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TRANSPLANTATION OF MOTOR NERVES AND MUSCLES IN THE FORELIMB OF THE RAT

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EIGHT FIGURES

Previous experiments have shown that in the rat a reversal of foot movement results when flexor and extensor muscles of the shank are transposed or when the nerves to these muscles are crossed. This reversal of foot movement, although extremely awkward and in many activities a distinct hindrance to the animals, persists permanently in all activity without any correction of the distorted peripheral effect by central nervous adjustment. Special training, amputation of the contralateral hind food, or amputation of both forelimbs fails to induce reeducation (Sperry, '40, '41).

The present paper deals with similar experiments carried out on the front leg to find out if the central mechanisms for forelimb coordination are any more adaptable to peripheral disarrangements than are those for hind limb coordination. There are several lines of evidence which suggest that readjustments in motor coordination impossible in the hind limb might occur in the forelimb. It has been reported that in man reeducation is effected more readily after transposition of arm muscles than after transposition of leg muscles (Scherb, '38). Histological studies indicate that in rodents there is a richer supply of fibers distributed from the cortex to the forelimb centers of the spinal cord than to the hind limb

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centers. In many lower mammals the cortico-spinal tract does not extend beyond the brachial segments, though in the rat and other rodents it is traceable into the lumbar segments (Kappers, Huber and Crosby, '36). The effects of cortical lesions (Van der Vloet, '06), electrical stimulation of the cortex, and transection of the cortico-spinal tract (Barron, '34 b) in the rat also indicate a greater and more direct influence of cortical activity on forelimb movement than on hind limb movement. In addition front leg movement in the rat shows greater variation than hind leg movement, enters more frequently the visual field, and has more direct effect on the orientation and posture of the animal. Thus conditions in the case of the forelimb would seem to be more favorable than in the hind limb for the dissociation and reorganization of the innate coordination patterns to meet experimental alterations of the motor periphery.

Voluntary control of individual muscles of the arm is possible in man and the contraction phase of any arm muscle, after transposition, can be shifted by training to that of any antagonistic muscle (Scherb, '38). In amphibians, on the contrary, the normal motor coordination patterns of the entire forelimb are unalterable by learning and remain unmodified after peripheral disarrangements that make their persistence more disadvantageous than would be no movement at all (Weiss, '37).

In forms intermediate in the vertebrate scale between man and amphibians the situation is less clear. Flourens (1842) reported recovery of flight in the fowl after crossing the median and ulnar nerves of the wing. Osborne and Kilvington ('10) reported recovery of coordination in the forelimb of the dog after the original median nerve trunk had been substituted by that from the contralateral forelimb. Like Flourens they attributed the recovery to a learning process. According to Kennedy ('14) recovery of coordination occurs immediately after regeneration of crossed flexor and extensor nerve trunks in the forelimb of the dog without any training period and probably is not due to a learning process but rather to direct modification of central activity by the altered sensory stimuli. By nerve anastomoses Barron ('34 a) forced the median and ulnar trunks of the forelimb to innervate the hind limb in the rat and found that in some cases the resultant associated movements of fore- and hind limbs became gradually dissociated. The dissociation of function in the forelimb centers was attributed to a learning process dependent on a substantial supply of afferent fibers in the crossed nerves. In contrast to the above reports, Cunningham (1898) found no corrective adjustment whatever in the forelimb coordination after crossing the musculospiral with the ulnar and median nerves in the dog. He directly opposed the contention that central nervous mechanisms adjust their impulses through practice to suit an altered peripheral innervation.

Whether the basic central mechanisms for forelimb coordination can be disintegrated and reorganized in the lower mammals and if so, by what means and to what degree, are questions that still remain unsatisfactorily settled in the light of these conflicting reports and interpretations. In all of these previous experiments the nerve sutures were made on large nerve trunks. It is uncertain whether reeducation is possible even in man after the haphazard reestablishment of peripheral connections which results from the random regeneration of complex nerve trunks (Ford and Woodhall, '38; Stookey, '22).

The present experiments were undertaken in the hope that results of a more conclusive nature could be brought to bear on the problem by crossing only terminal nerve branches to specific muscles and by transposing muscles with their nerves intact. The nature of the peripheral derangement produced by these methods can be more exactly determined and controlled. Moreover, these methods produce less extreme shuffling of the original neuron connections between the centers and the periphery. And finally, readjustment is not prevented by the termination of different branches of the same neuron on end organs of different kinds. Control operations were performed and control cases run throughout with the experimental groups. All but the test muscles acting on the joint in question were excised to prevent readjustment by "trick" movements produced by non-test muscles.

The object of the experiments was to find out if the rat would be able to interchange the timing of the central discharges for elbow flexion and extension in order to restore normal limb coordination after the flexor-extensor relations of the periphery had been reversed by muscle transposition or nerve crossing.

ONE-WAY CROSS: FLEXION REVERSED TO EXTENSION BY MUSCLE TRANSPOSITION

In view of the complete refractoriness to adjustment exhibited by the rat after experimental reversal of hind foot movement shown in the previous experiments, an attempt was made in the first series of operations to establish the simplest and most favorable conditions for reeducation. In these cases only flexor muscles of the elbow were transposed, no extensors, so that readjustment of flexor action only was necessary. Possible reflex inhibition of learning by proprioceptive stimuli from antagonistic muscles, as reported in human patients (Scherb, '38), was excluded by removal of all the extensor muscles of the joint. To make unnecessary a dissociation of function within the agonist group of elbow flexors itself, the other flexor muscles which were not transposed were also removed. Thus all that was required for adjustment was a chronological shift in the functional relations between the brachial flexors and the musculature of the other limb segments.

The operation

The tendons of the biceps and brachialis muscles were cut from their insertions and sutured to the distal stump of the severed tendon of the long head of the triceps muscle (fig. 1) so that these two flexor muscles were made to act as extensors.

All other brachial muscles including the anconeus and pronator teres muscles were excised, leaving only the two crossed flexor muscles acting on the elbow joint. It was necessary in most cases to cut the cutaneous branch of the circumflex nerve to the skin over the shoulder; all other nerve branches save those to the excised muscles were left intact. All shoulder

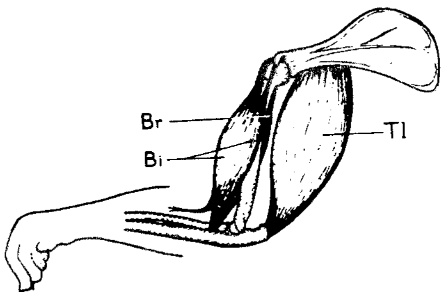

Fig. 1 Diagram of the test muscles in their normal anatomical positions. Br, M. brachialis; Bi, M. biceps brachii, caput longum and caput breve; Tl, M. triceps longus.

