VARIATIONS FROM NORMAL GAIT AFTER MUSCLE SECTION IN RABBITS

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In this paper an account is given of an investigation which was made to determine what changes could be observed in the gait of an animal after the throwing out of action of one or more of a group of muscles acting on a joint. For this purpose, the rabbit was selected, and the muscles which were chosen upon which to perform the operations were the superficial and deep muscles of the calf. These include all the muscles which are responsible for the flexion of the ankle joint, and, except the small intrinsic muscles of the foot, they are the only ones which flex the toes and the joints of the foot. It was felt that by eliminating these one after the other it would be possible to determine the alterations in the ability of the animal to flex its ankle and the joints of the foot and toes.

The muscles of this group in the rabbit vary in some important details from the arrangement seen in the human, and this must be borne in mind when the results of the experiments are considered. In a series of twenty rabbits, the outer head of gastrocnemius weighed on the average 2·35 g. and the inner head of gastrocnemius 1·59 g. Their origin and insertions were similar to those found in man. The plantaris is relatively a large muscle and weighed 1·62 g. on the average. Its tendon of insertion winds round that of the gastrocnemius and passes over the heel to run into the foot. As it passes over the heel it gives off two lateral expansions which are inserted into the sides of the calcaneal process. The tendon, upon arrival in the foot, broadens out and sends slips to each of the individual toes. These slips are perforated by the corresponding tendons of the deep flexor muscles. The soleus, on the other hand, is relatively small, weighing on an average 0·55 g. It arises only from the head of the fibula, and its tendon of insertion joins with that of the gastrocnemius to be inserted into the os calcis. It is made up of "red" fibres, this differentiating it from the other muscles which consist of "white" fibres. In this investigation, the deeper muscles have been grouped together as the deep flexors and weigh on the average 1·67 g. This has been done because it was found difficult to separate them into individual muscles. This mass arises both from the tibia and the fibula, and its tendon of insertion divides into slips which after perforating the corresponding tendons of the plantaris are inserted into the distal phalanges of the toes. From the above description it will be observed that the gastrocnemius and soleus are plantar flexors of the ankle joint and the deep flexor, a flexor of the toes. The plantaris, from its arrangement, can be both a plantar flexor of the heel and a flexor of the toes, and it is difficult to state which of these actions is the more important, but these experiments show that it is a powerful flexor of the toes and suggest that it is relatively less important as a plantar flexor of the heel. The weights given for each of these muscles are for the purpose of comparison and are not the average of full-grown individuals, as a fair number of the animals in the series from which the measurements were taken were young. The average weight for the group was 890 g.

The method which was adopted for destroying the action of the muscle was to remove a portion of its tendon of insertion. This had the advantage of destroying the individual action of the muscle while its nerve supply was preserved intact, and thus afferent impulses could still be conveyed from the muscle to the central nervous system.

A few preliminary experiments showed that dissection of the tendon of insertion of any one muscle influenced the gait to such a small extent that it was impossible to detect this by means of the naked eye. It was felt that such alterations might be more readily detected by means of slow-motion cinematography, and this was employed in the series of experiments which are described in this paper. The routine of the experiments was as follows. A record of the normal gait of the experimental animals was obtained by exposing films at the rate of 64 frames per second. As these are afterwards run through the projector at 16 frames a second, the rate at which the animal appears to move as seen on the screen is a quarter of that of the normal gait. After a record of the normal gait had been obtained, the tendons of the individual flexor muscles were divided at 2-daily intervals, and on the intervening days similar records to those of the normal gait were made with the ciné camera. As the group of muscles consisted of the outer head of gastrocnemius, the inner head of gastrocnemius, plantaris, soleus and the deep flexors, an experiment was completed within 10 days of the section of the first muscle. This was well within the time required for reformation of the tendon and return of function to the muscle which, as the author has been able to show (1), does not occur until after 3 weeks from the date of tendon section.

