagonistic to the primary reaction in its influence on the muscles. Similarly with the vasomotor centre and the heart, activity of the general vaso-constrictor centre by raising the arterial blood-pressure stretches the aortic wall and by so doing mechanically excites *n. depressor*, the afferent nerve of the aorta[1], and thus reflexly moderates the activity of the vasomotor centre itself, the originator of the whole reaction. In these cases the primary reaction generates a secondary antagonistic to the primary itself.

Thus there recurs rhythmically during reflex stepping a conflict between two stimuli exerting opposed influence on the motoneurones of the limb musculature. The case of the concurrence of two stimuli having opposed influence on one and the same group of motoneurones has been examined[2], and for the case of two muscles which the reflex step actually engages. The result of the conflict between the opposed influence is found to fall into one or other of three types determined by the relative intensities of the two opposed stimuli. We may take the case of S, the remote and primary stimulus, being excitant for motoneurons E and inhibitory for motoneurons F. If while S is in operation a stimulus Σ arises whose influence is inhibitory for motoneurons E and excitant for motoneurons F, the three types of result actually observed are as follows. (α) If Σ be much weaker than S its inhibitory influence is unable to outwardly modify S's excitatory influence as expressed by the contracting muscle; similarly, S's inhibitory influence wholly prevents Σ's excitatory effect from showing on the opponent muscle. (β) If Σ is much more intense than S the former's excitatory effect, to judge by the muscle, overcomes S's inhibitory effect wholly, and Σ's inhibitory effect wholly suppresses S's excitatory effect. (γ) If S and Σ are of not widely unequal intensity the excitatory influence of S is partially suppressed by the inhibitory influence exerted by Σ and the inhibitory influence of S only partially suppresses the excitatory of Σ. In effect there results contraction of the muscles E' which S excites and of their antagonists the muscles F' which Σ excites; but the grade of contraction of E' is less than when S is acting without Σ, and the grade

---

[1] A. Tschermak and Koster, *Pflüger's Archiv*, XCIII. 1902.

[2] Sherrington, *Roy. Soc. Proc.* B. 80. Nov. 1908, Vol. 81, 249. March, 1909.

of contraction of F' is less than when Σ is acting without S. In short *double reciprocal innervation* is at work and the influences of stimuli S and Σ add themselves algebraically in their effect on the muscles E' and F', and therefore on the motoneurones E and F.

In the limb-reflex therefore when the stimulus S by the mechanical effect of its reflex on the limb generates there a local proprioceptive stimulus Σ antagonistic to S itself, the particular result which will accrue will depend on the relative intensities of S and Σ. When S is very intense in comparison with Σ, as is the case when a nocuous cutaneous stimulus is applied to the limb itself, Σ is unable to modify the effect of S and there results the usual *nociceptive unalternating* reflex, the protective reflex folding up the limb out of harm's way. When the local centre is brisk and the skin stimulus not too powerful even with this nociceptive reflex Σ sometimes breaks through S in a brief partial and irregular manner.

When S is remote and for that reason relatively less intense even though cutaneous and nocuous the intensity of the secondary generated Σ is not so unequally matched with it; Σ then interferes with the effect of S regularly, and the rhythmic alternating reflex "stepping" ensues. And frequently in spinal stepping the to and fro movements of the limb oscillate not about a neutral position of the pendent limb but about a position in which the limb is somewhat extended or somewhat flexed. For instance, stimulus S when in the median line of the perineum causes bipedal stepping of remarkably symmetrical character right and left, operating especially the knees and ankles. But if the point of application of the stimulus be shifted to one side of the midline the stepping is characterised by the greater flexion of the limb of that side especially of hip, while the stepping of contralateral limb exhibits increased extension of hip. That is, throughout the stepping the ipsilateral limb retains a somewhat flexed posture while the contralateral limb retains a somewhat extended one. Here clearly the relaxation of the flexors in the one limb and of the extensors in the other is incomplete. Now the cutaneous stimulus S is responsible for the flexion of the ipsilateral limb and for the extension of the contralateral. In the ipsilateral limb throughout and even at acme of extension phase there remains some contraction of flexors; and in contralateral limb throughout and even at acme of flexion phase there remains some contraction of extensors. The persistence during a protagonist's contraction of some contraction in its antagonist is as regards spinal reflexes characteristic of the simultaneous operation of two antagonistic stimuli of nearly balanced action on the muscle couple. The case is 3, *i.e.* (γ) of the three cases experimentally tested above. The solution indicated therefore for these forms of the spinal stepping is two antagonistic stimuli and double reciprocal innervation. And similarly with the scratch-reflex where the to-and-fro movement of thigh oscillates about a position in which the thigh is even at completion of the extension phase still somewhat flexed[1]. Similarly with the respiratory movements, when they are quick and deep the contraction of the diaphragm does not wholly cease during expiration[2]; the diaphragm relaxes but its relaxation is incomplete. In the above instance the incompleteness of the relaxation of the flexors in ipsilateral limb indicates that Σ in that limb is relatively weak as against S; and the same relative weakness of Σ is indicated by the incompleteness of the flexion of the contralateral limb for there S is an extensor stimulus.

Hence it is evident that the particular form assumed by the reflex stepping of a limb is influenced by the nature (locus, etc.) and intensity of the remote initiatory (cutaneous or other) stimulus S in relation to the secondary proprioceptive one Σ. The exact degree of rhythmic relaxation being graded by the grading of the intensities of the two opponent stimuli S and Σ, the reflex step can assume in consequence various forms appropriate to this or that circumstance. Just as the plasticity of the tonus allows various modifications to the standing posture.

Whether the intensity of the secondary proprioceptive stimulus Σ is ever high enough in comparison with that of the initiatory remote (cutaneous) stimulus S to give the second type of result (β) remains without direct answer from my observations. My impression is that in the vigorous more perfect reflex stepping of the spinal hind-limbs of the dog after the period of shock has passed, such a combination usually occurs. The amplitude of the excursions of the step is then great. It may well be that flexors and extensors then alternately fully relax, just as in natural breathing[3] the diaphragm not unfrequently during the expiratory phase shows for a short time complete absence of all contraction. The reflex stepping of the spinal hind-limbs of the dog after the period of shock has passed, proceeds with remarkable freedom from

---

[1] This *Journal*, XXXIV. 1. 1906; T. Graham Brown, *Quart. Jnl. of Expt. Physiol.* II. 243. 1909. *Ibid.* III. 21. 1910.

[2] R. Dittler, *Pflüger's Archiv.* 130, p. 400–443. 1909. For an interesting comparison between the nervous regulation of the respiratory movement and of a limb-joint, see F. H. Scott, this *Journal*, XXXVII. 301. 1908.

[3] R. Dittler, *ibid.*

fatigue. It will continue for a quarter of an hour or more without obvious abatement. This is intelligible in light of the fact that the muscles whose contraction, *i.e.* the motoneurons whose discharge, produces the movement of the one phase of the step are none of them those whose contraction, *i.e.* discharge, produces the movement of the other phase. It is obvious that fatigue is least likely to affect such a reflex when primary stimulus S and secondary proprioceptive stimulus Σ are so balanced that Σ on each recurrence suffices to reduce to complete quiescence S's motoneurons and muscles, and S in its turn to completely quell any after-discharge due to Σ. The advantages of such a balance seem to explain the common experience and every day teaching that there is a proper way of walking, etc., as distinguished from bad habits of walk, etc. Walking for instance with a crouched posture of the limb must entail that the extensor stimulus never renders the flexor neurons fully quiescent, so that the action of the walk entails an ingravescent fatigue. And this would be avoided were the limb freely extended at each extension phase. A full and free extension phase connotes a full and free relaxation of flexors and a phase of complete quiescence for their neurones: and vice versa.

The reaction caused by the secondary stimulus Σ, the proprioceptive stimulus, tends itself in its turn to generate a proprioceptive stimulus of opposed influence to the secondary stimulus Σ, and harmonious with the original primary stimulus S. Evidence of this is given by the fact that the stepping reflex once started often outlives for many seconds the duration of the primary stimulus which originally evokes it, it continues for a time after the primary stimulus is altogether withdrawn. Where, as in the spinal preparation, there is nothing to restrain it. It proceeds for a time by its own intrinsic stimulation of the limb. The same holds true for the scratch-reflex, and constitutes one of a number of resemblances between these two rhythmic alternating reflexes of the limb. And in both this after continuance of the reflex can be cut short by mere mechanical passive arrest of the moving limb.