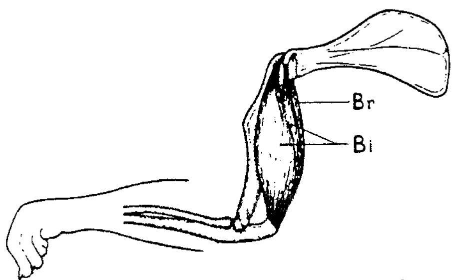

Fig. 2 Diagram of flexor muscles of the elbow (M. biceps, Bi; M. brachialis, Br) after being transposed to act as extensors.

muscles were left in place except the small coracobrachialis muscle which was removed to make more room for the crossed biceps muscle. The diagram in figure 2 illustrates the resultant anatomical relationship of the flexor muscles after transposition. Two control rats were prepared also in which all the brachial muscles acting on the elbow joint were excised except the long triceps [2] extensor which was left intact. The

[2] For the sake of brevity, the long head of the triceps and long head of the biceps will be referred to as the long triceps and long biceps respectively.

operations were performed under a combination of ether and sodium amytal anesthesia with a single lateral incision. The tendons were sutured with fine silk thread.

Results

Active elbow extension began to appear at varying periods from 7 to 19 days after the operation, recovery being quicker in the younger animals. The extensor movements occurred from the beginning in reverse phase. The elbow was sharply extended in the suspended flexor phase of locomotion instead of in the supporting extensor phase. In the flexion or withdrawal reflex the elbow was extended strongly; whereas it remained limp or was extended only weakly in the controls. In landing on the front legs, the forearm, instead of extending to support the body weight as in controls, remained loose and was flexed passively so that the animal's weight fell on the elbow. In reaching to free a binding placed about the neck, an action involving elbow flexion in the normal animal, the elbow was stiffened out in extreme extension so that the paw reached far beyond the binding. When the rats were suddenly rotated toward the side of the operated limb, the limb remained limp instead of extending against the floor to counteract the rotation as it did in normal and control animals.

Fifteen successfully operated cases were obtained which showed this extension of the elbow in movements normally involving elbow flexion, and a looseness of the elbow joint in movements normally involving elbow extension. Extension of the elbow by the crossed flexor muscles and passive flexion by the body weight prevented ankylosis of the joint. The fifteen cases with the transposed flexor muscles ranged in age from 20 days to 60 days at the time of operation. These cases were kept under observation and tested to see if they could learn to support themselves on the operated limb by using the transposed flexor muscles to extend the elbow.

The first three rats successfully operated upon continued to move the elbow in reverse for several weeks, meantime relying on the unoperated limbs for support during locomotion and other activity. It therefore became necessary to make the use of the operated limb in unreversed fashion more crucial to the animals. This was accomplished effectively by amputating the contralateral forelimb, the ipsilateral foot, and the tail which the rats used considerably for balance and support. The absence of the contralateral limb also made it possible to determine more reliably just how much the animals were actually depending upon the operated limb. All cases, therefore, were treated uniformly in this manner thereafter as soon as the transposed muscles had begun to function. In this condition, the only way in which the animals could raise their forequarters off the floor while moving about was by use of the operated forelimb. They were thus in a state of training whenever they moved. Moreover, these extreme measures served another important purpose in that they tended to break up the normal automatic patterns of coordination and bring out new, more voluntary activity. Such conditions have been shown to favor reeducation after muscle transposition in man (Scherb, '38).

After this treatment all but one of the rats managed to support themselves to some degree on the operated front leg with the elbow extended. They accomplished this, however, by a trick method quite different from that used by normal rats. Reversed action of the transposed flexors frequently brought the elbow joint into a locked position in extreme extension. Once the joint became thus fixed, it was used in the mechanically stabilized position aided by an inward rotation at the shoulder to support the forebody. In locomotion the limb was moved from the shoulder in a stiffly extended locked position. It was swung forward out at the side and then used for support much like a crutch. Whenever the joint slipped out of the locked position, the limb caved in and the rat came down on its elbow. The one case which never showed this trick adjustment was found to have a partial ankylosis which prevented extreme extension and locking of the joint. The controls never displayed the characteristic locked joint method of supporting themselves shown by the experimentals. Like normal rats, they raised and upheld the forequarters with the elbow joint maintained in varying degrees of extension.

The elbow joint of the rat does not lock completely by extending beyond 180 degrees as does the elbow in many human beings. When the forelimb is fully extended in the supporting position, however, it is capable of upholding a weight several times the body weight of the rat. The downward pressure is taken up almost entirely by the mechanical structure of the bones and ligaments with only a slight and relatively insignificant amount of active muscular work being required to hold the joint in the mechanically stabilized position. The use of the forelimb in this manner so that the body was supported primarily by the mechanical features of the elbow joint, rather than by muscular work at the joint, is referred to here as a locked joint reaction.

No training period was observed in the onset of the trick locked joint reaction. It appeared abruptly on amputation of the other limbs. In most of the cases it appeared for the first time as soon as the animals began to move on coming out of the anesthesia after the amputations. As the animals' excitability subsided and they became more relaxed, there was a certain amount of relapse back to discrete reversed action. In the early stages thereafter when the limb went into the locked position, it was held out sidewise from the body and only occasionally, apparently by accident, was the body weight shifted directly on top of the extended limb. As time went on, however, the effective use of the locked limb in a supporting position became less accidental and more consistent and somewhat more proficient. This gradual though slight improvement in the use of the locked joint reaction for support after it had once appeared apparently involved a training process.

The initial appearance of the locked joint reaction was not completely dependent on the amputations. In a few of the cases the reaction appeared before the amputations were made. In these cases, however, very little of the body weight was shifted onto the operated limb. The reaction could be readily elicited in cases which had only the contralateral forelimb amputated and which had not yet shown it spontaneously, by holding the rat up by the hind quarters and pushing it slowly along the floor on its forebody. The amputations merely favored the appearance of the reaction and made its retention and improvement thereafter more necessary to the animals.

There was considerable range in the degree of success with which the various cases used the operated limb to support themselves. In some cases elbow extension remained in reverse most of the time, and it was only exceptionally that the animals happened to raise their forequarters off the elbow and lean on the straightened locked forelimb. This occurred most frequently while they were pivoting about on the hind quarters and only rarely during locomotion. At the other extreme were cases that came to use the extended limb for support with considerable certainty and in which it was only on occasional instances that the joint gave way under them. One of these cases after 9 months is pictured in figure 3 supporting itself on the operated limb while stretching for food. At times these rats were able to maintain their support in the position shown in figure 3 during extreme and rapid shifts of head, neck, and trunk posture.

When the joint slipped out of the locked position, the animals usually fell from the platform. But two of the rats were observed to avoid falling sometimes by quick extension of the elbow before the joint had become more than slightly flexed. Except for these corrective movements that appeared in the advanced stages of the two most proficient cases, the act of extending the joint to the locked position was always performed in the reverse phase of coordination, that is, in the normal flexor phase of limb movement when the body weight was being shifted off the limb, not onto it. Even in the case of these corrective movements it is probable that although the weight of the forequarters was falling onto the operated limb, the muscular contractions of the back and hind legs were of a nature to counteract this fall and were thus similar to those involved in shifting weight off the forelimb, rather than onto it.

In any case, the act of getting the limb into the beneficial locked position in most instances demanded no adjustment in the function of the transposed muscles. It was only the ability to maintain this position during the supporting phases of activity that involved a corrective modification of the reversed

Fig. 3 Rat with transposed flexor muscles feeding from training platform. The training apparatus was so constructed that the rats, in order to reach food contained in the self-feeder at upper left, had to climb stairs to platform, span distance to prop, and then support forebody on the operated limb as shown in picture. Photograph illustrates most proficient case of the series. Even this animal usually fell to floor 22 cm. below when the elbow joint slipped out of the locked position (see text).

movement of the elbow. There was some tendency, though not very marked, for the cases operated young to show greater proficiency than the old ones.

