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INFLUENCE OF DORSAL RHIZOTOMY ON ACQUISITION OF A SUSTAINED AVOIDANCE RESPONSE IN RATS

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INFLUENCE OF DORSAL RHIZOTOMY ON ACQUISITION OF A SUSTAINED AVOIDANCE RESPONSE IN RATS

by

BARBARA E. RODIN

A dissertation submitted to the Graduate
Faculty in Psychology in partial fulfillment
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Introduction

Experimental Problem

A large body of experimental data, involving a variety of species, has indicated that discrete responses, of short duration, can be acquired with a dorsal rhizotomized (DR) limb, even when vision of the limb is precluded. It has not yet been unequivocally determined, however, whether responses which involve a sustained change in limb position can be acquired after dorsal rhizotomy. The few reports of positive findings concerning this problem are subject to question because, in all cases, response requirements might have been satisfied with a series of discrete changes rather than a sustained change in limb position. In the present study, an attempt was made to resolve the question of whether a sustained response, involving a change in limb position that is maintained over a considerable period of time, can be acquired after dorsal rhizotomy. An unequivocal answer to this question is important in that it can specify at least some of the limits of central nervous control of movement in the absence of peripheral feedback.

Background

The mechanisms of neural control of movement have long been a subject of debate. This is not surprising, when one considers the many aspects and varieties of movement. Humans, for example, can produce rates of joint displacement on the order of 10,000 degrees per second, can sustain forces exceeding ten times body weight (Smith, 1976), can accurately execute rapid ballistic movements, but can also acquire the delicate, skilled movements exemplified by a violinist of microsurgeon.

Peripheral control theory. One theory concerning movement control was proferred by Mott and Sherrington (1895) who stressed the importance of peripheral feedback in movement by maintaining that instrumental movement is constructed from individual spinal reflexes which are "chained" together by proprioceptive feedback from each discrete phase of the movement. For example, in his chained reflex model of ambulation, Sherrington (1910) proposed that species-typical locomotor patterns consist of mutually interacting stretch reflexes of agonist and antagonist muscles.

More recently, peripheral feedback has been used to explain conditioned serial behavior, or response chaining (Guthrie, 1935; Powers, 1973; Weiner, 1961). It has been proposed that, if the appropriate environmental contingencies are operating, non-reflexive movements can be associated by the process of feedback from one movement cueing the initiation of the next movement.

The first test of peripheral control theory was performed by Mott and Sherrington (1895), who investigated the effects of unilateral cervico-thoracic dorsal rhizotomy on forelimb movement in monkeys. This approach was based upon the belief that all sensory fibers subserving a particular body part entered spinal segments via dorsal roots (Bell, 1811; Magendie, 1822). Thus dorsal rhizotomy was assumed to abolish segmental reflexes along with sensory information from muscle, skin, tendon and joints. Mott and Sherrington reported that, after unilateral dorsal rhizotomy, instrumental movement in the affected limb disappeared. Although some movements in proximal musculature were observed, these were believed to be associated with reflexive movement in non-rhizotomized body parts. These findings were later relicated by Lassek (1953a) and Twitchell (1954). Peripheral control theory was seemingly upheld.

There were data which cast doubt upon the general validity of peripheral control theory as early as the late nineteenth and early twentieth centuries. At this time, reports appeared sporadically in the literature which indicated that instrumental movements are in fact possible after either unilateral or bilateral dorsal rhizotomy. Bickel (1897) found that stepping movements survived bilateral dorsal rhizotomy of the hind limbs in dogs. Munk (1909) reported that, after unilateral dorsal rhizotomy, a monkey could be trained to use the affected forelimb to bring food to its mouth, and Lashley (1917) reported that a patient could accurately position his legs, even though the legs were without sensation. Until quite recently, strangely, these reports were overlooked by researchers interested in movement control.

The apparent contradiction in early descriptions of the effects of dorsal rhizotomy on movement can be attributed to the fact that some investigators studied the effects of unilateral dorsal rhizotomy (Lassek, 1953a; Mott & Sherrington, 1895; Munk, 1909; Twitchell, 1954)), while others studied the effects of bilateral dorsal rhizotomy (Bickel, 1897; Lashley, 1917). In addition, when dorsal rhizotomy was unilateral, some investigators restrained the contralateral sensate limb (Munk, 1909), while some did not (Mott & Sherrington, 1895; Lassek, 1953a; Twitchell, 1954). If one examines the results of studies using the same experimental situation, the contradiction disappears. Thus, studies have confirmed that instrumental movements in the free situation do disappear after unilateral dorsal rhizotomy, as Mott and Sherrington reported (Knapp, Taub & Berman, 1958, 1963). However, instrumental movements in the free situation have been observed when dorsal rhizotomy was bilateral (Knapp et al., 1963), or when dorsal rhizotomy was unilateral and the affected limb was induced to move via restraint of the contralateral sensate limb (Knapp et al., 1963; Stein & Carpenter, 1965; Taub, Barro, Parker & Gorska, 1972) or by amputation (Berman, Teodoru & Uygur, 1971) or encasement of the contralateral sensate hand (Berman, Derasmo, Marti & Berman, 1978).