Certain difficulties however attach to the explanation of the rhythmic reflex of stepping by interference between remote and secondary intrinsic stimuli. These are (1) that passive movement especially flexion does not so regularly and potently excite opposite active movement, especially extension, as might on the above view be expected: (2) that sartorius when isolated and detached except for nerve and blood supply will still sometimes "step" on faradisation of cervical cord: (3) that a hind-limb when deafferented (3rd to 9th post-thoracic afferent roots inclusive severed) still gives traces of the reflex step on faradisation of ipsilateral side of spinal cord at 1st cervical level; and that the scratch-reflex which in many ways resembles the stepping-reflex is under similar circumstances still elicitable. These difficulties suggest that generation of a secondary local stimulus and its interference with the operation of the primary remote stimulus, although *regulative* of the rhythm (cf. vagus and respiratory rhythm) is of itself not the sole rhythm-producing factor in the reflex. Other factors (*vide* following subsections ii, iii, and v) to be considered are "Umkehr," rebound, and influence from contralateral fellow limb.

ii. "*Umkehr*" (*v. Uexküll, Magnus*). In the ray-arm of the Brittle-star, *Ophioglypha*, v. Uexküll[1] has found that a given stimulus tends to excite contraction in whichever of the two opposed muscles is at the time the more stretched. Magnus shows that the same phenomenon is exhibited by the tail (cat)[2] when rendered spinal. Also[3] that it is clearly seen in the spinal reflexes of the hind-limbs of the dog. He has demonstrated this influence in two limb reflexes especially interesting in connection with the step, namely in crossed extension reflex and the crossed reflex-flexion of hip elicited by passive extension of the other hip. From these observations we learn that in mobile parts furnished with antagonistic muscles passive extension tends to make the reflex effect of a given stimulus flexion of that part whereas passive flexion tends to make the reflex effect extension. This reversal (Umkehr) would in such a reflex as the step explain the anterior turning point by the mechanical flexion of the limb when it had reached a certain grade diverting the excitatory effect from flexor motoneurons to extensor motoneurons; and the posterior turning point conversely. Such an explanation would be a welcome solution of the problem; and the observations already obtained by Magnus show that this reversal is potent in mammalian spinal reflexes just as in the reflexes of the Echinoderm. Can the "Umkehr" of itself explain the rhythmic alternation of flexion-extension and extension-flexion in the reflex step? Were it by itself able to produce the turning points of the reflex step one would, I think, expect passive flexion and passive extension of the limb to determine still more easily than at present they seem to movements of opposite direction to their own.

Further, in the step reflex when isolated muscles are under observation I have several times seen a muscle still exhibit the rhythmic

---

[1] *Zeitsch. f. Biol.* XLVI. I. 1904; *Ergebn. d. Physiol.* III. 2. 1. 1904; cf. also Mangold, *Pflüger's Archiv*, CXXVI. 371. 1909. *Zeitschr. f. Physiol.* XXIII. 141. 1909.

[2] *Pflüger's Archiv*, CXXX. p. 251. 1909.

[3] *Ibid.* CXXX. p. 219. 1909.

response when quite severed from its insertion and lying unstretched and retracted, and when rhythmic movement of the limb was practically excluded and what slight movement still persisted in the limb could not mechanically affect the tension of the isolated muscle itself. Muscles in which the rhythmic response has under these circumstances still persisted have been sartorius and semitendinosus. Thus, in sartorius good rhythmic response was seen when the muscle lay retracted on the front of the thigh attached only at its upper origin, and after complete severance of the popliteal, peroneal, hamstring obturator and vasto-crureus nerves, and after psoas magnus, psoas parvus, tensor fasciæ femoris, the glutei and all the muscles attached to the trochanters and intertrochanteric line had been resected up from their insertions. Yet the muscle on stimulation of the cross-section of spinal cord at 1st cervical segment responded with its usual rhythmic contraction. It lay retracted into a short lump and formed a rhythmically jumping heap when the step reflex was elicited. It is true that the rhythmic "stepping" of the muscle thus isolated is always relatively weak: but it is difficult to see how under such circumstances Umkehr could produce the rhythmic response. I have seen a similar reaction with scratch-reflex. Professor Magnus does not indeed suggest that the "Umkehr" is responsible for the rhythmic alternation either of the scratch-reflex or of the step-reflex. But the importance which the "Umkehr" phenomenon assumes in the light of his own and v. Uexküll's fundamental papers, makes it natural in seeking an explanation of the "turning points" in these reflexes to consider the influence of "Umkehr" as a possible factor. It seems to me a contributory factor but unable of itself alone to explain the alternations in these reflexes.

The alternating movement of the reflex step of the limb may open either with flexion phase or extension phase. Which phase it is which forms the opening phase in any particular case is clearly a matter of rule. The opening phase is flexion in the hind-limb when the exciting stimulus is applied to contralateral fore-limb or to ipsilateral column of the spinal cord, and usually when applied to ipsilateral pinna or neck. It is extension when the stimulus is applied to crossed hind-limb, and generally ipsilateral fore-limb, and sometimes to ipsilateral pinna. Magnus[1] has shown that in the spinal hind-limbs of the dog when reflex stepping is elicited by dropping one thigh the primary movement of the crossed hip which is flexion when the initial pose of the crossed limb is extension often becomes extension when the initial pose of the

---

[1] *Pflüger's Archiv*, cxxx. p. 245. 1909.

crossed limb is full flexion (Umkehr). In the decapitate cat on exciting stepping in the hind-limbs by stimulating the tail, the preparation being symmetrically supine, I find, following Magnus's plan with the crossed-reflex, that if the initial pose of one hip be full flexion the opening phase of the reflex step in that limb is extension, whereas if initial pose be extension, the opening phase of the step is flexion. Similarly in decerebrate rabbit. Pinching tail gives there a symmetrical hopping movement of both hind-limbs. If the initial pose of the hind-limbs be extension the opening phase of the reflex is bilateral flexion of hips, if the initial pose be flexion the opening movement is extension. I have not determined the latencies of the movements, but in view of Magnus's observations I think these reversals of direction of the opening phase of the step, obtained by following the procedure described by him, may be instances of the "Umkehr" influence he has demonstrated.

iii. *Central Rebound.* Passive movements of the limb by inducing proprioceptive stimulation certainly produce reflex effects in it and the fellow limbs. *Active* movements however are as sources of reflex influence probably more important, and involve moreover central nervous changes excitatory and inhibitory additional to those accruing to passive reactions.

In each phase of the reflex step certain muscles are by appropriate isolation ascertained to relax (*v. supra,* p. 82). They are found in each phase to be the antagonists of the muscles which contract. The inference is that in this case as in the ordinary flexion-reflex and crossed extension reflex, there is reciprocal innervation of the prime-movers and their antagonists and that the relaxation of the antagonists is due to central inhibition. This inference can be tested as follows. A character of decerebrate rigidity is that it suppresses the recurrent refractory phase of the limb reflexes which are alternating in the decapitate preparation (*v. supra,* Sect. III, p. 70). The same stimulus which in the decapitate preparation excites reflex stepping with extension as its opening phase, excites when exactly similarly applied in the decerebrate preparation the same movement, namely, extension, but there then supervenes no reverse movement, it simply becomes a posture which is maintained as long as the stimulus. This gives time for examining the conditions of the muscular arcs in the reaction. The flexor arcs are found to be under inhibition. If the reaction be induced at a time when the flexors are already actually contracting in response to an appropriate reflex stimulus they immediately relax in spite of continuance of the excitatory stimulus[1]: and when the reaction is over they immediately show their previous contraction again. I have ascertained this both for sartorius and semitendinosus, two of the most active flexor muscles in the step; and venture to assume that it applies to the rest of the "flexor" group. Similarly the stimulus which in the decapitated preparation excites reflex stepping beginning with flexion phase, produces in the decerebrate simply maintained flexion. Examination in the above way shows that here again the relaxation of the extensors is due to central inhibition. This has been ascertained individually for vasti, crureus, soleus, gastrocnemius, biceps femoris anterior, quadratus femoris and adductor minor, and presumably applies to the whole group.

It seems clear therefore that in the flexion phase of a step-reflex which begins with flexion, excitation of the flexor motoneurons is accompanied by inhibition of the extensor motoneurons; and in the extension phase of a step-reflex which begins with extension excitation of the extensor motoneurons is accompanied by inhibition of the flexor motoneurons. We may assume that this obtains at every repetition of these phases.

Inhibitory depression of spinal motor centres is followed on removal of the inhibition by a state of activity greater than that obtaining in them before the inhibition[2]. This is the case alike in decapitate, spinal and decerebrate preparations. An instance illustrating it is the following. Suppose a crossed extension reflex elicited at regular interval by a given stimulus. The reflexes form a series of practically constant amplitude and duration. If in the interval between two such successive reflexes a strong flexion-reflex be elicited in that limb whose extensor muscles are replying, the extensor reflex next following is ampler and longer lasting than the previous one[3]. The flexion-reflex laid the extensor motoneurons under inhibition. On cessation of the flexion-reflex the inhibition subsides and subsequently for a short time an exciting stimulus (crossed-reflex) finds the extensor motoneurons in a condition of exalted responsiveness and excitability. Similar post-inhibitory exaltation was noted in the inspiratory centre by Head[4]. He stimulated central end of one vagus with faradic currents just too weak to produce complete tetanic contraction of the diaphragm. During

---

[1] *Roy. Soc. Proc.* LXXXI. B. 249. 1909.

[2] *Integrative Action of the Nervous System*, p. 206.

[3] Sherrington. *Roy. Soc. Proc.* LXXVII. B. 478. 1906.

[4] This *Journal*, x. p. 1. 1889.

this condition an inflation of the lung at once produced relaxation of diaphragm by reflex inhibition. After the inflation on the lungs returning to their normal volume the stimulus previously ineffectual to produce complete tetanus of diaphragm became at once effectual. As in this case the inspiratory centre so in the case of the limb the extensor centre after a period of inhibitory depression exhibits a period of increased responsiveness to excitation.