Cutting the nerves to the transposed muscles in one case and the tendons of the transposed muscles in another case abolished the reversed action of the elbow and the locked joint adjustment. In another case the nerves to the transposed muscles were merely crushed. Both the adjusted and the reversed action of the elbow disappeared and reappeared after 4 weeks when the nerves had regenerated. Clearly the reversed extension of the elbow was produced by contraction of the transposed muscles and this contraction was necessary to bring the joint into the locked position where it could be used for support.

Four additional experimental cases were prepared similarly to the others except that in two of them the biceps muscle was excised and only the brachialis muscle crossed, while in the other two the brachialis was excised and only the biceps crossed. All four cases showed the typical locked joint adjustment, while all actual movement of the elbow remained reversed. Since it appeared after crossing either muscle alone, the trick adjustment was not linked up with the two-joint action of the biceps muscle nor with any reaction peculiar to either one of the muscles.

The cutaneous nerve to the skin over the shoulder regenerated in all cases. No loss in sensitivity over the rest of the limb was detected. The elbow and shoulder joints remained normally loose and flexible. Function of the forearm and paw muscles was unimpaired. The wrist was extended and flexed in normal phase while the elbow moved in reverse. The digits were extended in the landing reaction and grasped tightly the wires of the cage when the animals were lifted out.

Two additional controls were prepared like the other controls except that the large triceps muscle was sheared down to a size no larger than the combined size of the biceps and brachialis muscles. These cases never resorted to locking the elbow joint for support, but maintained themselves with the joint in various degrees of extension with tension on the reduced triceps muscle. The same was true of two other controls in which all brachial muscles were excised except the small medial triceps. This muscle is smaller in size than the combined size of the flexor muscles, and its mechanical relations are quite similar to those of the transposed flexor muscles.

The experimental cases when examined under anesthesia showed no atrophy of the transposed muscles (note transposed flexors in fig. 7). On the contrary a slight hypertrophy was apparent in many of the cases. The length of the muscles was nicely adjusted. The anatomical conditions for this transposition at the elbow are very favorable. That the operated limb was capable of strong and vigorous elbow extension was also evident from struggling movements made during manipulation. That the transposed muscles were strong enough to lift the full weight of the forebody was shown by the fact that they did so during random struggling movements when the rats were held by their hindquarters with the forebody resting on the floor. The use of the joint in the locked position for support instead of in the normally somewhat flexed position, cannot be ascribed, therefore, to weakness of the transposed muscles.

Ten of the experimental cases were kept longer than a year. The four cases showing greatest adjustment were kept for 16 months. In all cases the withdrawal reflex remained in reverse to the end. When the palmar surface of the paw was pricked with a needle from behind, the paw, instead of being withdrawn, was driven harder against the needle by extension of the elbow. All cases continued permanently to extend the arm sharply in trying to locate points about the face or in trying to brush off a binding placed about the neck. When the operated limb was lifted over obstacles or over steps in climbing up stairs, the transposed muscles continued to work in reverse so that the limb was stiffly extended and had to be raised upward far out to the side in order to clear the steps and other obstacles. In the controls the elbow remained loose in these reactions in a neutral position of half flexion which was more advantageous than the stiffly extended position. In order to get to the platform shown in figure 3 the rats had to climb up stairs. To get down they usually jumped to the floor from the platform or from halfway down the stairs rather than descend the stairs, which was difficult for them. None of the cases ever learned to break the fall in landing by contraction of the transposed muscles. The muscles relaxed so that the limb caved in and the animal's weight fell on the elbow. Like normal rats the controls landed on the forepaw, not on the elbow. Use of the limb in the extended, locked position for support was thus the only reaction which seemed to involve any adaptive alteration in elbow movement.

To determine whether maintenance of the joint in the locked position during the supporting phases of movement involved any muscular contraction or was dependent entirely on the mechanical relations of the joint and ligaments, the following operation was performed (fig. 4). A small hole was drilled in the humerus at the point where the olecranon process of the ulna closes against it in extreme extension. A small peg made from a metatarsal bone was inserted firmly into the hole

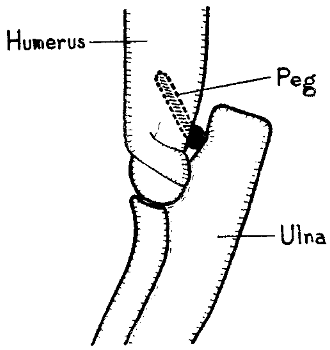

Fig. 4 Diagram illustrating how peg inserted into humerus prevented elbow joint from locking.

in the humerus so that only the epiphysis of the metatarsal peg protruded. This was filed down until it was just long enough to prevent the elbow joint from locking. The joint could thus be extended approximately 170 degrees but could not be brought into complete extension. This operation was performed on one of the cases that had been using the operated limb consistently for support for more than 10 months and had learned to feed from the training platform as shown in figure 3. The forelimb was rendered practically useless as a means of support by the pegging operation. Whenever any appreciable weight was put on the forelimb, it caved in at the elbow. The rat was no longer able to support itself on the training platform so as to obtain food when tested 2 weeks after the peg was inserted. On some occasions, however, during rapid locomotion and especially when the animal was at rest with most of its weight on the hind quarters, extension of the elbow was maintained during the supporting phase of coordination. A certain amount of weak muscular tension was apparently present at this time. The muscular tension involved in the trick adjustment shown by all but one of the rats in this series was too weak evidently to furnish any appreciable support itself, even after 10 months of practice, but was sufficient to maintain the joint in the locked position so long as most of the body weight was taken up by the non-muscular, mechanical structures.

Contraction of the shoulder muscles as well as of the test muscles could have produced the slight tension required to hold the joint in the locked position during the supporting phases of movement. Adduction of the forelimb accompanied by an inward rotation of the humerus would necessarily produce also a secondary extensor action at the elbow joint when the fore foot was fixed against the floor. That it was actually the shoulder muscles and not the test muscles that were primarily responsible for maintaining the joint in the locked position during the supporting phases of movement was shown by the following: Cutting the tendons of the latissimus dorsi and pectoral muscles on two cases 12 months after operation completely abolished the trick adjustment. On the other hand, severing the tendons of the spinodeltoid, acromiodeltoid, and infraspinatus muscles on two other cases produced no deleterious effect on the locked joint adjustment. Normal and control animals were able to support themselves on the forelimb in locomotion and other activity with little noticeable deficiency after severance of the tendons of either the above adductor or abductor group of shoulder muscles.

Whether the transposed flexor muscles were aiding the shoulder muscles to some slight degree to keep the joint locked could not be determined by observation alone and, hence, action potential recordings were made. Two fine enameled silver wires, one for the active lead and one for ground, were cemented together side by side. The two cut ends of the wires almost in contact served as the electrodes. These electrodes were fastened under the skin just over the muscle or in some cases directly under the perimysium of the test muscles. Records were taken from the three cases which after 14 months showed the greatest proficiency in supporting themselves on the operated limb. The action potentials, amplified and recorded through a loudspeaker and oscillograph, were correlated with the rats' limb movements.

