

INNERVATION AND FUNCTION OF HIND-LIMB MUSCLES IN THE CAT AFTER CROSS-UNION OF THE TIBIAL AND PERONEAL NERVES

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SUMMARY

1. Peripheral nerves to flexor (common peroneal) and extensor (tibial) nerves in a hind limb of seven 2–6 month old cats were cut and cross-united to study the plasticity in the spinal cord. The extent to which motoneurons from extensor and flexor motor pools were misdirected to their antagonistic muscles was determined by measuring the potentials generated at the spinal roots from the crossed nerves. The axons contributing to the extensor nerves normally leave the cord in the L7 and S1 ventral and dorsal roots while the axons contributing to the flexor nerves normally leave the cord in the L6 and L7 ventral and dorsal roots. Following cross-union, medial gastrocnemius (m.g.) and lateral gastrocnemius–soleus (l.g.s.) nerves were primarily supplied by L6 and L7 ventral and dorsal roots, and common peroneal (c.p.) nerves were primarily supplied by L7 and S1 ventral and dorsal roots. A method for quantifying the completeness of cross-reinnervation was developed.

2. The pattern of e.m.g. activity in cross-reinnervated muscles during locomotion was primarily determined by the innervating nerve with the reinnervated flexor muscles being activated during the extensor phase. However, the cross-reinnervated extensor muscles showed evidence of extensor activity in addition to the double-burst pattern typical of flexor nerves. This extensor activity was more prominent when the nerve cross was less complete.

3. We conclude that during locomotion the activity of spinal motoneurons was not substantially modified by inappropriate peripheral connexions, even when the nerve cross was carried out in young animals. This conclusion is discussed in relation to previous studies which suggested some degree of functional modification.

INTRODUCTION

The alternating swing and stance phases of locomotion result from spinally generated patterns of activity in the nerves to the flexor and extensor muscles of the hind limb (Shik & Orlovsky, 1976; Grillner, 1981). During one step cycle, the extensor muscles typically fire when the limb is on the ground (stance), while the flexor muscles show a double burst pattern with one short burst when the limb is off the ground (swing) and another during the stance phase (Grillner, 1975). By surgically cross-uniting the common nerve innervating all of the distal flexor muscles with the

common nerve innervating all of the distal extensor muscles, the reinnervating motor axons can be deliberately misdirected to muscles with antagonistic functions. The present study was designed to determine to what extent the output of the spinal locomotor generator was affected by inappropriate target organs.

By surgically cross-uniting two motor nerves, the reinnervating axons will generally be directed to a muscle formerly innervated from a different motor pool and responsible for a different muscle function. Unless there can be some rematching of central neural activity to peripheral nerve and muscle properties, the reinnervated muscle will function inappropriately and generate the activity pattern appropriate to its antagonist. In experiments where a single muscle has been cross-reinnervated by a nerve with a different function, alterations in the physiological, biochemical and histochemical properties of the muscle fibres have been studied (Jolesz & Sréter, 1981). How cross-reinnervation of muscles influences movement patterns has not been examined as carefully.

Early studies to assess movement performance following cross-reinnervation of muscles failed to assess the completeness of the nerve cross or to record e.m.g. activity during movement to support the behavioural observations (Sperry, 1941, 1942, 1947). Cross-union of the nerve to a flexor and extensor muscle in the forelimb or hind limb of the rat resulted in full reversal of flexor and extensor movements of the elbow and ankle joints respectively. These functional reversals were observed to persist with little compensation in stereotyped movements like locomotion (Sperry, 1941, 1942). More recently, similar results have been reported in studies in which e.m.g. activity was recorded during locomotion following cross-reinnervation of an elbow flexor and an elbow extensor muscle of the rat or cat (Cohen, 1978; Tsukahara, Fujito, Oda & Maeda, 1982).

Both monkeys and cats were able to perform goal-directed movements accurately, despite their crossed forelimb nerves (Sperry, 1947; Tsukahara *et al.* 1982). In cats, this ability to perform co-ordinated voluntary movements may result from sprouting of corticorubral neurones onto the proximal portion of red nucleus neurones. Such results suggest a reorganization in the brain with a switching from cerebellar to cerebral dominance of the red nucleus (Tsukahara *et al.* 1982). Spinally controlled movements like locomotion were largely unaffected by such reorganization, although both Cohen (1978) and Tsukahara *et al.* (1982) suggested that some change might have occurred in the walking pattern. Monkeys apparently develop good co-ordination in doing common cage activities after a nerve innervating the flexor muscles of the distal forelimb is surgically cross-united with a nerve innervating extensor muscles (Brinkman, Porter & Norman, 1983). However, e.m.g. activity was not recorded to support these observations of appropriate muscle function.