The order in which the tendons were cut varied throughout the series of animals, so that it was possible to study the effects of eliminating the action of different combinations of the members of the group of muscles. Complete cinematograph records were obtained at all stages of the experiments and were examined by being projected on the screen.

Investigation in which the cinematograph is used offered difficulties in publication in that it is impossible for the reader to see the actual film. To surmount this difficulty to a certain extent, the author has made use of the same method which he employed in a recent paper (1), by projecting the film on to a roll of paper and tracing the position of the limb in every consecutive frame throughout the cycle of movement. If the animal was moving very slowly, the number of frames in the cycle was very large, and to reduce this, outlines were made from every other frame in the cycle, or occasionally every third frame. It is hoped by this means that the reader will be able to follow the description of the changes observed in the projected films, but it must be remembered that in the film, movements could be seen more clearly than in the outline drawings.

The author has also examined these movements by comparing the variations in the amplitudes of the movement of the individual joints, but as these, although more accurate, merely confirm what has been seen on the film, it is not thought necessary to add to the length of the paper by giving them here.

RABBIT 13

Fig. 1. Rabbit 13. *a*, Normal gait; *b*, outer head of gastrocnemius cut; *c*, both heads of gastrocnemius cut; *d*, gastrocnemius and soleus cut; *e*, gastrocnemius, soleus and deep flexors cut; *f*, all muscles cut.

In this animal, the tendons were cut in the following order:

(1) Outer head of gastrocnemius,
(2) Inner head of gastrocnemius,
(3) Soleus,
(4) Deep flexors,
(5) Plantaris.

After section of the outer head of gastrocnemius (Fig. 1*b*), no alteration in the gait of the animal could be detected. After both heads of gastrocnemius had been divided (Fig. 1*c*), the movements of the knee and the ankle still remained unchanged. There was, however, a slight difference in the position of the toes, and during the support period, while the feet were on the ground, the toes appeared to be rather less dorsiflexed than during the earlier stage of the experiment. This would suggest that the plantaris and deep flexors are now more strongly contracted. After section of the gastrocnemius and soleus, there is a distinct increase in the amount of the dorsiflexion of the ankle during the suspense period while the feet are off the ground. This is clearly due to the anterior muscles now having less opposition to overcome. During the support period, the raising of the heel is now delayed and only occurs late in the support period just before the foot is leaving the ground. The position of the toes is clearly altered, and there is now no doubt that the plantaris and the deep flexors are kept in a state of marked contraction. Fig. 1 *d* shows that the toes are flexed at all stages of the locomotory cycle, and even when the extensors are active during suspension they are unable to counteract the action of the flexor muscles. These changes which have occurred through the division of the soleus are most striking. As has been mentioned above, it is in the rabbit a relatively small muscle, yet, so long as it remains intact, the loss of locomotory power from the division of the tendons of the large gastrocnemii is negligible. This would suggest that the soleus, in at least certain stages of the cycle, must be in a state of hypercontraction and exerting a power much above that which it normally attains. Such a hypercontraction is clearly present in the two remaining muscles, the plantaris and the deep flexor, for, as has already been mentioned, the toes are in a condition of marked plantar flexion which the extensors of the toes are unable to counteract. These findings therefore suggest that when a muscle or muscles are divided, the remaining muscles, acting upon a joint, attempt to counteract this loss by greater contraction, and if the quantity of muscle which has been thrown out of action is not overwhelmingly great, they succeed in doing so. After section of the gastrocnemius, soleus and deep flexors, there is little further change in the movement of the ankle joint. The toes are slightly less flexed than in the last experiment, but this diminution in the amount of flexion is very slight when it is considered that a considerable amount of the flexor force, as represented by the deep flexor muscle, has been thrown out of action. It would suggest that once more the remaining muscle, the plantaris, is acting with still greater force. It is able to counteract the whole of the extensors of the toes, because at no stage of the cycle are the toes anything but flexed. After all the muscles have been cut (Fig. 1*f*), the foot is carried forward during the suspense period in a state of very marked dorsiflexion and the toes are also dorsiflexed. One interesting feature was observed which is not clearly brought out by the tracings. When the foot was brought forwards it made contact with the ground with the heel, and then the forepart of the foot fell to the ground with great rapidity and afterwards oscillatory movements of the toes occurred. Although these movements are not shown very clearly on the outline drawings, they were quite obvious in all the animals after all the muscles had been divided.