Although the DR preparation was initially used by Sherrington to support peripheral control theory, in more recent years, it has been repeatedly used to question peripheral control theory and to demonstrate that somatosensory feedback is not essential for either the execution of species-typical movement patterns or the acquisition of movement sequences. Species-typical movements that have been reported to occur following bilateral dorsal rhizotomy include locomotion, swimming and jumping in frogs and toads (Bickel, 1897; Harcombe & Wyman, cited in DeLong, 1971; Székely, Czeh & Voros, 1969; Weiss, 1936), swimming in fish (Lissman, 1946a, 1946b), and locomotion, climbing, reaching, grasping and thumb-finger prehension in monkeys (Bossom, 1974; Liu & Chambers, 1971; Taub, 1976a, 1976b; Vierck, cited in Taub, 1976b). Following unilateral dorsal rhizotomy, stepping (Brown, 1911), locomotion (Goldberger, 1977), scratching (Jankowska, 1959) and cleaning movements (Gorska, Jankowska & Kozak, 1961) have been observed in cats and locomotion and scratching movements have been observed in rats (Jankowska, 1959).

Response acquisition with DR forelimbs has been demonstrated in various circumstances and, in most instances, when vision of the responding limb and other forms of peripheral topographic feedback were prevented. In avoidance training situations, for example, monkeys have acquired responses with DR limbs which involved primarily proximal (Knapp et al., 1963) or distal musculature (Taub, Ellman & Berman, 1966), when an exteroceptive cue signalled the correct response (Knapp et al., 1958, 1963), or in the absence of exteroceptive cues (Taub, Bacon & Berman, 1965; Taub & Berman, 1963). Monkeys have also learned to compensate with DR limbs for constant loads, in the absence of exteroceptive cues (Taub, Schlossberg, Teodoru & Berman, Note 1; Wylie, 1978; Wylie & Tyner, 1978), and for frequent load changes, when an exteroceptive cue signalled the correct response (Taub et al., Note 1), and to inhibit acquired responses with DR limbs in a go; no-go auditory discrimination task (Taub, Teodoru, Ellman, Bloom & Berman, 1966). Acquisition with DR limbs has been demonstrated when positive reinforcement was used to establish the response, whether reinforcement was delivered on a continuous schedule (Berman, Blau, Herskovic & Berman, 1978; Levine & Ommaya, 1971, cited in Taub, 1976b; Polit & Bizzi, 1978; Taub, Goldberg & Taub, 1975; Wylie, 1978; Wylie & Tyner, 1978), or fixed ratio schedules of increasing magnitude (Taub, Williams, Barro & Steiner, 1978).

The dorsal rhizotomized preparation can be used to test peripheral control theory, only if somatosensory feedback associated with movement of the affected limb is completely and permanently abolished. In this regard, the possibility of regeneration of dorsal root fibers cannot be entertained since, under normal physiological conditions, severed fibers do not cross the neuroglia-neurilemma barrier into spinal cord (Kimmel & Moyer, 1947; Paskind, 1936; Westbrook & Tower, 1940). Recent evidence has indicated, however, that after dorsal rhizotomy alternate sources of peripheral somatosensory feedback may mediate behavior. This feedback may be provided by afferents entering ventral roots (Coggeshall, Coulter & Willis, 1974) or by afferents from intact body parts contiguous to the DR limb (Goldberger, 1977).