This post-inhibitory exaltation manifests itself not only by increased responsiveness to stimuli externally applied. It gives also the "rebound extensions," namely, those seemingly spontaneous extensions which follow on reflex flexion when the stimulus for the latter is withdrawn. In decerebrate and spinal reactions the withdrawal of a flexion stimulus is commonly followed by an active extension. Thus a brief nociceptive flexion-reflex is in the decerebrate preparation generally diphasic, active extension following as a rebound on the flexion when the external stimulus is withdrawn[1]. These rebounds are seen with fore-limb as with hind-limb, and in dog and rabbit as in cat. In my experience they follow better on cessation of a relatively short stimulus than on one prolonged for several seconds[2]. They ensue on centrally applied stimuli[3] as well as on peripheral. They are exhibited by muscles, *e.g.* vastocrureus, isolated from all but their own nerve supply and attachments, that is when all other nerves except that of the muscle in question have been severed in both hind-limbs of the decerebrate preparation[4].

In the decerebrate preparation these rebounds are although seemingly spontaneous probably not truly so. In the decerebrate preparation there is a tonic reflex excitation of the extensor centres and this is temporarily blocked by inhibition during the flexion stimulus. When that stimulus is withdrawn the tonic reflex excitation finds the extensor centres in post-inhibitory exaltation and produces a reflex extension greater than that it was producing prior to interruption by the flexion stimulus. But in the decapitate preparation it is more difficult to find a reflex explanation of the rebounds. They are in that preparation less common and less vigorous, but they occur. In that preparation there is no reflex excitation playing tonically upon the extensor centres. The extensor rebounds are perhaps then really spontaneous discharges of the extensor centres due to their state of

---

[1] Sherrington. This *Journal*, XXXVI. 135. 1907; *Roy. Soc. Proc.* B. LXXX. 53.

[2] *Proc. Roy. Soc.* B. LXXX. 61. 1908.

[3] *Ibid.* B. LXXIX. 348. 1907.

[4] *Proc. Roy. Soc.* B. LXXX. 53.

post-inhibitory exaltation; an autochthonous autonomic (E. Hering[1], A. v. Tschermak[2]) back swing following on allonomic inhibitory disturbance.

When the musculature of the limb is examined by the methods given above to determine which particular muscles exhibit the rebound on withdrawal of a flexion stimulus, these are found in the hind-limb to be the following:

Semimembranosus
Biceps femoris anterior
Vastus lateralis
Crureus
Vastus medialis
Adductor minor
Gastrocnemius
Quadratus femoris
Soleus
Sartorius (distal end of lateral division).

No muscles or part of muscles engaged in the flexion phase of the step show this rebound contraction ensuent on withdrawal of a flexion stimulus. In fore-limb muscles observed to exhibit rebound on withdrawal of a flexion stimulus have been

supraspinatus and humeral head of triceps.

Doubtless there are others but the above are those in which the phenomenon has been observed in the muscle when actually isolated.

The muscles responsible for the rebound extension both in hind-limb and fore-limb so far as observed are those which as shown above participate by contraction in the extension phase of the reflex step. When therefore the flexion phase of the step has been excited by an appropriate stimulus and in that way an incomplete step—incomplete because consisting of flexion phase only—has been produced, the reflex reaction is of itself competent to complete it in virtue of post-inhibitory rebound of the extensor centres giving the extension phase of the step.

Taking the case where a stimulus excites reflex stepping with flexion as its opening phase, for instance in the hind-limb when the stimulus is applied to the contralateral fore-limb or to the pinna, or to ipsilateral *funiculus gracilis* of the cord. When the refractory phase arrives and the stimulus ceases to have its excitatory effect on the flexor centres of the limb it may be presumed that its reciprocal inhibitory effect on the extensor centres similarly ceases. Post-inhibitory exaltation then ensues in the extensor centres and a rebound discharge occurs from them producing the extensor phase of the step. But when the refractory phase is past excitation of the flexors with

---

[1] *Lotos*, 1888.

[2] *Arch. d. Sciences biologiques, St Pétersbourg.* 1904.

inhibition of the extensors reappears, and a feature of rebound extension is the ease and promptitude with which it can be arrested by inhibition. An alternating reflex consisting of successive flexions and extensions will then result.

And post-inhibitory rebounds are not confined to extension. On cessation of an extension stimulus rebound contraction of flexors is often seen, though in my experience of less common occurrence than extension rebound after reflex flexion. With the crossed extension reflex in the decerebrate preparation there not unfrequently occurs on withdrawal of the stimulus a flexion of the crossed limb synchronous with the rebound extension in the ipsilateral limb. Taking the case of the stepping reflex initiated in one hind-limb by stimulation of the contralateral foot or of the ipsilateral fore-foot, the opening phase of the reflex step is extension. On supervention of the refractory phase under this stimulation a flexor-rebound will execute flexion until the refractory phase is past when the external stimulus reacquiring its original power will produce extension again, the reflex thus becoming alternating. It was shown above that the extension of the limb tends to produce in the limb itself a stimulus excitatory of flexion. This stimulus exciting the flexors concurrently inhibits the motoneurons of the extensors. The interference of an intrinsic limb stimulus causing flexion with a distant continuously applied stimulus causing extension will convert the latter's effect into a rhythmic alternation of extension and flexion.

iv. When the continuous remote (*v. sup.* p. 74) stimulus which evokes the rhythmic reflex of the step is increased in intensity the stepping movement is not only more forcible but is quickened in rhythm. This is so both when the stimulus is applied to appropriate points of skin and when it is applied to the cross-section of the cervical cord itself. With intenser stimulus the refractory phase occurs sooner. This agrees with the view[1] of Verworn, Baglioni, and F. Fröhlich who relate refractory phase to fatigue. But it is also compatible with the above view of the origination of the rhythm from two antagonistic stimuli a remote and an intrinsic which interfere. The more intense stimulus excites a quicker and more powerful opening phase of the step, and this tends more quickly and powerfully to generate the secondary proprioceptive reflex of the limb antagonistic to itself. A stronger step with higher frequency of rhythm in this way ensues.

If two separately located distant stimuli provoking the stepping

---

[1] *Biogenhypothese, Jena,* 1903; Verworn's *Zeitschr. f. allg. Physiol.* IV. 113, X. 110. Cf. also Verworn, *ibid.* VI. 11. 1906; and Fr. Fröhlich, *ibid.* VIII. 393. 1908.

reflex in a hind-limb be concurrently applied the result is an intensification of the stepping. This is so not only when the two stimuli are such as produce reflex stepping commencing with the same opening phase, but also when the two stimuli are such as to excite stepping of opposite opening phase, *i.e.* flexion from one stimulus, extension from the other. On the view above given this is what would be expected since the excitation phase of one reflex reinforces the rebound phase of the other, and conversely.

The observations indicate a difference between (*a*) the stimulation exciting the spinal step from distant skin-points or by direct faradisation of the cross-section of the cervical cord, and (*β*) the step-producing stimulation generated by simply allowing the hind-limb to drop pendent under its own weight. In the former case the primary stimulus although continuously in operation is interrupted in its effect by the rhythmic generation of a limb-reflex antagonistic to that which it itself excites. In the latter case a stimulus (passive extension) is applied which generates a reflex whose movement is opposed to the original passive one; and this active movement generates in its turn an active (reflex) movement opposed in sense to its immediate predecessor, and reinforced in its execution by the passive posture in which the animal is being held. In (*β*) two antagonistic reflexes alternate under alternation of two intermittent proprioceptive stimulations arising in the limb itself. In (*a*) one of the two intermittent proprioceptive stimulations is reinforced at each recurrence of it by a continuous distant stimulus and this latter by evoking the first phase of the whole movement originally initiated as well as continues to maintain the steps.

v. *Influence from the crossed fellow limb.* The reflex stepping of a limb is considerably helped by reflex stepping of the crossed fellow limb. This is readily observable in the spinal hind-limbs of the dog. When the animal is held clear of the ground with hind-limbs pendent under their own weight and the limbs performing stepping the passive arrest of one limb often stops the stepping in both. Arrest in a position of flexion at hip usually stops the movement more speedily than arrest in extension. When the reflex stepping is vigorous the passive arrest of one limb may not stop the stepping of the other, although it slows its rhythm.

Stimuli which applied to the limb itself evoke from it flexion excite in the contralateral limb extension (Sect. II). This holds equally for stimuli applied to the afferent nerves of the muscles of the limb

(Sect. II). Passive flexion of one knee excites reflex lengthening of its own extensor muscles and reflex contraction of the extensors of the opposite knee. The flexion phase of the step in one limb therefore tends by a crossed reflex which it excites to reinforce the extension phase of the step in the other limb.

Extension of a hind-limb can also excite reflex flexion of the opposite hind-limb[1]; this is so in spite of almost invariable failure to obtain such a crossed reflex by artificial stimuli applied direct to the afferent nerves (Sect. II). Crossed flexion is however the usual result, as Magnus[2] points out, when in the spinal hind-limbs of the dog, one limb being passively supported in flexion that limb is allowed to drop into extension under its own weight. Flexion of the crossed hip occurs almost as soon as the other limb drops. In this case the dropped limb very often appears to exhibit an active extension as it falls. This would be a "shortening reaction[3]" of extension of knee and probably of thigh. In this case an active extension of the dropping limb is accompanied by an active flexion of opposite hip (and knee).