During locomotion, when the forelimb was kept rigidly extended, the contraction of the transposed flexors was distinctly intermittent, instead of being sustained throughout the locomotor cycle. The bursts of contraction occurred, moreover, not during the supporting phase of walking to help maintain elbow extension but during the suspended flexion phase of walking as in normal animals. That this was the exact phase of contraction was further substantiated by synchronized motion picture and oscillograph records [3] (fig. 8). The slight muscular tension required to maintain the limb in the mechanically stabilized position of complete extension during the supporting phase was evidently furnished entirely by the intact adductor muscles of the shoulder and not at all by the transposed muscles. The transposed muscles after 14 months of practice were, therefore, still working in their original locomotor phase in spite of the fact that action in just the opposite phase would have been much more to the animals' advantage for either this stifflegged type of walking or normal walking.

At times when the rats were at rest supporting the forebody on the locked limb, there occurred a certain amount of weak discharge in the transposed muscles. This weak discharge, however, could not be distinguished from flexor discharge in normal animals under similar conditions. Regarding the action of the transposed muscles in other responses, the

[3] The synchronized action potential and motion picture records were taken with the aid of Paul F. Brown.

action potential records merely substantiated the previous conclusions based on observation of elbow movement, namely, persistence of the original time pattern of activation of the transposed muscles.

ONE-WAY CROSS: FLEXION REVERSED TO EXTENSION BY CROSSING NERVES

In the rat, unlike the situation in amphibians, there is no evidence that normal coordination is restored through modulation of nerve by muscle after nerves are crossed to foreign muscles. The discoordination produced by crossing nerves is similar to that produced by transposing muscles and can be used in the same way to test the modifiability of central mechanisms by experience and training (Sperry, '41). In the present experiments the normal timing of elbow extension was reversed by crossing the nerve of the biceps flexor into an extensor muscle, the long triceps.

The operation

The nerves to the biceps muscle and the long triceps muscle were severed, and the proximal stump of the biceps nerve was crossed to the distal stump of the triceps nerve. To prevent regeneration of the triceps nerve into its original muscle, the proximal stump was ligated tightly with silk thread and inserted into tissue as far distant as possible from the triceps muscle. To expose the nerves better, the tendons of the deltoid and pectoral muscles were partially severed from the humerus. The biceps and coracobrachialis muscles were excised and a section of the nerve to the brachialis muscle was removed where it crossed the humerus. The brachialis was thus paralysed to give the weakened extensors a better chance to extend the elbow completely and so prevent possible ankylosis of the joint during the period in which the crossed nerve was regenerating. The nerve crosses were tubulated in arterial sheaths as described by Weiss ('41 a). In a few cases the brachialis nerve as well as the biceps nerve was crossed to the triceps muscle but no detectable difference appeared in the results. The operations were done through a medial incision in the axilla. About a month and a half later when the flexor nerve had regenerated into the triceps muscle, the other brachial muscles including the brachialis, anconeus, and pronator teres were excised through a lateral incision. This left only the long head of the triceps muscle supplied by the biceps nerve to effect elbow movement as shown in figure 5. After the operated limb had healed, amputations were performed as in the muscle-cross group. In two control

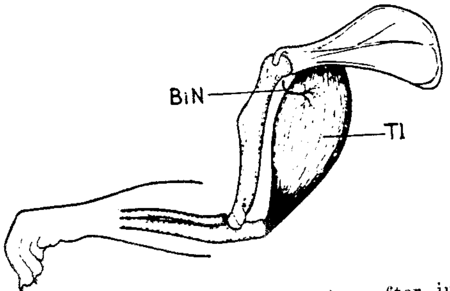

Fig. 5 Diagram illustrating anatomical situation after innervating the long triceps extensor (Tl) by the nerve (BiN) of the biceps flexor.

cases all brachial muscles acting on the elbow were removed except the long triceps which was left in its normal position with its nerve intact. The tendons of the pectoral and deltoid muscles were partially severed as in the experimental cases.

Results

Seven experimental cases were obtained which showed good elbow extension in reversed phase. Three of these cases were 15 days, the others ranged up to 30 days in age at the time the nerves were crossed. No reliable age difference was noted in the results. These animals were kept under observation from 4 to 15 months. When sacrificed they were carefully dissected and tested for misregeneration of nerve fibers. Electrical and mechanical stimulation of the cut end of the biceps nerve above the point of suture produced sharp strong contraction of the triceps muscle. No contraction occurred in this muscle when the trunk of the original triceps nerve was cut and stimulated. There was no sign of misregeneration in any of these seven cases. The triceps muscle after reinnervation by the biceps nerve was in no case reduced by more than one-seventh normal size, showing that a few nerve fibers from a small muscle are capable of reinnervating a much larger muscle by multiple axon branching. At postmortem dissections the nerve to the triceps muscle was found to be distinctly larger, by approximately one-third, distal to the region of anastomosis than proximal to it.

Anatomically these cases were quite comparable to the control cases, the only difference being that in the experimental group the triceps was supplied by the biceps nerve instead of its original nerve. Forelimb function in the experimental cases, however, was not at all comparable to that in the controls. Briefly its history was quite similar to that previously described for the cases in which the flexor muscles were transposed. These cases displayed the same type of reversed movement and the same kind of trick adjustment. In two cases the elbow moved in reverse most of the time and was used for support in the locked position only rarely. In other cases the adjustment was fairly good and the animals supported themselves much of the time on the stiffened, unnaturally extended limb. Those showing the greatest adjustment never became quite as proficient as did some of the animals in the preceding muscle-cross series. This may be attributed to the partial severance of the tendons of the shoulder adductor muscles during the operation when it was not foreseen that these muscles would be of such importance in postoperative adjustment. No compensating adjustment for this deficiency in the shoulder muscles ever appeared in the action of the test muscles in these cases. As in the muscle-cross cases the trick method of mechanical support constituted the only adjustment observed in elbow movements.

Since the same type of adjustment that followed muscle transposition occurred also in these rats in which the muscle attachments remained normal and only the nerves were crossed, its nature must not have been due in the muscle-cross series to any peculiarity of the unnatural mechanical conditions of the transplanted muscles.

It is important to note that this locked joint adjustment that occurred naturally in both series of cases furnished a better condition for testing the rats' learning ability than any training situation that could have been devised experimentally. In itself, it was a direct approach to the important first step of re-education, namely, the production of a favorable trial reaction which could be selected for and improved upon, while the unfavorable reversed movements were eliminated. Had the animals been capable, under any conditions, of correcting the innate action phase of the flexor motor neurons, one would expect them to have done so from this excellent point of departure by gradually improving upon the awkward unstable locked joint support until a more effective normal use of the elbow was restored.

As in the preceding series, the trick adjustment in these nerve-cross cases was followed carefully and tested for any signs of improvement that might indicate a corrective shift in the timing of the test muscles. In one of those cases which showed the greatest degree of adjustment and which had been using the operated limb for support for nearly 9 months, a bone peg was inserted in the humerus as illustrated in figure 4. After the operation the elbow joint was extended to about 170 degrees but could not be extended completely. As a result the rat was unable thereafter to support itself on the extended forelimb. The trick adjustment was likewise abolished by severing the tendons of the shoulder adductor muscles in a third case. Action potential records taken on two other cases 13 months after the primary operation showed that the triceps extensor supplied by the biceps nerve was still contracting in the uncorrected flexor phase of locomotion and other activities. Thus, as in the muscle-cross series, these various checks showed that the rats, even after 9 months and more of practice, had acquired no discriminate control over the flexor motor neurons during the extension phase of co-ordination.