Ventral root afferents, most having cell bodies of origin in dorsal root ganglia (Coggeshall et al., 1974; Maynard, Leonard, Coulter, Coggeshall & Willis, 1975), have been demonstrated in a number of species, including frog, rat, cat, monkey and man (Coggeshall, Applebaum, Fazen, Stubbs & Sykes, 1975; Coggeshall et al., 1974; Dimsdale & Kemp, 1966; Frykholm, Hyde, Norlen & Skoglund, 1953; White & Sweet, 1955; Windle, 1931). Their numbers are substantial; in cat lumbosacral cord, 15-29% of ventral root fibers are sensory (Applebaum, Clifton, Coggeshall, Coulter, Vance & Willis, 1976; Coggeshall et al., 1974). However, ventral root afferents are not believed to be involved in proprioception. Relatively few are myelinated, with conduction velocities adequate for effective feedback (Kato & Hirata, 1968; Kato & Tanji, 1971; Ryall & Piercey, 1970); the majority are unmyelinated (Applebaum et al., 1976; Coggeshall et al., 1974) and have slow conduction velocities. Most have receptive fields which are located in viscera; the few that have somatic receptive fields are apparently involved in nociception (Clifton, Coggeshall, Vance & Willis, 1976; Clifton, Vance, Applebaum, Coggeshall & Willis, 1974).

Even if it is true that somatosensory information is mediated by ventral root afferents, it appears that its access to central nervous system is dependent upon the integrity of dorsal roots (Frykholm et al., 1953). This view is supported by the finding that, after dorsal rhizotomy, somatic sensation is apparently abolished. Animals do not respond to noxious stimulation of a DR limb (Bossom & Ommaya, 1968; Taub & Berman, 1968), and segmental reflexes in the limb are absent (Polit & Bizzi, 1978). Electrical stimulation of peripheral nerves which originate in a DR limb evokes neither electrophysiological evidence of sensory input at segmental levels of spinal cord (Wylie, Barro & Taub, 1979), not a detectable scalp-recorded cortical response (Cohn, Jakniunas & Taub, 1972). Furthermore, dorsal root ganglionectomy in cats, which eliminates dorsal root afferents and the majority of ventral root afferents, has no more effect upon locomotion with the affected limb than does dorsal rhizotomy (Goldberger, 1977). Although it is difficult to interpret experiments such as these which were designed to prove the null hypothesis (Allison & Goff, 1973), the evidence indicates that residual function in DR limbs cannot be explained by somatic sensation mediated by ventral root afferents.

Peripheral somatosensory feedback concerning limb movement may be available from intact body parts contiguous to a limb. It has been demonstrated, for example, that animals use cues arising from these surrounding areas for accurate placement of DR limbs (Goldberger, 1977). When a limb is moved, the central nervous system receives feedback from receptors in the limb itself and from receptors in surrounding body parts. Since afference from contiguous body parts could signal the occurrence and magnitude of limb movement, this feedback may be sufficient to permit performance with a DR limb. This is an important consideration since, after dorsal rhizotomy of a limb, dorsal root fibers serving contiguous body parts increase their projection to central nervous system by sprouting collaterals (Goldberger, 1977) and the size of their receptive fields increases (Kirk & Denny-Brown, 1970).

To determine whether sensation from sensate adjacent body parts is necessary for movement in a DR limb, dorsal rhizotomy has been performed to include not only the responding limb, but also body parts immediately surrounding the limb. It has been reported that, whether areas surrounding a forelimb are dorsal rhizotomized before (Berman, Marti, Koss & Berman, 1977), at the same time as (Berman, Blau, Herskovic & Berman, 1978), or after (Bossom, 1974; Knapp et al., 1963; Taub, 1976b) dorsal rhizotomy of the limb itself, or if almost all roots on one (Knapp et al., 1963) or both sides of the spinal cord (Berman et al., 1977) are severed, movement patterns present before surgery are still performed, although the quality of movement is altered. In these cases, it could be argued that the behaviors tested may have been so well-practiced preoperatively that they had become independent of somatosensory feedback (Lashley, 1951). However, initial response acquisition with DR limbs has also been demonstrated after extended dorsal rhizotomy (Berman, Note 2).

Central control theory. Since instrumental movement is possible in the absence of peripheral topographic feedback, it is the present author's belief that peripheral theory of motor control is unsatisfactory. An alternative, central control theory, specifies that central nervous system is not dependent upon peripheral feedback; its control of the patterning and acquisition of movement is autogenous. For example, central control theorists explain the retention or reoccurrence of species-typical motor patterns after dorsal rhizotomy by postulating the existence of motor programs which are believed to be built into central nervous system and can be executed in open-loop fashion[1]. Convincing electrophysiological and behavioral evidence has been presented for the existence of motor programs within spinal cord (Grillner, 1973, 1975; Grillner & Zangger, 1974, 1975), and within brain areas controlling respiration (Salmoiraghi & Baumgarten, 1961) and deglutition (Doty, 1967; Doty & Bosma, 1956; Doty, Richmond & Storey, 1967).