During the support period, the delay already mentioned in the raising of the heel from the ground is prolonged, but this actually occurred towards the end of the support period just before the foot leaves the ground. It will be noticed that the heel can still be raised from the ground even although all the muscles on the posterior aspect of the ankle have been divided. This is probably carried on largely by the muscles of the forequarters dragging the body forward, but it shows again the point which has already been made, that when muscles are put out of action other muscles will attempt to carry on the work of those which have been lost, and the success which they achieve will depend largely on the quantity of muscle force which has been lost. The conception of muscles working as groups is very generally accepted, but it is here suggested that the whole of the musculature of the body should be looked upon as composed not of separate organs but as a continuum, united by means of their nervous connexion with the central nervous system and acting as a whole, so that, as long as the reciprocal innervation apparatus is intact, when one muscle fails another takes on its work.

RABBIT 14

a

b

c

d

e

f

Fig. 2. Rabbit 14. *a*, Normal gait; *b*, deep flexors cut; *c*, deep flexors and plantaris cut; *d*, deep flexors, plantaris and soleus cut; *e*, deep flexors, plantaris, soleus and outer head of gastrocnemius cut; *f*, all muscles cut.

The tendons were cut in the following order:

(1) Deep flexors,
(2) Plantaris,
(3) Soleus,
(4) Outer head of gastrocnemius,
(5) Inner head of gastrocnemius.

After division of the deep flexor tendons, no alteration takes place in the movements of the ankle. The toes are held in a very slightly dorsiflexed position but this is only very slightly marked (Fig. 2 *b*). After section of the deep flexors and the plantaris (Fig. 2 *c*), there is little change in the movements of the ankle and none that can be perceived in the outline drawings. A careful measurement, however, of the variations of the angles of the long axis of the foot and the tibia showed that the plantar flexion and the raising of the heel were slightly retarded, but this did not reveal itself on the screen. The toes, however, became markedly extended. This, of course, is to be expected, as the whole of the flexor musculature of the toes, except for the small intrinsic muscles of the foot, has been thrown out of action and therefore the extensor muscles are able to work without any opposition from antagonists. During the time the foot is on the ground, the hyper-extension is much less marked, presumably due to the extensors of the toes not being in active contraction.

Section of the deep flexors, plantaris and soleus makes no further difference to the gait. After division of the deep flexors, plantaris, soleus and the outer head of gastrocnemius, there is a definite increase in the dorsiflexion of the ankle throughout the whole of the locomotory cycle. During the support period, the length of time the foot remains on the ground is definitely increased

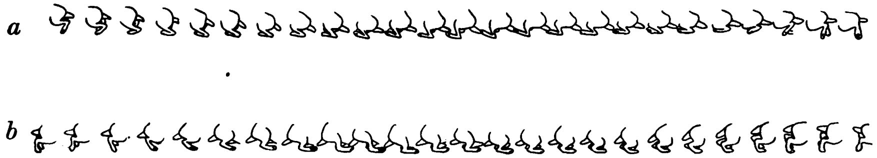

Fig. 3. Rabbit 12. *a*, *Left leg*: all muscles cut; *b*, *right leg*: all muscles *except soleus* cut.

and, following from this, there is a considerable delay in the raising of the heel. The toes show oscillatory movements similar to those seen in rabbit 13 after all the muscles are divided, but they are much less marked. When all the muscles had been sectioned the movements were similar to those described in rabbit 13.