To clarify the effects of cross-reinnervation on movement performance, we chose to cross-unite the common flexor and extensor nerves which supply the distal hind limb of young cats, thereby producing misdirection of the motoneurons from many different motor pools to muscles with antagonistic functions. Cross-reinnervating all major flexor and extensor muscles of the distal hind limb might provide a more potent stimulus for central adaptation than crossing single muscle nerves. Also, we felt that young cats of age 2–6 months might have greater plasticity than adult cats. However, the short length of the nerves crossed at this age made it essential to check the

completeness of the cross-reinnervation. We assessed the completeness by adapting the method of charge contributions developed by Hoffer, Stein & Gordon (1979).

During normal locomotion the flexor muscles in the distal hind limb function synergistically, as do the extensor muscles, and the alternating flexor and extensor activity is characteristically repeated during each step cycle. Thus, by recording flexor and extensor e.m.g. activity we were able to show that the timing of activity in the reinnervated flexor and extensor muscles was inappropriate during locomotion. The results indicated that the muscles were mainly activated according to the patterns of the antagonist nerves that now supplied them and that the central connexions to these nerves were not greatly altered a year or more after cross-union. A preliminary account of these experiments has been published in abstract form (Thomas, Gordon & Stein, 1984).

METHODS

Seven 2–6 month old cats were used in this study. They were given injections of penicillin 1 day before and immediately after surgery. The animals were anaesthetized with sodium pentobarbitone and maintained on this anaesthetic at a depth such that withdrawal reflexes could not be elicited during surgery. Under fully aseptic conditions, the tibial and peroneal nerves to the left hind limb were exposed in the popliteal fossa, cut 5–10 mm below the sciatic branch point and surgically cross-unioned using fine sutures (8–0 silk). Normally the peroneal nerve innervates all of the flexor muscles while the tibial nerve innervates all of the extensor muscles of the distal hind limb. In the present study we used the common peroneal (c.p.) nerve as an example of a flexor nerve and the medial gastrocnemius (m.g.) and lateral gastrocnemius–soleus (l.g.s.) nerves as examples of extensor nerves. Following cross-reinnervation, nerve impulses were recorded distal to the nerve suture. Thus, the nerve distal to the suture line on the c.p. nerve is referred to as the crossed c.p. nerve while the nerves distal to the suture line on the m.g. and l.g.s nerves are referred to as the crossed m.g. and crossed l.g.s. nerves (Fig. 1A).

Recording e.m.g. activity during locomotion

The animals were trained to walk on a motor driven treadmill. An appropriate speed was determined for each animal during training. At regular intervals 10–18 months after surgery e.m.g. activity was recorded during locomotion using stainless-steel wire electrodes (nine-strand, Teflon-coated cables with a total diameter of 0.2 mm; Bergen Wire Rope Co., Bergen, NJ). The tips of the wires were bared of insulation and bent back to form a hook before being inserted into the vastus lateralis (v.l., knee extensor) and semitendinosus (s.t., knee flexor) or lateral gastrocnemius (l.g., ankle extensor) and tibialis anterior (t.a., ankle flexor) muscles of the normally innervated and reinnervated hind limbs of each cat. The animals were maintained under a volatile anaesthetic (Fluothane) during the insertion of three electrodes per muscle. The free ends of the three electrodes were braided and led to an amplifier by means of wire spring connectors. Two of the three electrodes provided for bipolar recording while the third served as an earth. The long lengths of wire external to the muscle enabled the wires to move freely with the limb movements during each step cycle while the electrodes remained inserted within the muscle because of the hooks at their ends.

The unrectified e.m.g. activity was recorded on tape while rectified and filtered e.m.g. (30 Hz Paynter filter) was monitored on an oscilloscope, a pen recorder and superimposed on a video image of the cat walking on a motor driven treadmill at a comfortable speed. We were able to match the movements of each hind limb during the step cycles with the corresponding e.m.g. activity recorded on tape by playing back the signals recorded on the video tape recorder.