Response acquisition following dorsal rhizotomy cannot be explained simply by the spontaneous execution of endogenous motor programs. Rather, in this situation, there must be a mechanism by which central nervous system is informed of programs emitted, so that

[1] Open-loop: Without information from the periphery.

outflow can be associated with environmental contingencies. In the absence of somatosensory feedback, other peripheral sources of topographic feedback, such as vision of the responding body part, can inform central nervous system of movement patterns. However, in many cases, response acquisition after dorsal rhizotomy has been demonstrated even without peripheral topographic feedback. To deal with this problem, a theory of effernce copy has been proposed, in which it is suggested that the central nervous system can monitor its own outflow, without feedback from peripheral receptors.

There are two different views on how efference can be monitored centrally. On the one hand, it has been suggested that peripheral feedback is not necessary for knowledge of efference, because either the firing of motoneurons or the effort to move is sufficient to lay down engrams concerning centrifugal outflow from central nervous system (Helmholtz, 1866/1963, Mach, 1890/1959, Müller, 1840, as cited in Goodwin, 1976; Jones, 1971). On the other hand, it has been postulated that, regardless of whether or not peripheral feedback concerning movement is available, knowledge of efference can be provided via central feedback. Furthermore, when peripheral topographic feedback is absent, central feedback takes over its functions and becomes crucial to movement acquisition. The concept of central feedback, in the form of "corollary discharge" (Festinger & Caron, 1965; Holst, 1954; Sperry, 1950; Teuber, 1960) has also been used to explain differential perceptual experience resulting from active vs. passive movement (of the eyes, for example) and to explain error detection in motor learning (Schmidt, 1976; Schmidt & White, 1972).

There is considerable neuroanatomical evidence for the existence of central feedback pathways. Examples would include the neuroanatomical loop between cortex and the deep nuclei of cerebellum (Eccles, Ito & Szentagothai, 1967); collaterals from fibers of the medullary pyramids which project to dorsal column nuclei and from there to nucleus ventralis lateralis of the thalamus, which in turn projects to cortex (Kuypers, 1960); spinocerebellar tract cells which receive input from axons descending from supraspinal levels (Lundberg, 1964, 1971); fibers from corticospinal tract which terminate in laminae 4 and 6 of the dorsal horn (Fetz, 1968).

It is conceivable that movement acquisition, in the absence of peripheral topographic feedback, occurs via pairing of central efferent commands with reinforcement; knowledge of efference is believed to be provided by central feedback (Taub, 1976a, 1976b; Taub & Berman, 1968). This contention has been questioned on the grounds that no conscious sense of movement exists in humans without peripheral somatosensory feedback (Goodwin, McCloskey & Matthews, 1972). However, these data do not bear on the functional significance of central feedback in movement acquisition, since it is possible that central feedback information is utilized by central nervous system without conscious awareness on the part of the subject.

The view that central feedback is important in movement control following dorsal rhizotomy is supported by the results of experiments which have interrupted putative central feedback loops. Dorsal rhizotomy plus lesions in cerebellum (Gilman, 1970; Liu & Chambers, 1971), head of caudate nucleus (Bossom & Ommaya, 1968) or subthalamic nuclei (Stein & Carpenter, 1965) result in movement deficits which are more severe than after dorsal rhizotomy alone or after lesions in any one of these areas separately. Even though central feedback may not be utilized by central nervous system when peripheral feedback is available, it probably becomes essential for performance when peripheral feedback is reduced or lost.

The evidence thus indicates that central nervous system can autonomously control both species-typical movement patterns and response acquisition in the absence of peripheral feedback. This denotes considerable plasticity within central nervous system; behaviors which may be feedback-dependent in the intact animal can be controlled via open-loop execution of motor programs after peripheral feedback is lost. This switch from peripheral to central control of movement has been demonstrated in the oculomotor system following vestibulectomy. In the monkey, accurate saccadic and compensatory eye movements, which participate in eye-head coordination, are dependent upon an intact vestibular system (Bizzi, Kalil & Tagliasco, 1971). When vestibular input is lost, however, both types of eye movement eventually recover as the oculomotor system develops the appropriate motor programs for their execution (Dichgans, Bizzi, Morasso & Tagliasco, 1973). Similarly, descending systems in cat spinal cord become increasingly involved in the control of locomotion after peripheral feedback is lost (Goldberger & Murray, 1974, Murray & Goldberger, 1974). Thus, when there is somatosensory feedback from a hind limb, ipsilateral partial hemisection of the spinal cord at T13, interrupting descending tracts but sparing the dorsal columns, has little effect upon locomotion with the limb. After the hind limb has been deprived of somatosensation and locomotor movements have recovered, however, partial hemisection of the cord results in permanent loss of limb movement. It is noteworthy that, after dorsal rhizotomy, fibers in efferent tracts increase their projection to spinal cord by sprouting collaterals. A significant amount of sprouting occurs in fibers that project to Clarke's nucleus; this nucleus receives most of the proprioceptive input from the hind limbs. Thus, afferent centers are increasingly informed of motor output to a limb, after the limb has been deprived of somatosensory feedback.