The fact that the one peculiar type of adjustment reaction and no other type appeared consistently in so many cases, and the fact that its onset was abrupt without any training period, both indicated that the underlying pattern of muscular contraction involved was not one that was entirely novel to the action system of the rat, but rather a motor pattern normally present in the rat's repertoire of reactions which happened to work beneficially under the conditions of the experimental disarrangement. Action potential analysis and the results of severing the tendons of the shoulder muscles confirmed this conclusion and showed that the adjustment was achieved by the action of the intact shoulder musculature and not by a corrective shift in the timing of the test muscles. The gradual, but not very marked improvement in the proficiency with which the rats used the locked limb for support must be ascribed entirely to improvement in the action of the adductor muscles of the shoulder and to improvement in the general ability to balance on the straightened limb without throwing it out of the locked position.

The trick adjustment was in no sense a restoration of normal coordination, nor was it at all the best adjustment that might conceivably have been made in the centers to suit the altered peripheral conditions. The normal elbow extension of the controls was decidedly more beneficial to the animals in all activities than was the reversed movement and awkward unreliable stiff-legged support used by the experimental cases.

SPLIT CROSS: ONE FLEXOR MUSCLE TRANSPOSED FOR EXTENSION, ANOTHER LEFT IN NORMAL POSITION FOR FLEXION

In these cases the action of the group of elbow flexors was split by transposing one flexor muscle to act as an extensor against another flexor left in normal position. This type of operation in which a muscle is transplanted to act against its own original group of agonists is performed commonly on human patients. It requires for restoration of normal coordination a dissociation and reorganization of the functional relations not only between muscles of different limb segments, but also between muscles belonging to the same agonist group within a single limb segment.

The operation

Through a medial incision in the axilla the nerve to the long biceps was crushed and the short head of the biceps muscle and coracobrachialis muscle were excised. Two or 3 days later the brachialis muscle was transposed and the remaining brachial muscles except the long biceps and the small pronator teres muscle were removed entire as in previous operations. The nerve to the biceps was crushed, thus temporarily paralysing the muscle, in order to prevent it

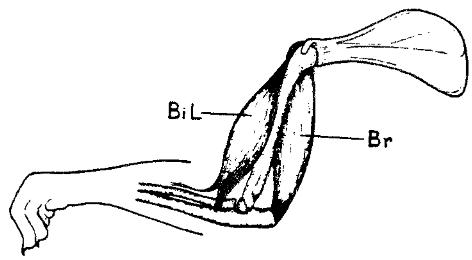

Fig. 6 Diagram showing long biceps (BiL) left in normal position and brachialis flexor (Br) transposed to act as an extensor in antagonism to its former co-flexor, the biceps.

from pulling loose the newly sutured tendon of the brachialis muscle. Nine cases, all between 20 and 30 days of age, were so operated. The anatomical effect of the operation is diagrammed in figure 6. The pronator teres muscle, the flexor action of which proved to be so weak as to be easily overpowered by the transposed brachialis muscle, did not figure in the results and is omitted for the sake of clarity in the figure. The experimental cases were compared with controls in which all brachial muscles were excised except the long biceps and long triceps, and also with the two experimental cases in the first series in which only the brachialis muscle was transposed.

Results

Four of the cases began to show active elbow extension in reverse within a week after the muscles were transposed. This reversed extension disappeared, however, in a few days when the biceps muscle began to recover function. The biceps, contracting at the same time as the mechanically antagonistic brachialis, easily overpowered the newly transposed muscle. By the tenth day the biceps muscle in all nine cases had recovered function and was overpowering the brachialis muscle so that extension of the elbow no longer occurred in any of the animals. Either the biceps nerves had regenerated very rapidly or had not been completely crushed. Two of the rats that had previously shown elbow extension in reverse were allowed to continue without further operation except that the unoperated limbs and tail were amputated as in the previous series. The flexor action of the biceps continued to predominate permanently over the extensor action of the brachialis in these animals. They never managed to dissociate the action of the brachialis muscle from that of the biceps so as to extend the elbow joint during the relaxed phase of the biceps. Nor did they learn to inhibit the action of the biceps so as to extend the elbow in reverse phase and bring it into the locked position.

In the other seven animals the nerve to the biceps was crushed again on the tenth day so thoroughly that in some cases it was severed completely. Five days later all seven rats displayed active extension of the elbow in reverse phase. Their contralateral forelimb, ipsilateral foot, and tail were then amputated as in the other cases. In one animal the biceps began to function again within a week and extension of the elbow was permanently prevented thereafter by the predominance of flexion.

It was 5 weeks after the second crushing of the nerve before there was any sign of biceps recovery in the other six animals. In the meantime all six of these rats had come to use the operated limb in the typical locked joint manner for supporting the forebody in locomotion and other activities with varying degrees of proficiency. During the fifth and sixth weeks a partial loss in the ability to use the operated limb for support was apparent in three of the cases. After 9 weeks two of the animals were no longer able to maintain extension of the elbow during the supporting phases of movement. One of these two cases 5 weeks earlier had been the most proficient of the group in supporting itself on the operated forelimb. Of the other rats, one had lost the ability to support itself during locomotion but managed to do so occasionally while at rest. The remaining three still used the operated limb for support without any noticeable impairment.

The three animals that showed no impairment of the locked limb adjustment were examined under anesthesia 9 weeks after the biceps nerve had been recrushed. The nerve had regenerated and the biceps muscle was full-size and looked perfectly healthy in all three cases. When the biceps nerve was stimulated electrically, the muscle contracted strongly as indicated by change in shape but produced only a small degree of flexion of the elbow instead of the vigorous complete flexion produced by similar stimulation of the biceps nerve in normal animals. Evidently the persistent stretching of the biceps by the transposed brachialis during the period of paralysis had increased the resting length of the biceps muscle. Thus the muscle, although being activated in these cases, was too long for its contraction to have sufficient mechanical effect on the joint to counteract the action of the brachialis muscle. This interpretation received further support from action potential records which showed that during stiff-legged walking in these cases the biceps was clearly discharging regularly in its original flexor phase in synchronism with the transposed brachialis muscle.

In none of the nine experimental cases was there any sign of dissociation of function between the two flexor muscles, the biceps and the brachialis. Although made to act as antagonists mechanically, the muscles continued to contract synchronously.

Depending upon the strength of the muscle and mechanical relations with the joint, one or the other muscle came to overpower the other in different cases so that the joint was either predominantly flexed or predominantly extended but was never flexed and extended reciprocally in the same animal. Even after the brachialis muscle had been used successfully for 6 weeks in two cases to bring the limb into the locked position, the biceps, on complete recovery of function, automatically counteracted the beneficial action of the brachialis muscle so that the rats thereafter were forced to crawl about on the elbow.

TWO-WAY CROSS: FLEXION REVERSED TO EXTENSION AND EXTENSION REVERSED TO FLEXION

In order to support themselves with an extensor as well as flexors acting in reverse, the rats would have to inhibit the action of the transposed extensor during the supporting phases of movement as well as maintain tension in the adductor muscles of the shoulder. These operations were designed to find out if the animals would be able to inhibit the action of the transposed extensor in this fashion and whether they could in addition adaptively modify its positive contraction phase.