Determination of success of nerve regeneration

If regeneration is unsuccessful sensory fibres may atrophy while motor nerve fibres atrophy initially and then stabilize (Hoffer *et al.* 1979). The voltage (V) generated at the dorsal and ventral spinal roots by stimulating these nerves will depend on the number of nerve fibres contributing to the potentials, their cross-sectional area, the dispersion of the potentials and the electrical

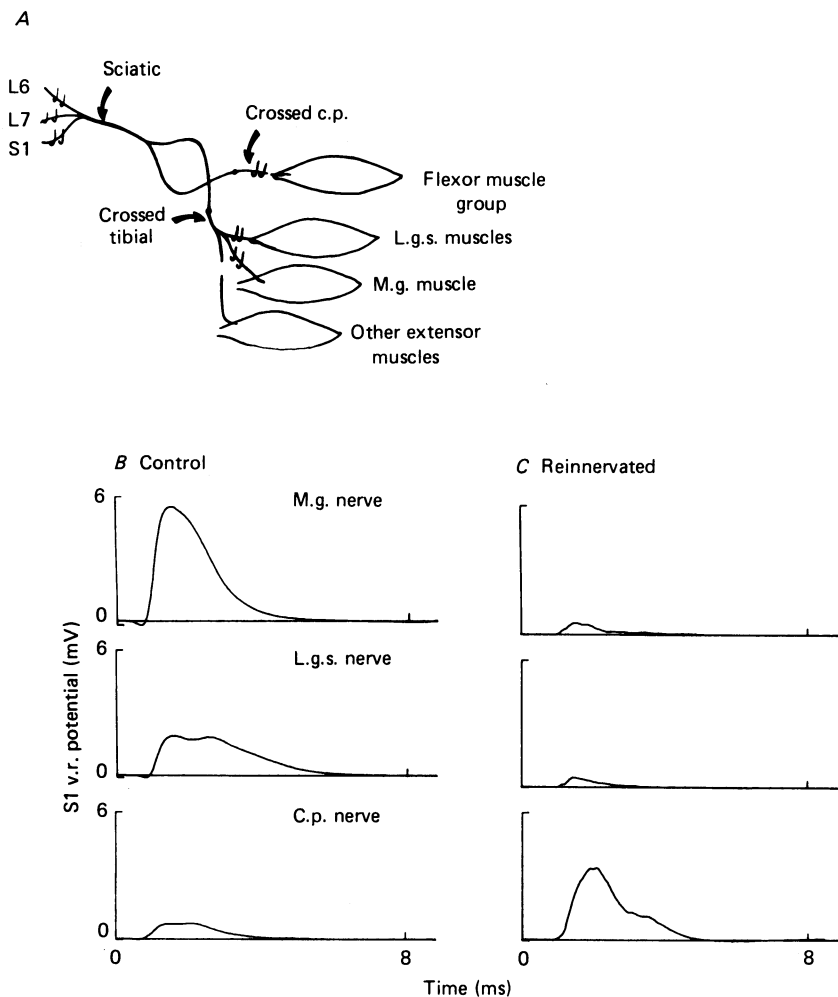


Fig. 1. Schematic diagram (A) of the method used to record compound action potentials on the L6, L7 and S1 ventral and dorsal roots in response to stimulation of the normal and crossed m.g., l.g.s. and c.p. nerves. Note that the c.p. nerve normally innervates all of the distal flexor muscles while the tibial nerve normally innervates all of the distal extensor muscles of the hind limb. Following a complete cross-union, the innervation of flexor and extensor muscles would be reversed. Below are examples of compound action potentials recorded on the S1 ventral root (S1 v.r.) in response to stimulation of the control m.g., l.g.s. and c.p. nerves (B) and crossed m.g., l.g.s. and c.p. nerves (C). At the time of recording, the nerves to flexors and other extensor muscles were cut (broken lines in A) to minimize e.m.g. artifacts.

resistance (R) of the root. Hoffer *et al.* (1979) suggested using monophasic recording conditions to measure the current ($I = V/R$) integrated over time from cut roots. This gives the charge (Q) as a measure of the electrical contribution of a nerve to a root. The charge from different roots can be summed and compared (Hoffer *et al.* 1979). Thus an indication of the success of the nerve regeneration was obtained in acute experiments (see below) by comparing the difference in the charge generated at the L6, L7 and S1 ventral and dorsal roots in response to supramaximal electrical stimulation of the control and crossed m.g., l.g.s. and c.p. nerves. A further indication

of the success of nerve regeneration was obtained by measuring the tetanic tension that could be developed in the control m.g., l.g. and soleus muscles, compared to that developed in the corresponding reinnervated muscles as described previously (Gordon & Stein, 1982).