Since movement following dorsal rhizotomy is apparently controlled by central processes when vision of the responding body part is prevented, careful study of movement and response acquisition in a dorsal rhizotomized preparation can elucidate the degree to which central control mechanisms produce normal movement patterns without peripheral topographic feedback. Furthermore, once this information is obtained, the role of peripheral feedback in movement and response acquisition can be inferred.

Peripheral-central interaction theory. Following dorsal rhizotomy of a limb, the quality of movement is altered, with certain classes of movement more severely affected than others. This indicates that central mechanisms alone cannot adequately control all aspects of movement. Rather, central nervous system must utilize peripheral feedback to control certain components of movement and must do so more for some classes of movement than others. It would thus appear that peripheral and central mechanisms continually cooperate to produce normal movement patterns.

In terms of quality, movement in DR limbs tends to be phasic (Taub, 1976b) and ataxic (Bossom, 1974; Taub, 1976a), particularly in the early postoperative period, and it also tends to be less accurate than movement in sensate limbs (Berman, Blau, Herskovic & Berman, 1978). The phasic nature of movement in a DR limb indicates a tonic function for sensory feedback in maintaining the excitability of motoneurons (Wilson, 1961, 1964) and setting a proper "operating point" for the initiation and maintenance of muscular contraction (Smith, 1976). The ataxia results because sensory feedback is involved in intersegmental coordination (Roberts, 1969) and in the timing of motor responses (Schmidt, 1973). Electrophysiological studies corroborate the latter contention. After dorsal rhizotomy, muscular contractions develop more slowly and are more prolonged, and the transmission delay between cortex and muscle is more variable than when somatosensory feedback is present (Vaughn, Gross & Bossom, 1970). In addition, after dorsal rhizotomy, normal output to agonist-antagonist muscle groups involved in movement is disrupted. Structured activity in antagonist muscles is absent and the timing pattern of output to agonists is altered (Terzuolo, Soechting & Ranish, 1974). Finally, inaccuracy of movement with DR limbs reflects the fact that the gamma loop is believed to be a servo-device which assists in the accurate execution of movement (Granit & Burke, 1973) and involved in the termination of movement (Merton, 1972; Stark, 1968).

As far as the classes of movement which are believed to be dependent upon somatosensory feedback, these include slow movements involving small adjustments (Woodworth, 1899), discontinuous movement (acceleration of movement crosses the zero line more than once) (Koslovskaya, Atkin, Horvath, Uno & Brooks, 1973), rapid alternating movement (Conrad & Brooks, cited in Brooks, Cooke & Thomas, 1973), fine movement involving distal musculature (Frank, 1975; Granit & Burke, 1973; Laszlo & Bairstow, 1971) and accurate tracking movement (Eidelberg & Davis, 1976).

Since it has been demonstrated that somatosensory feedback is important for the execution of certain classes of movement in situations where the response requirement has been previously defined for the animal, it also may be important for the <u>acquisition</u> of certain classes of movement, when the response requirement must be determined by the animal through pairing movement patterns with reinforcement contingencies. Therefore, investigation of the classes of movement that can be acquired after dorsal rhizotomy is critical for a better understanding of the role of peripheral topographic feedback in response acquisition.

<u>Movements acquired after dorsal rhizotomy</u>. Careful examination of the response requirements in previous studies of movement acquisition after dorsal rhizotomy indicates that, although many types of movement were studied, they were in all cases discrete responses of short duration. Such discrete movements have included limb flexion in monkeys (Knapp et al.,1958, 1963; Taub et al., 1978; Wylie, 1978; Wylie & Tyner, 1978) and dogs (Gorska & Jankowska, 1961; Koslovskaya, Gasanova & Ivanova, 1966), and wrist extension (Vaughn et al., 1970), pointing (Berman, Blau, Herskovic & Berman, 1978; Polit & Bizzi, 1978;

Vierck, 1976), tapping (Gianutsos, 1975) and grasp responses (Levine & Ommaya, 1971, cited in Taub, 1976b) in monkeys. Since central efferent commands must initiate active movement, knowledge of efference, provided by central feedback, and knowledge of the movement's success or failure, provided by reinforcement contingencies, are sufficient to explain the acquisition of these responses.