In view of the evidence in Sect. II it might be thought that the extension phase of the reflex step is simply a crossed reflex from the opposite limb. Such a supposition fails however to satisfy a number of facts. (1) The supporting of one thigh in the flexed posture often arrests the reflex stepping of both limbs, but it does not do so always. (2) In the spinal hind-limb (dog) skin lesions about the outer malleolus are apt to occur owing to pressure and rubbing in the stall. A common result of this is that the limb the seat of the lesion is retained in flexion at hip and knee, the lesion appearing to act as a chronic stimulus inducing continual ipsilateral flexion. Such a dog when held up from the ground performs the usual reflex stepping freely with one limb and much less freely with the limb the seat of the lesion. When such a dog is set on its feet it stands on its fore-limbs and on the spinal limb which is not the seat of the lesion. That is, it stands on three legs, the partially flexed limb being off the ground. All trace of stepping movement then ceases in the standing hind-limb, but in the other the stepping movement, though it sometimes ceases at once, often persists for twenty seconds or more before it gradually dies out. (3) A continued faradic stimulus applied to an afferent nerve of one of the spinal hind-limbs causing in that limb steady flexion maintained so long as the stimulus is continued, often excites regular stepping in

---

[1] *Q. J. of Expt. Physiol.* II. 1909.

[2] *Pflüger's Archiv*, CXXX. 1909.

[3] *Q. J. of Expt. Physiol. loc. cit.*

the crossed hind-limb though there is none in the ipsilateral[1]. (4) In the decapitated preparation faradisation of the cross-section about *funiculus gracilis* at first cervical level can excite stepping in the ipsilateral hind-limb without stepping in the other hind-limb or in the fore-limbs. (5) After section of sciatic, femoralis and obturator nerves of one hind-limb stepping of the opposite hind-limb by itself may be obtained in the decapitate preparation by skin-stimulation of the base of the paralysed limb.

Hence it seems clear that spinal stepping of the hind-limb can go on in absence of any reinforcement from the fellow hind-limb, although in bipedal stepping the stepping of each hind-limb does receive reflex reinforcement from the stepping of the other, and to a less extent from stepping of the fore-limbs (Sect. II).

As to deafferenting one hind-limb by severance of its afferent roots and the effect of this on the reflex stepping of that limb my observations are still incomplete. They make it clear however that a majority of the afferent roots of the limb may be severed and the limb still show stepping. Thus, in the decapitate preparation 14 days subsequent to section of 5th to 10th (inclusive) post-thoracic afferent roots together with posterior half of 4th, stimulation of perineal and prevulval skin excited stepping of both hind-limbs. Again, with 3rd to 8th (inclusive) post-thoracic afferent roots cut together with anterior half of 9th, faradisation in the decapitate preparation of ipsilateral side of cervical cord at 1st cervical segment evoked distinct traces of stepping in the limb with cut afferent roots. The scratch-reflex of that limb was clearly obtained. Again, after section of 3rd to 10th (inclusive) post-thoracic afferent roots of left side traces of slow stepping of left limb were evoked from perineal skin. Here also passive alternate extensions and flexions of right limb produced regularly flexions and extensions of left, as in stepping. Skin stimuli appropriate for evoking stepping of left limb usually however produced simply the opening movement of a step in that limb and no further movement. The scratch-reflex of left limb was however well evoked both from skin of neck and by faradisation of cross-section of cord at first cervical level. The above observations have been on the cat. In the dog Prof. Magnus and myself have to some extent repeated an experiment originally made by Philippson[5], but in our experiment a considerable part of one of the afferent roots of the series escaped me in the operation, though

---

[1] *Integrative Action of Nervous System*, p. 66.

[2] *International Congress of Physiologists, Heidelberg.* 1907.

the missing of it was not observed by me at the time. The root only partially cut appears to have been the 6th lumbar. In a later experiment the roots were successfully cut from the 4th lumbar to 2nd sacral inclusive. In this case on the 5th day after the root sections sepsis appeared and the animal was thereupon destroyed. But the results as regards the stepping reflex were the same in both cases. On being held up with spine vertical and hind-limbs pendent the reflex stepping of the spinal hind-limbs appeared slightly different from what it had been before the severance of the afferent roots. The stepping was exhibited by both hind-limbs and the stepping movement was synchronous with opposite phase in the right and left limbs. Before the root severance passive support of one hip in flexion had usually arrested the stepping in both limbs. After the root severance (left limb) passive support of the right hip in flexion caused the stepping as before to cease in both hind-limbs, but similar passive support of the left hip made no obvious difference to the stepping movement of the right limb and did not stop it entirely in the left.

7. The view at which the above observations arrive regarding the successive coordination of the reflex taxis of the spinal step may be summarised thus. It is a rhythmic reflex which may be excited by continuous stimuli applied either to various peripheral points outside the limb or to the cross-section of the spinal cord itself. In stepping a pair of antagonistic reflexes *E* and *F* alternately operate, the stimulus which generates and maintains the action is however not intermittent but continuous. The production of this intermittent reflex response from a continuous stimulus occurs in the following way. The primary generating stimulus excites its reflex movement of the limb. The reflex thus excited constitutes the opening phase of the step and is *E* or *F* according to the locus of the primary stimulus. The active movement thus executed excites in the limb a proprioceptive reflex diametrically antagonistic to that of the primary stimulus. If the primary stimulus evoke *E*, this secondary reflex is *F*. Three main factors combine to produce the secondary reflex which interrupts the primary one; (i) centripetal impulses from the deep structures passively moved by the primary reflex, (ii) centripetal impulses from the muscles actively used by the primary reflex, (iii) the central change underlying rebound in the spinal limb-centres reciprocally excited and inhibited by the primary stimulus. "Umkehr" has also to be reckoned with as an accessory factor. Also perhaps under certain circumstances the "extensor-thrust." When the secondary reflex is *F* the factor (i) is

especially marked; when the secondary reflex is E the factor (iii) is especially marked. Where the limb has been largely or completely deafferented by severance of its afferent roots factors (i) and (ii) fall out, but factor (iii) remains and there remain crossed effects of factors (i) and (ii) from the stepping fellow limb.

When both limbs are engaged in reflex stepping the extensor phase of the step in one limb is reinforced by a crossed extension reflex whose stimulus arises in the flexion of the other limb; and similarly the flexion phase is reinforced by a crossed flexion-reflex derived from the other limb. The influence of the fore and aft limb-pairs on each other is less. The observations indicate that in natural stepping the excitatory influence descending from the brain to the spinal limb-centres is not intermittent but is continuous, although it results in rhythmic alternating movement of the limb.

III. Reflex Standing.

1. *Spinal.* The execution of stepping movements by the limbs does not of course in itself amount to walking. For this latter act the reflex stepping of the limbs has to be combined with reflex maintenance of the erect posture of the body. In regard to this the question rises can the spinal preparation stand. In my experience the decapitate preparation (cat) certainly cannot stand. Placed in the erect posture it immediately sinks; limbs, neck and tail drop; they are without power to antagonise gravity. The stepping movements of the limbs so readily excited in this preparation are ineffective for locomotion; the extension phase of the step is usually unable to straighten the limbs effectively under the superincumbent weight of the body.

But a different condition is observable after a period has elapsed following the spinal transection, *e.g.* at 10th thoracic level. In the course of some months or weeks the hind-limbs become able to stand (dog)[1]. If placed symmetrically in the standing posture with the hind-feet together and the fore-limbs supported by an assistant, the hind-limbs are found capable of maintaining the extended posture and supporting the weight of the hindquarters, even for minutes at a time. In some experiments as was mentioned above the standing can be executed by one hind-limb without help from the other, so that the animal stands on three legs, but such standing lasts in my experience only for a short time, rarely a full minute. Spinal standing is subject to sudden lapses.

---

[1] Cf. Philippson. *International Congress of Physiologists, Heidelberg*, p. 130. 1907.

At times by no device can the spinal limbs be made to stand. And there is little latitude in the exact pose of the limbs compatible with the standing. In my experience the limbs need to be symmetrically placed, and there must be no wide departure from the vertical. In short there is in the tonic reflex which maintains standing in the purely spinal condition little of that plasticity which the natural act exhibits.