Determination of the completeness of the nerve cross

The success of the motor and sensory nerve crosses was determined in acute experiments 18–24 months after the initial surgery. Details of the methods used have been published earlier (Hoffer *et al.* 1979). Briefly, under sodium pentobarbitone anaesthesia, a laminectomy was performed from S1 to L6. Apart from the m.g., l.g.s., c.p., and crossed m.g., l.g.s. and c.p. nerves, all nerves to both hind limbs were cut. The intact nerves were dissected free of other tissue in the popliteal fossa and each was placed as far distally as possible on a separate pair of electrodes for electrical stimulation. The L6, L7 and S1 ventral and dorsal roots were cut sequentially and placed on an array of six electrodes to measure: (i) the impedance of each root with respect to the cut end of each root using a 10 kHz sinusoidal signal, and (ii) the average of twenty compound action-potential responses to supramaximal stimulation of the m.g., l.g.s. and c.p. nerves (Fig. 1*B* and *C*).

Data were similarly recorded from the contralateral control ventral and dorsal roots of the cross-reinnervated cats and from one side of two control cats. The value computed for the area of the compound action potential in mV ms (Hoffer *et al.* 1979) was divided by the impedance of the root in k Ω to give the electrical charge (nC) generated by the control and crossed m.g., l.g.s. and c.p. nerves at the L6, L7 and S1 ventral and dorsal roots in units of μ A ms.

By expressing the charge generated at one root by one nerve as a fraction of the total charge generated at all the ventral or dorsal roots supplied by that nerve, we could determine how the charge generated by the normal and crossed m.g., l.g.s. and c.p. nerves was distributed between the ventral and dorsal roots. A large proportion of the charge was generated at the L7 ventral and dorsal roots by the m.g., l.g.s. and c.p. nerves.

The remaining charge from these nerves was predominantly generated at either the L6 or the S1 ventral and dorsal roots. To determine whether this remaining charge contribution tended to be more lumbar or sacral we used L7 as a neutral zone and arbitrarily assigned the fraction of the charge generated at L6 a weighting of -1 , and the fraction of the charge generated at S1 a weighting of $+1$. By summing the weighted charge contributions to the L6 and S1 roots, we could then determine for a particular nerve its mean root entry relative to L7. Thus a negative root entry value indicated more charge generated at the L6 root than the S1 root while a positive root entry value indicated more charge generated at the S1 root than the L6 root.

By comparing the mean root entry values for control animals with those determined for experimental animals, we were able to establish the completeness of the motor and sensory nerve crosses. Thus, let $F - E$ be the difference in mean root entry of control flexor and extensor nerves. We could then determine how far a crossed extensor nerve (m.g. or l.g.s.) had been reinnervated by a flexor by calculating the following percentage:

$$\text{crossed m.g. or l.g.s. completeness (\%)} = \frac{E_c - E}{F - E} \times 100, \quad (1)$$

where E_c is the mean root entry for the crossed extensor nerve. If $E_c = F$, the computed value is 100% (complete cross), whereas if $E_c = E$ the value is 0 (no cross). Similarly, for a crossed flexor nerve (c.p.) reinnervated by an extensor:

$$\text{crossed c.p. completeness (\%)} = \frac{F_c - F}{E - F} \times 100, \quad (2)$$

where F_c is the mean root entry of the crossed flexor nerve.

RESULTS

Fig. 1*A* illustrates the method used to measure the compound action potentials on the L6, L7 and S1 ventral and dorsal roots following stimulation of the normal and crossed m.g., l.g.s. and c.p. nerves. Shown in the other parts of the Figure are typical examples of the compound action potentials measured on the control (*B*) and

reinnervated (C) S1 ventral root of one cat. Much larger potentials were generated on the control S1 ventral root by the m.g. and l.g.s. nerves than the c.p. nerve. Following reinnervation the situation tended to be reversed with larger potentials on the S1 ventral root from the crossed c.p. nerve than the crossed m.g. and l.g.s. nerves.

TABLE 1. Total charge generated on dorsal and ventral roots by stimulation of the nerves indicated. Each value represents the mean and s.e. of mean for six cats

Nerve	Total charge (pC)			
	Dorsal roots		Ventral roots	
	Control	Reinnervated	Control	Reinnervated
M.g.	81 ± 11	76 ± 18	160 ± 37	141 ± 19
L.g.s.	101 ± 9	81 ± 10	229 ± 39	136 ± 22
C.p.	864 ± 55	541 ± 97	659 ± 81	639 ± 122

Mean charge distributions

To compare potentials with different time courses on roots of different sizes, a computation was made of the electrical charge contributed by each nerve to each root (see Methods and Hoffer *et al.* 1979). The mean charge distribution of each nerve to all the ventral and dorsal roots was obtained by pooling data from all animals. Table 1 outlines the total charge (\pm s.e.) generated at the ventral and dorsal roots by the control and crossed m.g., l.g.s. and c.p. nerves. As the mean charge generated by each crossed motor and sensory nerve was less than the mean charge generated by its respective control nerve, fewer than normal motor and sensory axons innervated these muscles, or alternatively their axons remained somewhat atrophic. An indication of the success of the regeneration was also given by measuring the tension developed in the reinnervated extensor muscles. The mean tetanic tension developed in the reinnervated m.g., l.g. and soleus muscles was 91, 68 and 92% of that developed in the corresponding normally innervated muscles.