To acquire a response involving a sustained change in limb position, on the other hand, it would seem that central mechanisms alone could not provide the necessary information. Knowledge of efferent commands and of their success or failure would be insufficient for response acquisition because passive drift (such as that produced by gravity), following active movement, could not be associated with reinforcement contingencies because such drift would not be detected by central monitors. In addition, even if the demands of the conditioning situation could be determined by the animal, execution of sustained responses might be difficult, since somatosensory feedback is involved in tonic changes in musculature. This contention is supported by a number of lines of evidence. First, motor units in muscle that are suitable for tonic use are innervated by alpha motoneurons that are powerfully excited by muscle spindle primary afferents (Granit & Burke, 1973). Second, EMG studies have indicated that, after cervicothoracic dorsal rhizotomy, sustained firing of motor units was replaced by bursts of activity (Weisendanger, cited in Granit & Burke, 1973). Third, it has been reported that, for a period of time following dorsal rhizotomy or dorsal column section, and before the neural control of peripheral feedback-dependent behaviors has been reorganized, animals seem to have difficulty maintaining postural change (Bizzi, Polit & Morasso, 1976; Melzack & Bridges, 1971; Taub, 1976a). Fourth, additional corroborative evidence for the role of somatosensory feedback in maintaining tonic activation of muscles comes from the work of Shambes (1969) who reported that, after the gamma loop was blocked, body sway increased when the subject was in standing position.

In spite of evidence suggesting that acquisition of sustained responses should not be possible in the absence of peripheral topographic feedback (including vision), the empirical data bearing on this question are sparse and equivocal. For example, Koslovskaya, Gasanova and Ivanova (1966) and Koslovskaya, Ovsjanikoff and Gasanova (1966) reported that dogs learned to flex DR forelimbs in a shock avoidance situation, but did not learn to sustain the change in position. In contrast to the negative findings with dogs, Taub, Schlossberg, Teodoru and Berman (cited in Taub, 1976b), working with monkeys, and McLoon and Buerger (1974), working with rats, reported that animals could learn to sustain changes in the position of DR limbs for varying periods of time.

It is possible that these contradictory findings are the result of species differences in plasticity. The studies which report positive findings can be criticized on a number of methodological grounds, however, and their results are thus questionable.

The Taub et al. study, which Taub cited (Taub, 1976a, 1976b), but has not published as an experimental report is first of all suspect on the grounds that the authors did not describe the topography and temporal characteristics of the response. Animals were required to break a photoelectric beam by flexing the DR forelimb 12.5 cm in the vertical plane against a constant load and to maintain the flexion for variable periods of time. However, it is not clear from the brief description available that the animals could not have satisfied the requirements of the task via a number of discrete responses, rather than with one sustained response. In addition, restraint of intact body parts in this study was inadequate so that the topography of the supposed sustained response was noted to involve non-rhizotomized trunk musculature (Teodoru, Note 3). As the authors reported that a considerable amount of shaping was required for response acquisition, it is quite possible that animals learned to use cues from normally innervated trunk musculature to mediate the response.

McLoon and Buerger (1974), working with DR rats, used an experimental paradigm based upon one originally devised by Horridge (1962) for the study of instrumental changes in limb position in headless insects and later used with spinal amphibians (Farel & Buerger, 1972; Horn & Horn, 1969; Peters & Wirth, 1976) and spinal rodents (Buerger & Fennessy, 1970, 1971; Chopin & Buerger, 1975). This paradigm involved suspending an animal over an electrolyte solution with an electrode attached to one hind limb. Contingencies were such that whenever the electrode was in solution, the animal received footshock. Successful performance required that animals sustain a change in limb position in order to hold the electrode above the fluid surface. Each experimental animal had a yoked control partner for whom the pattern of shock was identical. There was a short period of training (usually 15 min.), during which shock delivery was contingent upon limb position of the experimental animal but not that of their yoked partner. Upon completion of training, there was a five minute rest period after which the animals were "tested". During "testing", shock delivery to each member of an experimental:yoked pair was contingent upon each animal's own limb position.

In such studies with headless insects and spinal animals it was found that, at the completion of training, experimental animals maintained the electrode above the fluid surface while yoked controls did not. During the "testing" phase, experimental animals showed evidence of retention, as expected, while their former yoked controls showed evidence of acquisition (Buerger & Fennessy, 1970; Farel & Buerger, 1972; Horridge, 1962).