2. *Decerebrate.* If however we turn to the decerebrate preparation the condition is different. The state of that preparation is as regards the innervation of its skeletal musculature more constant and homogeneous than that of the decapitate or spinal. The decerebrate preparation is exhibiting a steady reflex in continuous operation. It is in a state of reflex equilibrium such as the purely spinal preparation rarely approaches to. In the decerebrate preparation there obtains a characteristic rigidity[1]. The limb muscles are stiffened by tonic reflex action to the extent that they successfully counteract the weight of the body. In short in the limbs a static reflex is in progress. A tonic reflex keeps the limbs extended, the neck and tail lifted, the back and head horizontal, and the lower jaw closed against the upper. This reflex rigidity maintains the preparation in a definite posture. The tonic contraction which thus maintains a reflex attitude does not involve all muscles in the limb and other regions; it is confined to certain muscles and is absent from the antagonists of these (Sect. III, p. 60). It is present in the extensors of the limb, the retractors of the head, and the elevators of neck and tail and lower jaw. The tonic reflex contraction is therefore confined to those muscles which counteract gravity in the usual erect posture of the animal. And the grade of contraction of these muscles in the decerebrate state commonly just suffices to support the creature in the erect attitude when passively set upright. This static reflex though its effect covers a wide field of musculature is nevertheless a homogeneous entity. The tonic excitation produced by it is distributed to muscles which form one functional system compassing one common result, namely, the counteracting of gravity in those parts whose weight has to be duly supported for the maintenance of the erect posture of the animal. The source whence proceed the centripetal impulses maintaining this reflex has been traced to be in those muscles which themselves exhibit the tonic reflex contraction. The reflex arises therefore from a source which is itself of unitary functional character, namely, that system of muscles which in the erect posture of the animal antagonises the displacements which gravity would produce. This

---

[1] This *Journal*, XXII. 339.

reflex employs a pre-spinal centre situate between anterior colliculus and hind edge of pons. It ceases when that region is removed. Originated *via* one particular set of proprioceptive afferents and subserving one unitary purpose the reaction constitutes a single though composite proprioceptive reflex.

In it, as in the kinetic reflexes (flexion-reflex, crossed extension reflex) analysed above, reciprocal innervation of antagonistic muscles seems to obtain. The tonic excitation is supplied only to one member, the extensor, of antagonistic muscle pairs. There is evidence that the flexors are under a mild tonic inhibition, the counterpart of the tonic excitation of the extensor motoneurons.

(1) The reflex contractions of the flexors in decerebrate rigidity show less prolonged after-discharge than they show in the purely spinal condition. (2) The threshold stimulus for reflex contraction of the flexors of the limb is often seen to be slightly lower in the decapitated preparation than in the decerebrate. (3) Alternating reflexes are facile in the decapitate preparation but are much less so in the decerebrate. The latter is occupied by the tonic extensor reflex, the former not. In the decerebrate preparation occasionally the tonic extensor reflex (rigidity) does not develop or lapses; when this happens the alternating reflexes are more facile than usual in the decerebrate preparation. Reflex flexion is involved in the alternating reflexes and some of them, *e.g.* scratch reflex, open with flexion. (4) In spinal preparations myographic work with the flexors is commonly disturbed by reflex twitchings of the muscles. This is especially the case when afferent nerves of the limb have been prepared for stimulation, etc. The twitches can be temporarily subdued by reflex inhibition. Work with the decerebrate preparation is not disturbed in this way. The twitching of the flexors seems suppressed. In decerebrate rigidity a stimulus *A* which reflexly excites the flexor muscles produces marked relaxation of the extensors of that limb. Conversely a stimulus *B* which excites the extensor muscles inhibits the flexor muscles as can be shown by its suppressing a contraction just previously produced in them. Yet in decerebrate rigidity stimulus *B* produces in the flexors no further elongation (relaxation) than they already show. The inference is that the flexors are already completely relaxed.

These points indicate that in the decerebrate preparation the postural reflex which keeps the extensors in tonic contraction is keeping the flexors relaxed by tonic inhibition. This static reflex which the decerebrate preparation so constantly exhibits is the attitude of "standing" reflexly executed. It seems unnatural that experimental search should find, so far as "acute" preparations go, reflex *stepping* obtainable as a purely spinal reflex but for reflex *standing* have to resort to a preparation retaining hindbrain and part of midbrain as well as cord. An explanation lies I imagine in the circumstance that the latter, the postural reflex (standing) is an extensor reflex, whereas the former is a flexor as well as an extensor reflex. Extensor reactions usually suffer more than flexor from loss of subcortical prespinal centres. After the "shock" has passed as pointed out above a modicum of standing remains even in the spinal preparation.

And to ascribe to "standing" such wide-spread muscular action as is seen in decerebrate rigidity may seem somewhat opposed to views in general acceptance which tend to attribute it mainly to ligaments, joints and organs of purely static function. But R. du Bois Reymond our best authority on such matters writes[1]: "In the study of joints the idea of the bones and ligaments acting as stops, which was at first only regarded, has with time become ever more restricted. In its stead the doctrine of the checking of the joint movements by muscles has arrived."

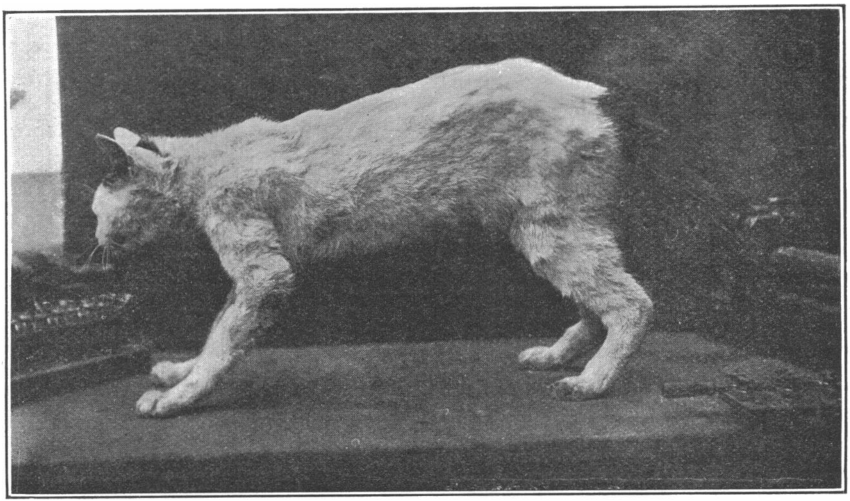

Fig. 11. Reflex of "standing"; decerebrate preparation: see text.

"Standing" appears to be the functional meaning of decerebrate rigidity. The preparation "stands" (Fig. 11) and maintains its "standing" as a continuous reflex even for hours at a time. The transection through midbrain seems to set into action or to free from higher control, probably from thalamus (Thiele[2]), a reflex "standing" which unfettered persists whatever the passive position of the animal as a whole. The tonic postural reflex still goes on when the preparation is laid upon its side. That the animal still stands when laid upon its side may seem an extravagant statement. It merely

---

[1] *Arch. f. Physiol.* p. 37. 1902.

[2] This *Journal*, XXXII. 358. 1905.

implies that in the decerebrate preparation the standing posture is largely beyond control by the otic labyrinths. Similarly in the dog with spinal hind-limbs the hind-limbs often execute for long periods the stepping reflex when lying in the stall sidewise and on the flank. The reflex standing of the decerebrate preparation is not broken down even by complete inversion of the animal. And that the reflex is in large measure independent of the otic labyrinth and nervi octavi is indicated by its not being annulled nor sometimes obviously impaired by removal of both labyrinths (cat) or severance of both nervi octavi (cat, monkey) subsequent to onset of the rigidity. Nor has it been by destruction of both labyrinths four days prior to decerebration. The longest period over which the observations on this point range has been in an experiment in which one labyrinth was removed eight days and the other three days before decerebration. In this and other experiments on this point I had the advantage of the able cooperation of Dr S. Sewell. After decerebration the tonic postural reflex appeared as usual and without obvious difference in the right and left sides. Nervus octavus can, it is true, regulate, adjust and modify the reflex standing of the decerebrate preparation. But the reflex posture of standing can be maintained even in complete absence of both otic labyrinths and after severance of both *nervi octavi.* These receptors and receptive nerves are therefore not essential to the fundamental execution of the standing posture. And this agrees with the fact that the spinal hind-limbs of the dog after spinal shock has passed are able to stand, although less perfectly than is the decerebrate preparation.

Although the tonic postural reflex persists even when the animal is completely inverted, its intensity is favoured by placing the animal upright on its feet. It is markedly increased by lifting the preparation from shoulders and loins and setting it briskly on its feet a few times in succession. With each setting down the extensor attitude of the limbs stiffens and the head and tail which before the manœuvre may be drooping rise with the increasing tonus of the neck and tail muscles. Centripetal impulses from the soles of the feet contribute, as with reflex stepping (*v. supra*, p. 76) little, perhaps nothing, toward the reflex. The afferent nerves of the feet may be severed without clear lessening of the reflex, just as similar severance does not obviously impair the execution of the standing posture when assumed naturally (horse[1], pigeon[2], cat[3]). The afferents from practically the whole of the skin of the limb may be severed without obviously lessening the reflex. The

---

[1] Chauveau. *Brain*, XIV. 153. 1891.

[2] *Ibid.*

[3] *v. supra*, p. 76.

skin may be removed from the whole preparation and the reflex "standing" of the preparation still continue. The reflex is clearly proprioceptive. In other words the stimuli exciting and maintaining it come not from the environment but from the body itself acting as stimulating agent to its own afferent nerves.

The reflex tonus which thus executes the posture of standing in the decerebrate preparation has "plasticity[1]," *i.e.* capacity for local modification in regard to the length of this or that particular muscle or muscle-group without disturbance of the tonic tension of the muscle.