The operation

In this series the operation was similar to that in which only the flexor muscles were transposed except that, instead of being excised, the long triceps was transposed to the flexor position. To do this, both the origin and insertion of the muscle had to be transplanted. The broad tendon of origin was sutured with silk thread to fascia and tendons about the anterior head of the humerus. The tendon of insertion was fastened to the medial surface of the ulna at the location of the distal stump of the severed brachialis tendon. Silk thread woven through the insertion tendon was looped underneath the ulna and tied to fascia on the dorsolateral face of the forearm. To make space for the transposed triceps muscle it was necessary to excise the bulk of the deltoid muscle of the shoulder and to remove part of the deltoid ridge of the humerus. Because the long triceps is very large it was sheared down to about two-thirds normal size. The anatomical effect of the operation is illustrated in figure 7 by photographs of the operated limb of one case dissected 13 months after the operation. The muscles were transposed in this manner on

Fig. 7 Medial (top) and lateral (bottom) views of limb with biceps and brachialis flexors transposed to act as extensors and long triceps extensor transposed to act as a flexor. Tl, M. triceps longus; Bi, M. biceps; Br, M. brachialis. Dissection made at time of sacrifice 13 months after operation. Shoulder and forearm muscles partially removed to expose tendons of test muscles. This is an average specimen. The muscles are somewhat shrunken after preservation for 3 months in formalin.

fourteen rats ranging in age from 22 to 48 days at the time of operation. The contralateral forelimb, the ipsilateral foot, and tail were amputated on all cases within 4 weeks after the operation. Three control rats were prepared in addition in which the operation was similar except that the brachialis muscle was excised and the biceps and long triceps muscles were left in normal position, uncrossed.

Results

Six weeks after the operation five of the fourteen animals showed active extension and flexion of the elbow. These elbow movements were always in reverse phase from that shown in control and normal rats. The elbow was extended in the suspended phase of walking and flexed in the supporting phase. In the withdrawal reflex the elbow was extended. It was flexed when the rats, in falling, landed on the forelimbs. When the rats reached upward toward regions about the ears and neck, the elbow was extended instead of flexed. When the animals were suddenly rotated onto the side of the operated limb, the elbow was flexed instead of extended. When they leaned on the operated limb while at rest, the elbow was flexed. In climbing and lifting movements, the elbow was always extended in the phase in which it was flexed in normal and control rats. Contraction of the transposed flexors in these reactions regularly produced complete extension of the elbow, but triceps contraction produced only about three-fourths complete flexion. Electrical stimulation of the triceps under anesthesia showed that the transposed muscle was incapable of producing as complete flexion of the elbow as does the normal biceps muscle.

All five of these cases were kept under observation for longer than 12 months. In all cases the elbow movements remained permanently in reverse. At the end the elbow movements in some of the test reactions were not so vigorous as at first. Apparently the rats had learned that the operated limb was of little use and tended to inhibit its action. When surprised or excited by rough handling, however, they moved the limb with the former intensity with reverse action at the elbow. None of them learned to support itself on the extended forelimb either while at rest or during locomotion. An attempt was made to train three of them to feed as in figure 3. The self-feeder was lowered time after time to within reach and then raised gradually day by day until it was so high that it could be reached only by using the extended forelimb for support. The controls had no difficulty in supporting themselves on the extended forelimb while feeding from the training platform. When no learning appeared in the experimental cases after 3 months, the self-feeder was left at a height such that the rats could just barely reach the food with difficulty when the limb was flexed. After 3 weeks more they still showed no sign of learning to extend the limb so as to raise the forebody to a position from which they could get at the food more easily, and this training was discontinued. The limb coordination in climbing the stairs to the platform and in landing on descent was also carefully watched during this period, but no adjustment in the action of the transposed muscles was observed.

Of the other nine rats, two showed active elbow extension which remained in reverse without adjustment. Active overt elbow flexion, however, was absent or at least so weak that it could not be distinguished from passive flexion of the joint. When the triceps muscle was stimulated electrically in these two cases, its contraction flexed the elbow only about 80 degrees, not as much as in the preceding five animals.

The forelimb coordination in the remaining seven rats was quite similar to that in the animals described previously in which only the flexor muscles were transposed. Within 5 weeks after the operation they all managed with varying efficiency to support themselves on the forelimb with the elbow joint in the locked position. There was no indication in any of these cases of active flexion of the elbow. When these rats were examined under anesthesia, it was found that in three cases the insertion of the triceps muscle had been pulled loose so that the muscle had no action on the elbow joint. In the other four animals the insertion and origin were both intact. In one of the four, the muscle was so lengthened that its contraction had no effect on the ulna. In the other three cases electrical stimulation of the triceps caused partial flexion of the joint by not more than 80 degrees.

These three animals in which the triceps on electrical stimulation was found to be capable of exerting an appreciable elbow in all fourteen cases can be attributed to the following factors. First, the origin as well as the insertion of the triceps was transplanted and neither of these could be as neatly and firmly sutured as could the tendons of the transposed flexors. Secondly, extensors are inhibited and flexors predominantly contracted in a newly operated or injured limb, a reaction which, under normal conditions, protects the limb. Contraction of the flexors in these animals and the resultant stretching of the passive triceps especially while its tendons were still regenerating would tend to make it recover finally with an abnormally long resting length. Thirdly, as soon as the flexors had recovered sufficiently so that the locked joint adjustment was used, the action of the triceps was further inhibited. These factors plus a better anatomical and mechanical adjustment to the joint all tended to favor the transposed flexors.

Pronounced action of the transposed triceps to produce overt flexion of the elbow was correlated with the absence of the trick adjustment in this series. Whether the locked joint reaction was prevented from the beginning by the early recovery of triceps function or whether the absence of the reaction permitted better recovery and function of the triceps is not certain. Both factors would tend to reinforce each other. Excision of the long triceps after 14 months in two cases which showed overt elbow flexion and no locked joint adjustment was not followed by an emergence of the trick adjustment. The lack of adjustment may have been correlated primarily with the effects on the shoulder muscles of removal of the deltoid ridge of the humerus in the original operation. Postmortem examination of the shoulder musculature, however, did not reveal differences significant enough to bear out this latter interpretation with certainty.

TWO-WAY CROSS: FLEXION REVERSED BY MUSCLE TRANSPOSITION, EXTENSION BY NERVE CROSSING

This series was similar to the preceding except that the difficulties and complications introduced by crossing the triceps muscle were avoided by crossing the triceps nerve into a flexor muscle.

The operation

Through an incision in the axilla the coracobrachialis muscle and the short head of the biceps muscle were excised. The proximal stump of the long triceps nerve was anastomosed to the distal stump of the long biceps nerve with an arterial sheath. The proximal stump of the biceps nerve was ligated and inserted into tissue as far distant as possible from the biceps muscle. Ten days later through a lateral incision, the brachialis muscle was transposed to the extensor position and the remaining brachial muscles except the long biceps were removed. The resultant anatomical condition is similar to that shown in figure 6 except that the biceps muscle was innervated by the nerve of the long triceps instead of its original nerve. Ten animals were operated upon. They were 24 and 25 days of age when the nerves were crossed. The controls in this series were the same as those in the preceding series.