The total charge was then subdivided to determine the mean charge distribution of each nerve to each ventral and dorsal root. As there was substantial mean charge generated by m.g., l.g.s. and c.p. nerves at both the ventral and dorsal L7 roots, the effects of cross-reinnervation were most clearly reflected by changes in the mean charge distributions to the L6 and S1 roots. In Fig. 2, the mean charge (\pm s.e.) generated by the control and crossed m.g., l.g.s. and c.p. nerves at only the L6 and S1 ventral and dorsal roots is expressed as a percentage of the total charge generated by each of these nerves. M.g. and l.g.s. nerves mainly contributed a substantial charge to the S1 ventral and dorsal roots while the charge from the c.p. nerve was greater at the L6 ventral and dorsal roots. Following reinnervation the opposite trends were observed. Major contributions of charge from the crossed m.g. and l.g.s. nerves were generated at the L6 ventral and dorsal roots and from the crossed c.p. nerves at the S1 ventral and dorsal roots. Similar trends were indicated by the over-all mean root entries which were positive for the m.g., l.g.s. and crossed c.p. nerves (0.66, 0.40, 0 for sensory nerves; 0.60, 0.22, 0.26 for motor nerves) but were negative for the c.p.

and crossed m.g. and l.g.s. nerves (-0.32 , -0.16 , -0.19 for sensory nerves; -0.35 , -0.07 , -0.14 for motor nerves). As described in the Methods, values of $+1$, 0 and -1 would indicate root entry of the axons centred about S1, L7 and L6 roots respectively.

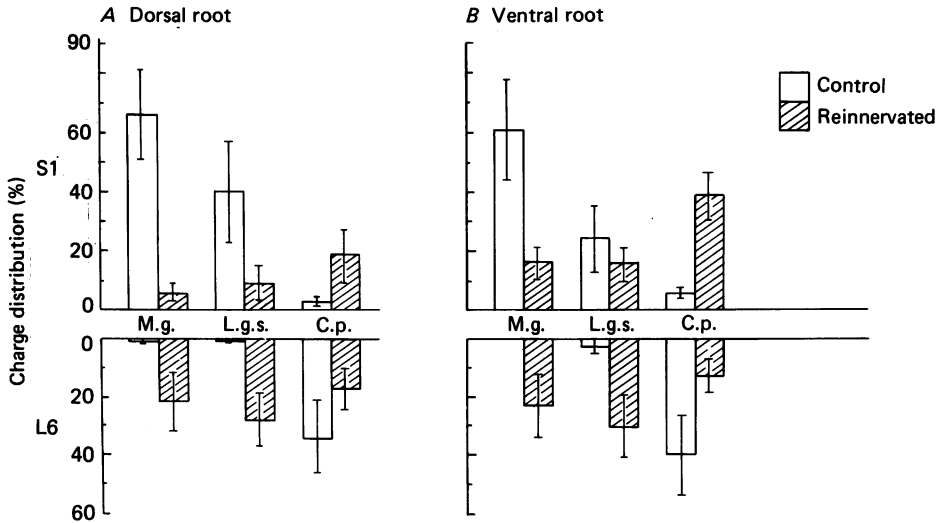


Fig. 2. Comparison of the mean (\pm s.e. of mean) charge distributions of normal m.g., l.g.s. and c.p. with crossed m.g., l.g.s. and c.p. nerves on the S1 and L6 dorsal (A) and ventral roots (B). Mean root entries can be obtained from the difference between the S1 (weighted by $+1$) and L6 (weighted by -1) mean root entries. The data represent mean values from six cats.

Completeness of the nerve cross

From the distribution of charge at the ventral and dorsal roots, we assessed the completeness of the motor and sensory nerve crosses. As shown in Table 2, the completeness of the motor nerve crosses was 65–96% for the crossed c.p. nerve, and from 41–99% and 39–73% for the crossed m.g. and l.g.s. nerves respectively. The success of the sensory nerve crosses was generally better than the motor nerve crosses for the crossed m.g. and l.g.s. nerves, being in the range 76–94% and 67–97% respectively, but was generally poorer than the motor nerve cross for the crossed c.p. nerve which was 25–52%. It should be noted that the tibial nerve supplies branches to the m.g., l.g. and soleus muscles as well as to some foot muscles, but our calculations of nerve-cross completeness only included the charge contributions from the m.g. and l.g.s. nerves. The tibial nerve branch to the foot normally contributes substantial amounts of charge to both the dorsal and ventral roots (Hoffer *et al.* 1979). Because the root entry of the m.g. and l.g.s. contributions is somewhat different, our estimate for the completeness of the sensory c.p. nerves is artificially low, while that for the motor c.p. cross is artificially high (see Discussion).