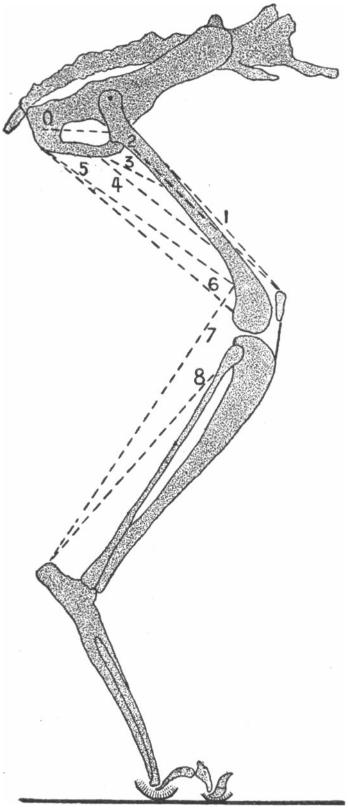

Fig. 12. Muscles observed by direct analysis to be engaged in the reflex tonic contraction of the standing posture (decerebrate preparation (cat, dog)).

1. Crureus and vastus medialis
2. Vastus lateralis
3. Adductor minor
4. Adductor major (a part)
5. Semimembranosus
6. Biceps femoris anterior
7. Gastrocnemius
8. Soleus (absent from dog)
0. Quadratus femoris

---

[1] *Q. J. of Expt. Physiol.* II.

Each such local modification is given by an intrinsic proprioceptive reflex. This plasticity appears to meet the requirement that in "standing" the posture of the limb may with advantage vary a good deal provided always that each joint maintain a resistance sufficient to counteract the tendency to double up under the weight it bears. Ordinary standing postures (*usustatus*[1]) include various degrees of flexion at hip and knee and extension is usually less at the former. One hind-foot may rest close beside the other or much in advance of or behind it. Yet the plastic tonus allows the tonic length of the muscle to vary without its tonic tension falling too low to bear the superincumbent load. In v. Uexküll's[2] terminology the extensors in this postural reflex of standing are acting as "sperr-muskeln." They secure that in the various positions of the joints in standing the tonic tension of the muscles shall still continue adjusted to the support the limb requires under the standing animal. Reflex "standing" is a "sperr-reflex."

The reflex standing of the decerebrate preparation differs from that exhibited by the spinal preparation in its equable steady long-persisting character, in its immunity from sudden lapses, in its reliability of occurrence and in its plasticity allowing latitude to the exact form of standing posture assumed.

In the hind-limb (cat, dog) the muscles observed to be contracting in this tonic postural reflex of standing in the decerebrate preparation are as follows (Fig. 12):

Biceps femoris anterior
Semimembranosus
Quadratus femoris
Vastus lateralis
Vastus medialis
Crureus
Adductor minor
Adductor major (in part)
Gastrocnemius
Soleus.

Other muscles as well—particularly I would suspect flex. long. digitorum—may be contracting, but only those in which observation by the isolation method has ascertained their contraction without any doubt are included in the above list. Similarly the following are muscles in which absence of contraction in this reflex has been ascertained clearly:

Psoas magnus
Tensor fasciæ femoris
Sartorius
Semitendinosus
Biceps femoris posterior
Gracilis
Tibialis anticus
Peroneus longus
Extensor digitorum longus
Tenuissimus.

---

[1] K. Schaefer, *Pflüger's Archiv*, xli. 582. 1887.

[2] *Ergebn. d. Physiol. loc. cit.* and *Umwelt u. Innenwelt der Thieren.* 1909.

These lists make clear that the same principles of coordination are adhered to in the execution of this static reflex as in that of the kinetic reflexes above analysed. Hence the term protagonists seems preferable to that of prime movers for the main muscles executive of the reflexes. For the latter term is inapplicable to the static reflexes since in them posture but not movement results. Contracting muscles used at one joint as direct executants of the posture serve also as fixators for the direct executants of the posture at another joint. Contraction is arranged to reinforce passive mechanical effects due to contraction elsewhere (*v. supra*, p. 50). Rotation of the limb at certain joints is avoided by balanced action of partially antagonistic muscles. All those items of taxis traced above (Sect. I and II) in the kinetic reflexes are observable also in this postural static one.

3. *The initiation of reflex stepping during reflex standing.* Between decerebrate rigidity signifying the reflex attitude of standing and the flexion-reflex or extension-reflex of the limb signifying the execution of a step the nexus is natural and close. When in the decerebrate preparation a stimulus is applied such as by quality and locus would in the decapitate preparation excite reflex stepping, the kinetic reflex of a step-phase breaks in on the static reflex of "standing." Suppose the stimulus one which gives flexion as the opening phase of the step, and the limb in which the reflex is initiated to be the right hind. The extensors of the limb are in reflex plastic tonus when the kinetic reflex opens. The kinetic reflex at once inhibits the tonic standing contraction of quadratus femoris, semimembranosus and biceps femoris anterior, extensors of hip; of vasti and crureus, extensors of knee, of gastrocnemius and soleus extensors of ankle and also of adductor minor and part of adductor major of thigh. While inhibiting the motoneurons of these muscles it excites the motoneurons of psoas magnus, sartorius, rectus femoris, tensor fasciæ femoris brevis, flexors at hip; gluteus minimus, a flexor and abductor of hip; semitendinosus, biceps femoris posterior, gracilis, sartorius and tenuissimus, flexors at knee; tibialis anticus, a flexor at ankle; extensor longus digitorum, a flexor at ankle and extensor of toes; extensor brevis digitorum, an extensor of toes; peroneus longus, an abductor of foot; and a part of the adductor of the thigh. These muscles the reflex found at its outset in a state probably of slight tonic inhibition. By these inhibitions and excitations the reflex flexes the limb, lifts it slightly from the ground and swings it forward.

This reflex effect on right limb is accompanied by a converse action on the left limb. There the muscles which are in tonic contraction under the postural reflex of standing are reinforced in their contraction by the kinetic reflex. This is proved for semimembranosus and biceps femoris anterior, extensors of hip; adductor minor and part of adductor major, adductors and extensors of hip; vastus lateralis, vastus medialis and crureus, extensors of knee; gastrocnemius and soleus, extensors of ankle. It is so sometimes with quadratus femoris but reflex stepping in the decapitated preparation only occasionally actuates this muscle. Late in its course the kinetic reflex causes contraction of flexor longus digitorum, but that this muscle is engaged in the tonic reflex of standing I have not been able actually to see. And in this left limb also the kinetic reflex exerts inhibitory besides excitatory influence. The inhibition is distributed to semitendinosus, biceps femoris posterior, sartorius, and tibialis anticus, and almost certainly to other flexors as well, but with these others my observations have not actually dealt in this respect. To detect the inhibition in this case meets with the difficulty as already mentioned that the muscles on which it is exerted are much relaxed at the time when the inhibitory influence is exerted. The combined effect of these inhibitions and excitations by the kinetic reflex in the left limb is an accentuation of the extensor position previously maintained in it by the "standing" reflex. The foot is pushed backward against the ground and the body forward and somewhat upward as the limb extends.

Thus the kinetic reflex of the step so grafts itself on the tonic postural reflex of standing that its flexion phase is an interruption of the static reflex, its extension phase is an accentuation of the static reflex. One of the features of the tonic postural reflex is that although systemic and unified in its effect it is of multiple origin. Its source although homogeneous in character is multiple in seat, arising in the afferents of the widely spread groups of muscles which it causes to contract. In each region it is originated by centripetal impulses from the muscles of that region. Thus, that part of the reflex which keeps the neck supported against gravity arises through the deep afferents of the neck; that part which supports the fore-limb under the weight of the fore-quarters arises through the afferents of supra-spinatus, humeral triceps, and other extensors of the fore-limb; that which keeps the hind-limb extended under the weight of the hind-quarters arises from the afferents of the hind-limb extensors, and so on. The reflex posture in each body-region is not of course *wholly* independent of afferents in other regions. Thus, passive flexion of elbow and shoulder often provokes in the decerebrate preparation heightening of the tonic extension of ipsilateral knee and ankle, and lowering of it in crossed knee and ankle. Again active or passive rotation of neck on its long axis in the decerebrate preparation inhibits extensor tonus in hind-limb on the side of the lowered prima and caused active flexion of knee; and does so after severance of both cranial Vths and both *octavi*. Again, in the deafferented vastocrureus (decerebrate preparation) though the steady enduring tonus ensuing on decerebration is characteristically absent from the muscle, nevertheless from time to time for relatively short periods tonic contraction of it occurs traceable to afferent sources altogether headward of hind-limb.

But apart from these exaltations and depressions of tonus which are *regulative* of the reflex posture but not part of its essential basis, the broad fact remains that the reflex maintaining the erect posture of each region has its source in the proprioceptive afferents of that region itself. This holds even to the extent that the source of the decerebrate posture of the extensor of the knee is traceable almost entirely if not absolutely entirely to afferents of the knee-extensor[1] itself. A result of this is that although the individual components traceable from these several sources all involve a central mechanism between anterior colliculus and hinder edge of pons, and combine to one united static reflex of "standing," the resultant systemic reflex can be modified piecemeal. Hence a kinetic reflex such as the flexion phase of a step upsets the systemic postural reflex of standing only in its own limb and leaves it unbroken elsewhere.