Results

About 7 days after the brachialis muscle was transposed, it began to recover function extending the elbow in reverse. These movements became stronger, and after 4 weeks all the animals were using the limb in the locked position to support themselves during locomotion and other activity. The unoperated limbs and tail were not amputated in eight of these cases because it was found that if enough time was allowed

Fig. 8 Synchronized motion picture and action potential records of locomotion. — A. Action potentials from flexor muscles transposed to act as extensors. — S. Synchronizer. Each phase (every tenth phase indicated) corresponds to one motion picture frame taken at 16 per second. — T. Time, in 1/60 second. — Motion picture frames 13–24 (numbers of frames correspond to phase numbers of synchronizer) illustrate typical crutch-like use of straightly extended forelimb. Frames 33–36 and 42–44 include additional suspended phases of locomotor cycle for correlation with oscillogram. Note that the transposed flexors do not contract in supporting phase (e.g., 15–19; 24) but discharge only in the original flexor phase, when limb is lifted forward (e.g., 13; 20–22; 34–36; 42–43). (Limb blurred in pictures during rapid lifting movement.) Lengthened discharge, phases 27–32, indicates an interruption of progression; elbow caved in and rat paused to lift forebody with back musculature, meanwhile extending elbow to position shown in frame 33. — Records taken 14½ months after operation.

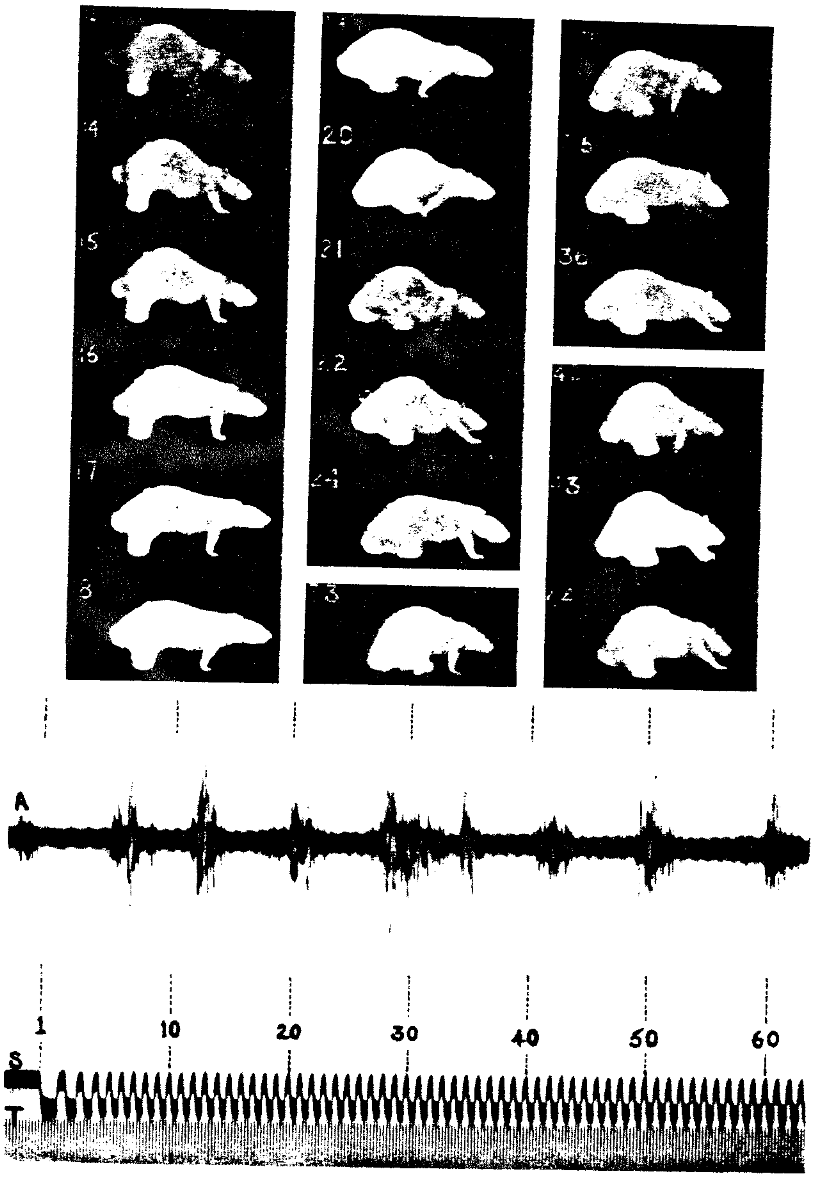

Figure 8

after the operation, the rats used the limb sufficiently so that there could be no question but that they were actually supporting a good portion of the body weight upon it. In two cases the amputations were performed after 5 weeks as a matter of control. There was no essential difference in the action of the transposed muscles in the amputated and unamputated cases.

The biceps muscle supplied by the triceps nerve did not recover function until after the trick adjustment had become firmly established in all cases. When the biceps began to function it did not abolish or hinder the adjustment. In none of the rats did the biceps ever come to produce complete flexion of the elbow. After $2\frac{1}{2}$ months, two of the rats were actively flexing the elbow about 105 degrees, one other about 90 degrees, two others somewhat less than that, and in the remaining three no overt active flexion could be distinguished for certain. On examination under anesthesia the biceps was found to be of full size in all ten animals. The nerve had regenerated and there was no sign of misregeneration. Electrical stimulation of the triceps nerve produced strong contraction of the biceps in all these cases as determined by change in shape of the muscle. The resting length of the biceps had been somewhat increased, however, and contraction of the muscle did not produce as complete flexion of the joint as does the normal biceps. Keeping the limb continuously in complete extension during the period of biceps paralysis had apparently stretched the biceps just as it had the triceps in the preceding series.

In two cases, $1\frac{1}{2}$ months after operation, the tendons of the latissimus dorsi and pectoral muscles were cut bilaterally. As a result the test limb caved in whenever the animals leaned on it while the contralateral forelimb continued successfully to support the forebody. After bilateral severance of the tendons of the infraspinatus and deltoid muscles in another case the rat continued to use the test limb for support in the locked position and the contralateral forelimb in the normal position of partial extension.

Action potential analysis showed that in all cases the triceps nerve was activating the biceps muscle in the original extensor phase of coördination except when the joint was kept locked. Biceps contraction was inhibited in the locked joint reaction. During relapses of the locked joint adjustment the biceps contracted in the normal triceps phase of coordination. In those six cases in which biceps contraction produced overt flexion of the elbow in behavior, elbow flexion always occurred when extension occurs in normal and control animals and never in the normal flexor phase of activity. Thus these results generally corroborate those of the preceding section.

In addition the fact that the biceps innervated by triceps motor neurons did not, on recovery of function, hinder or abolish the locked joint reaction indicates that the adaptive inhibition of the triceps centers that occurred in both this and the preceding series did not constitute a specific adaptation in the action phase of the triceps motor neurons, but that the inhibition was rather a normal component of the shoulder movement involved in the trick adjustment. This interpretation was supported by action current analysis which showed in both series that when the elbow joint gave way and the triceps, or biceps supplied by the triceps nerve, contracted in its normal extensor phase, this contraction followed rather than preceded the caving in of the joint. Evidently in acquiring the new method of supporting themselves, the animals had relied entirely upon the motor patterns of the normal intact musculature and had made no specific corrections in the timing of the test muscles.