Rabbit 14 was a repeat experiment of a series of operations which had been carried out in rabbit 12, but owing to some oversight in rabbit 12 the soleus on the right side was not divided. This oversight, however, gave a most interesting result because, at the end of the experiment, all the muscles of the left side had been divided and only the soleus on the right side remained intact. The movements of the two limbs are shown in Fig. 3. Note that the tracing for the right leg is to be read from left to right. These two tracings demonstrate very clearly the marked difference the preservation of the relatively small soleus makes to the movement of the limb. On the left side, where all the muscles have been divided, the movements of the limb resemble very closely the end result in the other animals, but on the right side the gait, although differing from that of the normal animal, resembles it much more closely than it does the movements of a limb in which all the muscles have been thrown out of action. This result gives further evidence in favour of the hypothesis that the muscles which remain perform extra work in an attempt to take the place of the muscles which have been lost. It has already been mentioned that the soleus is the one "red" muscle of the series, and the results of this experiment would suggest that the action of "red" muscles does not differ from the action of "white" muscles.

RABBIT 11

The muscles were cut in the following order:

(1) Plantaris,
(2) Soleus,
(3) Inner head of gastrocnemius,
(4) Outer head of gastrocnemius,
(5) Deep flexors.

Fig. 4. Rabbit 11. *a*, Normal gait; *b*, plantaris cut; *c*, plantaris and soleus cut; *d*, plantaris, soleus and inner head of gastrocnemius cut; *e*, plantaris, soleus and both heads of gastrocnemius cut; *f*, all muscles cut.

Section of the plantaris and soleus made little difference to the movements of the ankle. After division of the flexors, soleus and inner head of gastrocnemius, the movements of the ankle during the suspense period are unaltered, but during the time when the foot is on the ground there is a delay in the raising of the heel, otherwise the movements of the ankle are normal. The toes are now being held in a slightly more flexed position, showing that the deep flexor is in a hypertonic state. After the division of the outer head of gastrocnemius, when only the deep flexor remains, there is a very striking change in the gait. The toes are now hyperflexed indicating the additional work done by the flexor muscle. This, however, is inadequate for the purpose of moving the ankle, so that when the foot reaches the ground the heel is the first portion to make contact. The raising of the heel from the ground is very greatly delayed and only occurs near the very end of the support period. After section of all the muscles the usual condition is seen, but the oscillations of the toes are better marked than in the other experiments.

In rabbits 16 and 18 the same general tendencies were observed. In rabbit 16 the muscles were cut as follows:

(1) Soleus,
(2) Deep flexors,
(3) Inner head of gastrocnemius,
(4) Plantaris,
(5) Outer head of gastrocnemius.

It was only after the division of the plantaris that there was any delay in the time of the raising of the heel from the ground. In the toes there was a very slight amount of extension which appeared to be confined to the distal phalanx, and there was no further increase in the amount of extension until after section of the plantaris.

In rabbit 18, only the inner head of gastrocnemius, deep flexors, and plantaris were divided, as the animal unfortunately died before the experiment was completed. The results in this animal, however, resemble very closely those which had been obtained in the other experiments.

SUMMARY AND CONCLUSIONS

The muscles studied in this investigation were those which are found in the calf of the rabbit. After the section of any one muscle, little or no alteration occurred in the gait of the animal. Indeed, generally, it was not until three muscles were divided that noticeable changes could be detected. Evidence is brought forward which suggests that after muscles are divided the other muscles contract more strongly and take on the work of the muscles which have been divided. It is only after a relatively large quantity of the muscles to a joint have been thrown out of action that the remaining muscles are unable to act as efficient substitutes for those which are lost and that any marked alteration takes place in the gait. It is, of course, to be remembered that the movements which have been studied are relatively simple ones carried out by large muscles, and it does not necessarily follow that the evidence can be applied without modification to muscles and joints carrying out delicate and complex movements such as are found in the human hand.

In these experiments the innervation of the muscle remained intact.

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REFERENCE

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