Reflex walking therefore consists in an alterative[2] innervation locally disturbing in due sequence parts of a general tonic reflex. A rhythmic series of kinetic reflexes breaks a systemic static reflex in each limb in turn but leaves it in force elsewhere. In regions other than the limbs the erect posture continues maintained by the systemic tonic reflex during walking and running even as during standing. And the erect posture is as necessarily contributive to them as to standing itself. This does not of course mean that outside the limbs the static postural reflex necessarily remains everywhere wholly unmodified during the kinetic reflexes of progression: the tail exhibits rhythmic lateral movement during the spinal stepping of the hind-limb, and the same stimulus which excites the flexion phase of the step excites a lateral motion of the tail to the ipsilateral side[3]; the same is

---

[1] *Proc. Roy. Soc.* B. LXXIX. p. 345. 1907.

[2] A. v. Tschermak, *Folia Neurobiologica*, I. I. 1907.

[3] *Proc. Roy. Soc.* B. LXXIX. p. 345. 1907.

true of the neck in relation to the flexion-reflex of the fore-limb. Yet apart from these details the broad fact is that the general postural reflex which maintains the erect posture is modified only piecemeal by the kinetic reflexes which execute the step. The successive and simultaneous interruptions and reinforcements of the static reflex in its various parts by the kinetic reflexes grafted upon it in the several regions permute the general static reflex into the composite acts of walking and running. The fundamental relation of these reflex acts to the reflex posture of standing becomes clearer when this interweaving of the kinetic and static reflexes is recognised.

Why is the reflex stepping of the limb less easily evoked in the decerebrate preparation than in the decapitate and spinal? It certainly is so (*v. supra*, p. 70) especially in the hind-limbs. In the late spinal preparation (dog) reflex stepping of the hind-limbs immediately sets in on letting the limbs hang pendent: when the decerebrate preparation is so held stepping does not ensue. The spinal hind-limbs of the dog as the animal lies on its side in the stall often execute steps by the half hour together. The decerebrate preparation when laid on its side does not execute steps but lies with limbs simply steadily extended. Reflex "standing" engages the decerebrate preparation and reflex stepping may be said to engage the spinal preparation. Another rhythmic reflex exhibiting alternate flexion and extension is the scratch reflex. This reflex likewise is less readily obtained in the decerebrate than the decapitate or spinal preparation. It is the existence of rigidity, *i.e.* of reflex standing which in the decerebrate preparation seems the obstacle to the development of rhythmic alternating reflexes such as stepping or scratching. In those exceptional cases in which in the decerebrate preparation the rigidity does not develop or lapses the proneness to alternating reflexes is greater than when rigidity is present. In a series of experiments in which the vasto-crureus of one side was deafferented contralateral prolonged stimuli which after decerebration excited simply maintained contraction in the vasto-crureus of the normal side generally excited in the deafferented muscle the rhythmic contraction of stepping. The decerebration produced the usual tonic reflex contraction (standing) in the muscle of the normal side, but never in the deafferented. The influence of the standing reflex seems opposed to the development of rhythmic recurrent refractory phase in the kinetic reflex. Similarly stimuli which in the decapitate preparation excite rhythmic extension in the decerebrate excite steady maintained extension. Stimuli which in the former excite rhythmic flexion excite in the latter maintained flexion. In the former on withdrawal of the stimulus the rhythmic reflex usually still continues for a time and dies out gradually. In the latter on withdrawal of the stimulus the maintained contraction if extension still continues as a steady very slowly declining posture, if flexion is usually succeeded by rebound extension which then continues with slow steady decline. A nervous mechanism operative in the decerebrate preparation and absent in the decapitate suppresses refractory phase and thus transmutes alternating reflexes given by the spinal centres into continuous reflexes executive of posture. The explanation may be that remote stimuli are weaker in the decapitate preparation and hence allow of more easy interference by local proprioceptive stimuli.

Another effect of this mechanism is the accentuation and prolongation of extensor rebound (*v. supra*, p. 94). Examination of this marked rebound of the decerebrate preparation shows it (1) to be obtainable when all nerves of both limbs have been severed excepting only the nerve of the extensor muscle itself exhibiting the rebound; and (2) to be independent of actual lengthening of the muscle during the precurrent inhibitory period on which the rebound ensues. In one case it appeared that the rebound ensued even when the muscle itself had been deafferented. Flexor rebound in the decerebrate preparation is less readily obtained. But it occurs. Thus faradisation of central end of *n. femoralis* in one thigh, the semimembranosus and semitendinosus of the opposite thigh being isolated, causes contraction of the former muscle during the stimulus and contraction of the latter on withdrawal of the stimulus; the contraction of the latter was accompanied by cessation of contraction of semimembranosus. But this post-stimulation contraction of the crossed flexor is not always obtainable.

In the decerebrate preparation extensor rebound markedly ensues on the nociceptive flexion-reflex when the nocuous stimuli is not too prolonged. In this case the rebound obviously constitutes a compensatory reaction bringing the limb back to the state of reflex equilibrium which had been disturbed by the nociceptive flexion. Here the rebound resembles therefore such compensatory reactions as are seen in the skate, etc. on forced disturbance of an equilibrium posture and are ascribable to the otic labyrinth.

The distribution of the reflex motor discharge during the stimulus and of the rebound motor discharge following withdrawal of the stimulus, explains some results otherwise difficult to understand. If all the nerves of the limb be severed except superior gluteal and the branch of n. femoralis to vastocrureus; and if psoas parvus and magnus and the glutei and all muscles attached to the trochanters and intertrochanteric line be resected from their insertions, the muscles remaining operative on the limb are tensor fasciæ femoris and vastocrureus. The reflex result of stimulating the central end of an ipsilateral afferent nerve, *e.g.* n. peroneus, is then flexion at hip and slight flexion at knee during the stimulation. This is followed on withdrawal of the stimulus by active extension at knee, hip and ankle. That is tensor fasciæ femoris responded during the stimulus, vastocrureus after the stimulus. Again, if all nerves of the limb including superior gluteal be severed except hamstring nerve, and if psoas parvus and magnus be resected from their insertions the muscles remaining operative in the limb are anterior and posterior biceps femoris, semimembranosus and semitendinosus. The reflex result of stimulating an ipsilateral afferent nerve is then flexion at knee with, if the reflex be strong, slight extension at hip. This is the result during the stimulation but after withdrawal of the stimulus there follows strong active extension at hip, knee and ankle. That is, posterior biceps femoris and semitendinosus responded during the stimulus, anterior biceps femoris and semimembranosus after the stimulus. Other examples with tibialis anticus, gastrocnemius, etc. occur, all explicable in the same way.

IV. REFLEX WALKING.

Reflex stepping movements of the hind-limb (cat, dog) though less easy to evoke in the decerebrate preparation than in the decapitate are in the latter when evoked of a more effective character. Reflex stepping movements of the limbs even when including all four limbs timed in appropriate sequence yet of themselves alone do not constitute a complete reflex act of walking or running. For this they must be duly combined with the general static reflex maintaining erect posture of head, neck, trunk and tail. The greater efficiency of the reflex stepping when evoked in the decerebrate preparation as compared with the decapitate seems traceable to two factors.

(1) The extensor phases of the stepping movement are more vigorous. In other words that prespinal mechanism which importantly contributes to standing contributes also to the extensor phase of the movement of the step. It reinforces by its adjuvant action each extension phase whether primary or due to rebound. This adjuvant action is therefore added to the factors of the reflex step in the more complete form in which the step occurs in the decerebrate preparation.

(2) The stepping movements of the limbs are combined with the tonic reflex which maintains the erect position of the animal as a whole.

In virtue of these two factors the performance of mere stepping movements as exhibited by the decapitate preparation is amplified in the decerebrate preparation into the performance of actual walking and running—imperfect it is true especially in regard to equilibrium, the regulation of which is almost entirely wanting, but nevertheless amounting to a certain measure of effective locomotion.

As to what nervous mechanism it is which, present in the decerebrate preparation and absent from the spinal, contributes so importantly to reflex standing and to the extensor phase of the step, and tends to convert alternating reflexes into tonic postures by suppressing refractory phase, a main portion of it clearly lies between the levels of anterior colliculus and hinder edge of pons. It can hardly be the otic labyrinths for their bilateral destruction leaves these reactions still elicitable. The paracerebellar nuclei[1] are within the confines of the region to which the reaction is traced. Whatever the morphological field of the mechanism it is clear that its removal exerts at first a depression amounting to annihilation of reflex standing and to great weakening of the step especially of the step's extensor phase. Gradually in the course of weeks and months both reflexes recover partly. The recovery however never in my experience amounts to full qualitative restitution of the original reactions in which the prespinal mechanism participates.

SUMMARY OF CONCLUSIONS.

Sections I and II.

The reflex movement elicitable from all extero-ceptors of the limb except some at its attached base is (excluding extensor-thrust) primary flexion of the stimulated limb and extension of the contralateral fellow limb. This primary movement tends to be followed by active movement in the opposite direction. A similar reflex is obtained from the deep afferents of the limb and can be evoked by proprioceptive stimuli, *e.g.* passive and active movements of the limb.

The flexion-reflex and the extension-reflex exhibit in their reflex figures (simultaneous coordination of the musculature) the following features:—

1. Muscles the directions of whose main pull as prime movers at one and the same joint are opposed are dealt with by reciprocal innervation.
2. Protagonists at a given joint are used at the same time as fixators of that joint for protagonists at adjacent joints.

---

[1] Thiele, this *Journal*, xxxii. 358; Horsley, *Brain*, xxix. 455. 1907.