E.m.g. activity during locomotion

The alternating flexor and extensor muscle activation patterns of reinnervated and control muscles during locomotion are illustrated in Figs. 3 and 4. During each step cycle some control flexor muscles tended to show a double-burst pattern with a short burst during the swing phase and another early in the stance phase (Fig. 3C). Other control flexor muscles gave a single burst which increased during swing and gradually

TABLE 2. Completeness of motor and sensory cross-reinnervation. Values in % are given for six cats, as calculated from eqns. (1) and (2), together with the means and s.e. of means of the samples. See text for further description of the methods

Cat	Completeness of cross-reinnervation (%)					
	Dorsal roots			Ventral roots		
	M.g.	L.g.s.	C.p.	M.g.	L.g.s.	C.p.
1	88	72	52	75	54	88
2	84	78	38	57	39	65
3	94	90	25	99	68	96
4	78	67	52	75	62	81
5	85	89	30	60	73	81
6	76	97	26	41	57	90
Mean	84.2	82.2	37.2	67.8	58.8	83.5
S.E.	2.7	4.8	5.1	8.1	4.9	4.4

declined during the early stance phase (Fig. 4D). The control extensor muscles began to fire just prior to stance. Their activity increased and was usually maintained throughout the stance phase of the step cycle (Figs. 3D and 4C).

When normal animals are walking, ipsilateral flexor and extensor activity is approximately 180 deg out of phase with contralateral flexor and extensor activity. In contrast, the ipsilateral cross-reinnervated flexor muscle (t.a.; Fig. 3B) is essentially in phase with its contralateral control. Activity in the reinnervated flexor muscle (t.a.; Fig. 3B) begins shortly before foot contact (indicated by the downward pointing arrow below Fig. 3A) and continues throughout stance, which is the typical pattern for an ankle extensor (see above and Halbertsma, 1983), although the duration of contralateral extensor e.m.g. is longer. Similarly, a burst occurs in the cross-reinnervated extensor (l.g.) in phase with its contralateral control extensor muscle (cf. Fig. 3A and D). This burst in the cross-reinnervated extensor is in the swing phase (which begins with the upward directed arrows), as expected for an ankle flexor.

An additional burst of e.m.g. activity was present in the cross-reinnervated extensor muscle during the stance phase (Fig. 3A) which was comparable in amplitude to that present during the swing phase. Because the motor nerve cross for the l.g. was only 90% complete, the activity could have resulted from unsuccessful cross-reinnervation as well as other factors, rather than from genuine functional compensation (see Discussion).

Fig. 4 shows the same tendency for inappropriate timing of cross-reinnervated flexor and extensor muscle activity but in ipsilateral reinnervated and control muscles of a different cat. The cross-reinnervated flexor (t.a.) and control extensor

(v.l.) muscles both fired mainly in the stance phase while the cross-reinnervated extensor (l.g.) showed some activity in the swing phase, when the control flexor (s.t.) muscle was active. In this example, a larger burst in l.g. occurred during stance. However, since this cross was only 67% complete for the l.g., the additional e.m.g. activity could again have arisen from the 33% of fibres which were not cross-