DISCUSSION

In most reactions the transposed muscles in these rats continued to contract when they would have contracted normally had the muscles not been transposed, and the muscles innervated by nerves of antagonistic muscles continued to contract in the normal action phase of the antagonistic muscles which the nerves had originally supplied. One exception to the resultant reversal of elbow movement was the maintenance of elbow extension during supporting phases of coordination. This maintenance of extension was dependent upon the mechanical locking of the elbow joint and upon the action of shoulder rather than test muscles and hence has been referred to as a "trick" adjustment. It appeared abruptly, instead of being acquired by trial and error. The adjustment never appeared when the elbow was prevented from locking in the supporting phase of movement by a partial ankylosis of the joint or by either the action of the transposed triceps muscle or by severance of the tendons of adductor muscles of the shoulder. The degree of improvement in time was relatively slight. In no case did the trick adjustment ever become so well controlled that relapses were not common. When the elbow was prevented by a peg from locking in animals that had been using the trick adjustment for as long as 9 months, the forelimb was rendered uselss as a means of support. Cutting the tendons of the adductor muscles of the shoulder after 12 months abolished the ability to use the limb for support. In the adjustment the flexor motor neurons supplying the test muscles continued to the end to discharge in their normal flexor action phase instead of shifting their timing to suit the postoperative conditions. There was an inhibition of the transposed extensors as well as flexors supplied by extensor nerves during the adjustment, but whenever these muscles did work, they contracted in the original extensor phase of movement. This inhibition of the extensor motor neurons whenever the adjustment was used was evidently a normal part of the adductor movement of the shoulder used in the trick adjustment, instead of a specific correction in the timing of the extensor centers. When one flexor muscle was transposed and another left in position to oppose it, there was no adjustment in the action of either muscle. They continued to function synchronously although experimentally they had been made into anatomical antagonists.

The mechanical locking of the elbow joint, which made it possible for the rats to support themselves on the operated limb, furnished an excellent starting posture for learning to correct the reversed action of the elbow. Progression from the mechanical support to maintaining the joint more firmly in the extended locked position by contraction of the test muscles and finally to maintaining extension by the action of the test muscles alone and controlling the degree of extension by the intensity of their contraction, should have been easy successive steps in reeducation. The rats, however, after months of practice in which they were forced by amputations to use the operated limb continually, never learned to activate the flexor centers during the normal extensor phase of activity so as to use the forelimb in normal manner. Instead, the flexor centers continued to fire in their original innate action phase, and the animals remained permanently dependent on the unreliable and awkward mechanical support.

These experiments fail to reveal any essential difference between the forelimb and the hind limb with respect to the modifiability of the basic coordination patterns. The trick adjustment which appeared in these experiments furnished a set of favorable cues for reeducation that was absent in the hind limb experiments where no such favorable response occurred and the sensory cues for reeducation had to come entirely from unfavorable reversed movements. Also in the case of these forelimb experiments the reversed action of the test muscles produced a greater dissolution of the normal array of those proprioceptive stimuli from the rest of the limb segments that tend to reinforce the normal function of the test muscles. Both these factors increased the chances for readjustment in the forelimb. The fact that no corrective adjustment in the timing of the test muscles occurred in spite of the more favorable conditions, indicates that the basic motor patterns for forelimb as well as for hind limb coordination in the rat are too firmly established to be broken down and remolded to suit these experimental reversals of the motor periphery.

The stability of these normal coordination patterns suggests an inherited rather than an acquired basis. Some of the animals in these experiments could have had no more than

25 days including intra-uterine practice to acquire the normal coordination patterns whereas they failed for 15 months to develop new reversed patterns suited to the postoperative conditions. The age of maximum learning capacity of the rat is well beyond the stage at which the animals were operated (Liu, '28). These results, in line with similar data obtained on lower vertebrates (Weiss, '41 b), indicate that the central organizing mechanisms underlying the normal basic motor patterns in the rat are in large part inherited rather than acquired by experience.

The trick adjustment that appeared in these animals may be considered somewhat similar to those adaptations in coordination that follow the loss of limbs in mammals (see Bethe and Fischer, '31). Such adaptations involve coordination of the intact musculature which, although far from normal in superficial appearance, may be produced by mere quantitative modification and recombination of the basic motor patterns that, as units, remain qualitatively unmodified. In adjustment to limb amputations, the groups of closely related muscles in the remaining musculature must still function in their normal agonist-antagonist relations. Some elementary motor patterns are accentuated and others inhibited, but there is no necessity of directly reversing the action of individual muscles with respect to other muscles of the same functional group as there is after nerve crossing and muscle transposition. The trick adjustment, involving changes in the action of the intact musculature in adaptation to the abnormal elbow movement, enabled the rats to balance unsteadily on the straightly extended forelimb. However, the more basic form of adjustment that would have involved a reversal in timing of the test muscles themselves to restore the more effective, normal use of the elbow never appeared. This latter type of adjustment requires more drastic modification of the basic coordination patterns than do those adjustments that occur in an intact musculature.

The nervous system may be extremely plastic, as contended by Bethe, at the higher levels of organization. But the results of these experiments support the interpretation of Brown ('14), Weiss ('41 b), and others that at the base of the hierarchial organization in the nervous system are motor patterns the functional integration of which is extremely unplastic. The nervous system, particularly in the lower motor centers, is not merely a plastic, homogeneous connecting network whose patterns of activity are organized solely by the incoming sensory stimuli, but contains stable organizing mechanisms of its own.

SUMMARY

1. In fifteen rats the long biceps and brachialis flexor muscles were transposed so that they acted as extensors of the elbow joint instead of flexors.

2. In seven rats the nerve of the biceps muscle was crossed into the long triceps extensor muscle so that this muscle was activated from the spinal centers by flexor instead of extensor motor neurons.

3. In nine cases the biceps flexor was left in normal position and the brachialis flexor was transposed to act as an extensor in antagonism to its normal co-flexor.

4. In fourteen cases the biceps and brachialis flexors were transposed to the extensor position and the long triceps extensor was transposed to act as a flexor.

5. In ten cases the long triceps nerve was crossed into the biceps muscle and the brachialis flexor was transposed to act as an extensor.

6. In all cases all brachial muscles acting on the elbow joint except the test muscles were excised. The great majority of cases were operated upon at ages under 40 days, the youngest ones at 15 days. In all but eight of the animals the contralateral forelimb, the ipsilateral hind foot, and tail were amputated shortly after the test muscles recovered function. The animals were kept under observation well over a year after the operations. Operated control animals were run throughout with the experimental groups.

7. In most reactions the motor neurons to the test muscles continued permanently to discharge in their original innate

action phase without adjustment to the reversed anatomical arrangement.

8. The one exception to the general resultant reversal of elbow movement was the maintenance of the elbow in an extended locked position during supporting phases of activity. The forelimb was kept straightly extended and used like a crutch for support. This constituted a "trick" adjustment in that it was accomplished by the action of the intact musculature of the shoulder plus a mechanical locking of the elbow joint rather than by a corrective adjustment in the action phase of the test muscles.

9. This awkward trick adjustment appeared abruptly without practice and furnished an excellent point of departure from which to begin reeducation. In spite of long training, however, the rats never learned to improve upon the clumsy and unreliable mechanical method of support by correcting the reversed function of the test muscles.

10. The experiments demonstrate the unplasticity of the basic motor patterns for forelimb coordination in the rat.

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