3. Where a muscle (A) acts at a joint a and with less ample effect at another joint β and a muscle (B) opposes A's action at β but by so doing enhances it at a, the reflex deals with the two muscles, not by "reciprocal innervation" but by "identical innervation," *i.e.* A and B are excited together or are inhibited together.

4. A muscle pair AB such that both its members contribute a component pull in the direction of the general resultant movement of the reflex, but with the remaining component of A opposed to the remaining component of B, are dealt with not by "reciprocal innervation" but by "identical innervation."

5. Muscles which apart from contraction and simply as passive strings amplify the action of a flexor so that the latter besides flexing its own joint flexes other joints as well (Lombard, etc.) are thrown into contraction along with that flexor. And similarly with muscles which similarly amplify the action of an extensor, they are excited with that extensor or inhibited with that extensor. The passive behaviour of the limb-mechanism is thus not overridden or counteracted by the neural taxis but is reinforced by it.

6. Displacements which contracting muscles in virtue of their movements impose on joints situate beyond their actual attachments (Fischer) are not counteracted by the neural taxis but are supported and reinforced by it. The mechanical effect is enhanced by the contraction of additional muscles. The mechanical behaviour of the passive limb-mechanism is thus reinforced by the neural reflex-taxis.

7. Where a muscle group has a main action at right angles to the main direction of movement of the reflex, but of the group some members (A) exert in their pull a component parallel with the main action of the reflex and other members (B) a component opposed to the reflex's main direction, the A members are excited to contract along with the prime movers of the reflex, the B members are inhibited along with the antagonists of the prime movers.

8. A double-joint muscle such that its action is flexion at one joint and extension at the other is not used as a prime mover at both but only at one, probably always the same, joint. Hence in reflexes of diametrically opposed direction, *e.g.* flexion-reflex and extension-reflex of limb, no muscle in the limb appears to participate by contraction in both of the two reflexes.

9. The reflex action in many cases does not treat as entities muscles regarded as such by anatomical nomenclature.

10. A strong reflex does not necessarily employ more muscles than

does a weak example of the same reflex; it excites and inhibits the same muscles as the weaker reflex but excites and inhibits them more intensely.

Section III.

The reflex excites and inhibits in the decerebrate preparation the same limb-muscles as in the spinal preparation, *i.e.* the reflex-figure is the same in both cases. But the reflex response of individual muscles differs in the two cases in certain respects. In spinal preparations the reflex threshold for extensors tends to be higher than for flexors, and the intensity of extension reflexes to be less than of flexion-reflexes. In the decerebrate preparation the reflex contraction of an extensor is accompanied by an autogenous tonic reflex which prolongs the contraction; this is absent from the reflex contraction of flexors, and is also absent from that of extensors in the decapitate preparation.

In the spinal preparation both flexion and extension reflexes initiated by stimuli situate outside the responding limb itself tend if the stimuli be not quite brief to be rhythmic owing to development of central refractory phase. In the decerebrate preparation stimuli similar to the above move the limb into a position (flexion with flexion stimuli, extension with extension stimuli) which is steadily maintained during the continuance of the stimulus, and no refractory phase or rhythmic response is developed. On withdrawal of the stimulus there is however usually a rebound contraction opposite in sense to that of the opening movement. This rebound is traceable to post-inhibitory exaltation of the centres inhibited during the reflex. Extensor-rebound after a flexion-reflex occurs more regularly than flexor-rebound after an extension-reflex. These differences between the reactions of the decerebrate and spinal preparations are more marked when the former is exhibiting decerebrate rigidity than when as occasionally happens that rigidity does not develope or has lapsed.

Section IV.

The flexion-reflexes excited by stimuli applied to the skin of the reacting limb itself are elicited best by nocuous stimuli. The flexion-reflex is here nociceptive and its significance is self-protection. Besides the withdrawal of the limb itself the accessory reactions in other regions of the body testify to the protective "purpose" of the reflex.

But reflex flexion can be elicited from the limb by application to it of stimuli non-nocuous in character, eminently by proprioceptive stimuli in the form of passive movement. Thus in the dog with spinal hind-limbs, simply allowing the hind-limbs to hang freely pendent excites a rhythmic flexion and extension (Freusberg's reflex) which is reflex "stepping" and continues as long as the pendent position of the limbs is maintained.

Similar reflex stepping is obtainable in the decapitate preparation (cat, dog) even when lying on its side or inverted, by skin stimuli applied at any of a number of points outside the area of the reacting limb itself. These skin stimuli though continuous and equable evoke the rhythmic alternating movement constituting stepping. Stimuli which in the decerebrate preparation evoke during their continuance a maintained limb-flexion evoke in the decapitate and spinal preparation "stepping" with flexion as its opening phase. Stimuli which in the former preparation evoke maintained extension, in the latter evoke "stepping" with extension as its opening phase. Faradisation of certain points in the exposed cross-section of the cord causes stepping of the ipsilateral hind-limb with flexion as its opening phase, often accompanied by less vigorous stepping of contralateral hind-limb converse in phase but synchronous with that of the ipsilateral limb. In these cases there evidently occurs a central refractory period for the primary response and this recurs rhythmically and is at each appearance accompanied by a response of the previously irresponsive antagonistic centre for movement opposed to the primary movement. An alternating reflex thus results.

The suppression of the primary response and its replacement by one of opposite direction appears to arise in the following way. The movement of the primary response evokes in the limb proprioceptive stimuli which antagonise the primary remote stimulus and evoke a limb movement in the reverse direction, and this as it is accomplished generates a new proprioceptive stimulus operating in the same direction as the original primary stimulus, so that the original movement then sets in anew. From this interference of phasic secondary proprioceptive stimuli with the continuously applied exteroceptive (or centrally applied) stimulus a rhythmic alternating response results.

The muscles employed in the flexion phase of the reflex step are those employed in the nociceptive flexion-reflex and as regards their simultaneous coordination are employed in the same way as in that reflex. The reflex taxis of the flexion phase of the step exhibits therefore the same principles of coordination of the limb musculature as were shown for the flexion-reflex. Similarly the muscles employed in the extension phase of the step are those employed in the crossed extension-reflex, and the principles of simultaneous coordination of the musculature are the same as in that reflex.

Cutaneous afferents of the limb are inessential for the reflex step. The reflex step is as regards the afferents of the stepping limb itself essentially a proprioceptive reflex. Hence the normal stepping (cat, dog) is curiously little disturbed by denervation of the foot or anæsthesia of the limb-surface.

No muscle which contracts in the flexion phase of the reflex step appears to contract in the extension phase. The reflex centres excited in the one phase are inhibited in the other. Each of the centres has thus its systole and diastole and the reflex can continue for long periods without obvious fatigue. But in some cases the diastole of one or other of the opposed centres is incomplete.

In the bipedal form of the reflex step proprioceptive stimuli arising in the crossed limb reinforce by crossed reflex effects both the extension and the flexion phases of the stepping of the fellow limb.

Post-inhibitory central rebound reinforces the reversals of phase of the reflex step. This seems especially the case for that phase of the movement which corresponds with the refractory phase of the distant initiatory stimulus and especially when that phase is extension. Post-inhibitory rebound in the form of extension is ascertained to cause contraction in those muscles which contract in the extension phase of the step.

The decerebrate rigidity observable after mid-brain transection is a tonic postural reflex; it is in fact reflex standing, *i.e.* "standing" purely reflexly maintained. The plasticity of its reflex tonus has the effect of allowing considerable latitude to the exact posture maintained in the standing; the relative positions of the different body-regions may vary considerably and the reflex tonus nevertheless support the weight of the several parts and the preparation still "stand." The reflex is characterised by maintaining this plastic tonus in all those muscles which in the normal erect posture of the animal counteract gravity, and in no other. In the reflex all these muscles are therefore acting in v. Uexküll's sense as "sperr-muskeln." Standing is v. Uexküll's sense a "sperr-reflex"; it is significant that the cutaneous afferents of the limbs and indeed of the body generally have no share in it so that it like the step-reflex is entirely proprioceptive. Also the otic labyrinths are not indispensable to the reflex: both labyrinths may essentially under certain circumstances be destroyed or both *n. octavi* severed without abolition or marked impairment of the reflex standing; the labyrinths can modify the reflex posture but the execution of the posture is not essentially dependent on them.

It is this tonic reflex which in part causes the decerebrate preparation to suppress the refractory periods characteristic of the reflex response of the limbs shown in the decapitate and spinal preparation. It thus changes rhythmic stepping movement into assumption and maintenance of an attitude, namely standing.

Reflex standing employs contraction of the same muscles as contract in the extension phase of the step. In it as in the latter reflex the antagonists of the protagonist muscles are not contracting—there is some evidence that they are under tonic inhibition.

The prespinal mechanism involved in reflex standing cooperates also in the extension phase of the reflex step (in the decerebrate preparation). It also cooperates with the reflex stepping movements of the limbs amplifying their effectiveness by maintaining the erect posture of the body during the acts of walking, running, etc. In these acts there is a grafting of proprioceptive reflexes executing the phasic flexions and extensions of the limb upon a tonic proprioceptive reflex actuating the muscles which counteract gravity in the erect posture (*usustatus*) of the animal. The reflex-stepping of the decapitated preparation is thus in the decerebrate preparation amplified into reflex walking or running, although of imperfect kind.