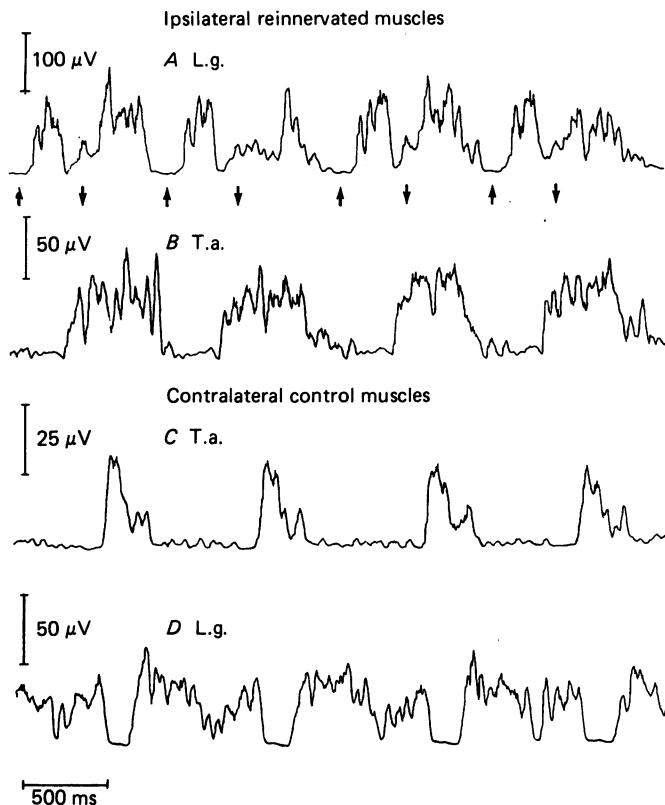


Fig. 3. Rectified and filtered e.m.g. activity recorded from ipsilateral cross-reinnervated extensor (A, l.g.) and flexor (B, t.a.) muscles and contralateral control (C, t.a.; D, l.g.) muscles during locomotion. The upward pointing arrows below trace A represent foot lift (beginning of swing phase) in the ipsilateral reinnervated leg while the downward pointing arrows indicate foot fall (beginning of the stance phase) in the same leg.

reinnervated, rather than genuine functional compensation (see Discussion). The data shown in Figs. 3 and 4 were typical of that recorded from all animals. The most common variation was in the relative amounts of stance related activity in the crossed l.g. (cf. Figs. 3A and 4A), which was largest in those animals in which the cross was least complete.

DISCUSSION

In the present study we cross-joined the nerve innervating all of the distal flexor muscles with the nerve innervating all of the distal extensor muscles in one hind limb of young cats. To assess whether genuine functional compensation during locomotion

resulted from alterations in central neural connexions following reinnervation, the success of the nerve crosses had to be determined.

Major contributions of the motor and sensory axons in the m.g., l.g.s. and c.p. nerves leave the spinal cord in the L7 ventral and dorsal roots. A large proportion of the axons to the c.p. nerves also leave from the L6 ventral and dorsal roots while for

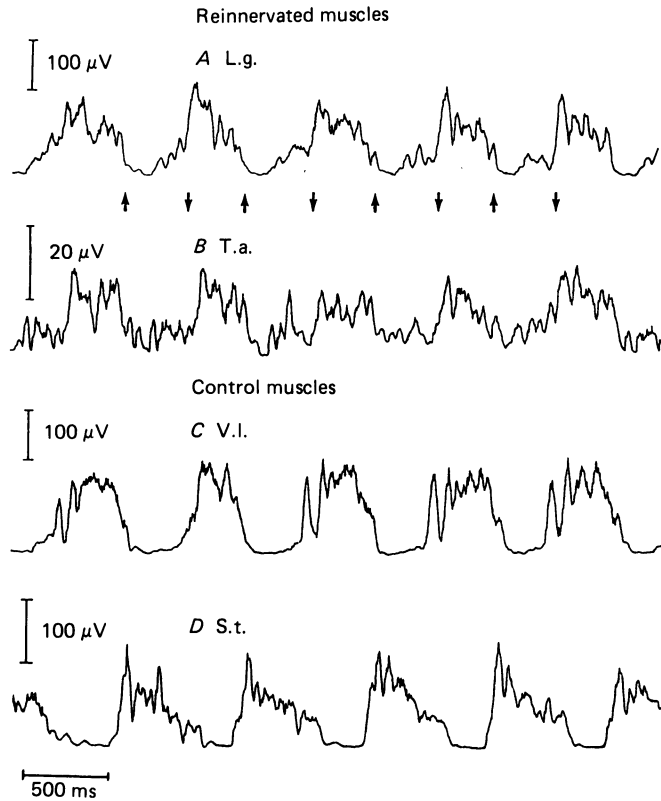


Fig. 4. Rectified and filtered e.m.g. activity recorded from ipsilateral cross-reinnervated ankle extensor (A, l.g.) and flexor (B, t.a.) muscles and ipsilateral control knee extensor (C, v.l.) and flexor muscles (D, s.t.) muscles during locomotion. Upward and downward pointing arrows below trace A correspond to the beginnings of the swing and stance phases in the ipsilateral leg.

the m.g. and l.g.s. nerves the remaining axons leave mainly in the S1 ventral and dorsal roots. The completeness of the motor and sensory crosses was therefore best reflected by a shift in the contribution of axons leaving the L6 and S1 roots to the motor and sensory nerve components of the crossed nerves. After cross-reinnervation, a complete reversal was not observed and there was some tendency for slightly more axons to be contributed by the L7 ventral and dorsal roots, although the difference was not significant.