McLoon and Buerger (1974) adapted the original Horridge paradigm slightly by changing the area of shock delivery from the foot, which is anesthetized after hind limb dorsal rhizotomy, to the sensate trunk. They initiated training three days after dorsal rhizotomy and reported that, within 15 min. of training, animals exhibited significant performance changes with DR limbs which the authors interpreted as acquisition of the sustained response. This conclusion is debatable, however, for four reasons.[2]

First, a description of the putative avoidance response was not provided by the authors. This omission was serious since the response might have involved many discrete changes rather than a sustained

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[2] The author wrote to Dr. A. A. Buerger concerning the criticisms which follow. He could not provide the additional information necessary to obviate the suggested problems with the study.

change in limb position.

Second, the evidence adduced for acquisition was a decreased insertion rate as training progressed. Since an insertion was defined as removal and subsequent replacement of the electrode into solution, the decreased insertion rate could have reflected sustained placement either above or below the fluid surface. Without data on insertion time, therefore, there is no way of knowing whether animals actually learned to sustain the response, or whether, after a period of response to shock, they gave up and allowed the monitoring electrodes to remain submerged. This interpretation should be entertained because nowhere in the report do the authors mention that animals actually maintained electrodes above the fluid surface.
In addition, it is improbable that, three days following dorsal rhizotomy, animals could acquire a response with DR limbs within 15 min. of training. This is at variance with data on monkeys which indicates that acquisition of an avoidance response after dorsal rhizotomy requires many sessions of training (Taub & Berman, 1963; Taub et al., 1965). It is also noteworthy that the pattern of insertions was similar for both training and testing; insertion rate was high when shock was initially turned on, but decreased as training or testing progressed. If acquisition had occurred during training, some "savings" across a five minute retention interval would be expected. It seems much more likely, therefore, that the behavioral change these authors observed in DR limbs reflected a non-associative process such as sensitization. For this reason, examination of the relative performance of experimental:yoked control pairs during

training was important. Unfortunately, these data were not presented.

Third, the nature of restraint used to suspend animals over the electrolyte solution was unclear. If restraint was inadequate and hind limb position could be changed by movement in non-rhizotomized body parts, the reported results would be of limited significance.

Fourth, no information concerning the completeness of rhizotomy was presented. The authors did not report using an operating microscope during surgery to help insure complete rhizotomy, nor did they report monitoring motor performance in the free situation or sensation in DR limbs postoperatively. This is a significant shortcoming because it has been reported that, if a critical root of the lumbosacral plexus (L5 or L7) in cat (Goldberger, 1977) or the brachial plexus (C6, C7, C8) in monkey (lassek, 1953b; Twitchell, 1954) is left intact, deficits of movement in an otherwise DR limb are difficult to detect.

The reports that animals can acquire a sustained response in the absence of peripheral topographic feedback are thus highly suspect. Since Koslovskaya, Ovsjanikoff and Gasanova (1966) are the only ones to report negative results concerning this question, it is unfortunate that the details of the study are available solely in abstract form and have been cited by the principal author only in passing (Koslovskaya, Vertes & Miller, 1973). It cannot be determined, therefore, whether failure of acquisition in this study reflected some methodological peculiarity such as insufficient training or incomplete recovery from surgery.

Experimental Purpose and Overall Methodology

The present study was designed to determine whether a sustained response could be acquired with a DR limb in the absence of all peripheral topographic feedback. A modified version of the Horridge paradigm was used, with rats, and care was taken to preclude vision of the limb and cues from sensate body parts. This methodology was considered appropriate for the study of acquisition of sustained responses since pilot data indicated that, after non-operated animals received training in the Horridge task, they avoided shock by maintaining a specific change in limb position. It was predicted that animals would not acquire a response which involved a sustained change in the position of a DR limb.

Dorsal rhizotomy involved the left hind limb. Two dichotomous training variables were manipulated: the first was the presence or absence of preoperative training, and the second was order of training of the two hind limbs. Training with sensate limbs could provide the animals with information concerning the nature of the task and the type of response required. Thus, preoperative training and/or initial postoperative training with the contralateral sensate limb might enable animals to acquire the sustained response with DR limbs, because these conditions would permit the nature of the task to be defined in a situation in which somatosensory feedback from the limb being trained was present. If these conditions were effective, failure of animals to acquire the response with DR limbs without prior training with the sensate limb could not be interpreted to reflect an inability by central nervous system to effect a sustained change in limb position after loss of facilitation of alpha motoneurons provided by muscle spindle afferents.

To assure that any positive results were not due to sensitization, or were not mediated by afference from sensate body parts, several control groups, in addition to the standard non-operated control, were included. Thus, yoked control animals were included to preclude sensitization; the performance of animals with dorsal rhizotomy of both the limb and contiguous body parts was examined to determine the role of afference from dermatomes surrounding the limb in postoperative performance.