Factors determining the completeness of the cross

Our data indicated that the motor nerve cross was generally better for the crossed c.p. nerve than for the crossed m.g. and l.g.s. nerves (Table 2). These results were expected because there are more than twice as many motor axons in the tibial nerve than in the c.p. nerve (Hoffer *et al.* 1979). However, our data for the crossed c.p. nerves were artificially high because the assessments of the completeness of cross-reinnervation only included the charge contributions from the m.g. and l.g.s. branches of the tibial nerve. When adjusted accordingly by using data from Hoffer *et al.* (1979), the mean completeness of the motor c.p. cross reduces from 83.5 to 69.5%. The least success was found for the sensory component of the crossed c.p. nerve and was probably due in part to there being generally more sensory axons in the c.p. nerve than in the tibial nerve (Hoffer *et al.* 1979). Similarly, the completeness of the sensory components in the crossed c.p. nerves was artificially low because of the absence of the tibial charge contribution to the foot. After the appropriate adjustment for the tibial contribution, the completeness of the sensory components in the crossed c.p. nerve was substantially increased.

In addition, there are important differences between motor and sensory reinnervation. Motoneurons reinnervate muscle fibres exclusively and non-specifically (Miledi & Stefani, 1969; Brushank & Mesulam, 1980; Gillespie, 1984). In comparison, sensory nerve fibres only make connexions with appropriate target organs. A fraction of the sensory fibres will be successful in reinnervating end organs, while other misdirected fibres will atrophy (Davis, Gordon, Hoffer, Jhamandas & Stein, 1978; Mackel, Kunesch, Waldhör & Struppler, 1983). Thus, motor reinnervation was expected to be better than sensory reinnervation. Because the tibial nerve also contains relatively fewer sensory fibres which innervate cutaneous receptors than the c.p. nerve, the likelihood of misguided sensory fibres is higher in a crossed c.p. nerve. As indicated by our data, the completeness of the sensory cross was high in the crossed m.g. and l.g.s. nerves.

E.m.g. patterns during locomotion

Cross-reinnervated extensor and flexor patterns of muscle activity were inappropriate in relation to the timing of control flexor and extensor muscle activation patterns in both ipsilateral and contralateral legs. E.m.g. activity in the cross-reinnervated flexor was in phase with ipsilateral extensor and contralateral flexor e.m.g. activity, while there was some reinnervated extensor e.m.g. activity in phase with ipsilateral flexor and contralateral extensor e.m.g. activity. Because the cross-reinnervated extensor and flexor muscles were largely reinnervated by flexor and extensor motoneurons respectively, these data indicate that the muscles were activated according to the normal patterns of activity of the antagonist nerves that now supplied them. Similar results were reported by Tsukahara *et al.* (1982) following cross-reinnervation of flexor and extensor forelimb nerves of cats.

As well as the reversed e.m.g. activity during locomotion, additional e.m.g. activity occurred in the cross-reinnervated extensor muscles during the extension phase of locomotion (see also Tsukahara *et al.* 1982, Fig. 3). In terms of movement patterns, this was reflected by incomplete movement reversals. Some cats initially placed the

foot dorsum on the ground, but quickly turned the foot over to take weight on the pad during the stance phase. The stance phase was shorter than normal with more weight bearing occurring in the contralateral limb. Several cats maintained an extended ankle joint during locomotion which, combined with shortening of the stance phase, prevented the ankle joint from collapsing onto the ground. In order to bring the leg through to the next flexion phase, the hip joint had to be lifted higher than usual during the relatively longer swing phase. Such compensation was necessary to maintain balance during locomotion. Note also that when the limb hits the ground, flexor reflex afferents will be excited which will now be directed to excite the crossed extensor muscles. If the muscle is stretched under the weight of the body, stretch reflexes may also be elicited in these muscles. Finally, since the motor nerve crosses were less than complete, some of the additional e.m.g. activity during locomotion could be due to extensor nerve axons which returned to their original muscles. For all these reasons, we feel that there was no compelling evidence for genuine modification of central neural connexions, as suggested by some previous authors (Cohen, 1978; Tsukahara *et al.* 1982).

Our data show that, even when cross-reinnervation was completed in young cats and when the success of the motor nerve cross was relatively high, a spinally generated behaviour like locomotion was still dominated by the original, inappropriate flexor and extensor e.m.g. patterns. Although the cats attempted functionally to compensate their movement patterns during locomotion, spinal synaptic connexions were not greatly altered even 1–2 years after surgery.

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