To insure that any negative results were not due to insufficient training with DR limbs, some animals were trained over a prolonged period of time. In most cases, when evidence of acquisition did not emerge in DR limbs after 15 sessions, training was terminated. This decision was based upon previous findings with monkeys which indicated that, after dorsal rhizotomy, acquisition of an avoidance response was retarded by a factor of 3.5 (Taub & Berman, 1963; Taub et al., 1965). Since pilot work indicated that non-operated animals acquired the response within two sessions of training, the fifteen session limit seemed quite generous. However, to obviate the possibility that animals might have acquired the response with additional training, four animals were permitted a maximum of 45 sessions with DR limbs.

Performance with right limbs, before and after contralateral dorsal rhizotomy, was also studied. These data were of interest since untoward deficits attributable to the general effects of surgery (e.g., spinal shock, edema) could be detected by assessing postoperative changes in performance with right limbs.

The experimental procedure used by McLoon and Buerger (1974) was adapted and improved in the following ways: restraint was arranged so that limb position could be altered only by movement of the limb itself; placement of animals in the apparatus was standardized, as were electrolyte levels, so that animals could be repeatedly tested; a complete description of performance was provided by recording insertions, electrode time in fluid and noting the characteristics of the avoidance response and, to help insure a complete lesion, dorsal rhizotomy was performed under an operating microscope and animals were postoperatively tested for sensation in DR limbs.

Method

Subjects

Thirty-five male Long Evans rats (200-250 grams), supplied by Charles River breeding laboratories, were randomly distributed among five experimental or two yoked control groups, as shown in Table 1. Experimental groups (total of 26 animals) were distinguished by extent of dorsal rhizotomy (T13-L6 or T11-S4, always involving the left hind limb), by maximum number of training sessions with the DR limb (15 or 45) and by whether or not animals were trained preoperatively. Yoked controls (n=9) were assigned to a subsample of animals in two experimental groups: in both, dorsal rhizotomy was T13-L6 and animals were trained for a maximum 15 sessions with DR limbs. However, animals in one group were trained both before and after surgery, while animals in the other group were trained for the first time postoperatively.

Apparatus

The apparatus was a modification of the one described by Buerger and Fennessy (1970) for use with spinal rats. An experimental animal and its yoked partner were each restrained on a separate plexiglas platform (18.3 x 10.0 x 0.3cm) so that their hind limbs were suspended over one edge. Restraint was arranged so that limb position could be altered only by movement of the limb itself. The platforms were mounted over an electrolyte solution (saline), and were separated from each other by an opaque partition. To monitor the position of the limb, a separate monitoring electrode (bared 12mm at the tip) was attached to the hind paw of each member of an experimental:yoked

Table 1

Summary of Experimental Plan

Maximum Number of Training Sessions with DR (T13-L6) Limb

	15		45
	Experimental	Yoked Control	Experimental
	n	n	n
Training Condition			
Preoperative/Postoperative Training			
Right limb trained first	5	3	-
Left limb trained first	5	2	2
Postoperative Training*			
Right limb trained first	5	2	-
Left limb trained first	5	2	2

*Two additional experimental animals were trained with the right limb after T11-S4 dorsal rhizotomy.

control pair so that it extended 30mm below the longest phalange (Figure 1). Current was supplied to the saline so that, whenever monitoring electrodes entered the fluid, they closed a circuit controlling shock delivery and/or data acquisition systems. Since the portion of electrode that contacted the animal's paw was insulated, current flow through the electrode did not result in footshock.

Each animal was shocked via two needle electrodes placed subcutaneously on the dorsal surface of the trunk, ipsilateral to the limb being tested. Electrode placement was standardized, with both electrodes placed 30mm (after T13-L6 dorsal rhizotomy) or 40mm (after T11-S4 dorsal rhizotomy) rostral to the ilial crest. The medial electrode was 15mm from the midline and interelectrode distance was 20mm. Shock electrodes of experimental animals and their yoked controls were wired in series (Figure 2) so that an experimental: yoked control pair always received the same intensity of current, regardless of their relative resistances. Monophasic square-wave pulses (6Hz, 0.1msec duration) were supplied by a Grass S6 stimulator. Voltage was set at a level just sufficient to produce behavioral arousal and limb movement in both animals (10-20 volts, 2.0-2.5 milliamperes).

Number of insertions and total electrode time in fluid were recorded for experimental and yoked control animals for each twenty successive seconds of training. An insertion was defined as removal and subsequent replacement of the monitoring electrode into the fluid.

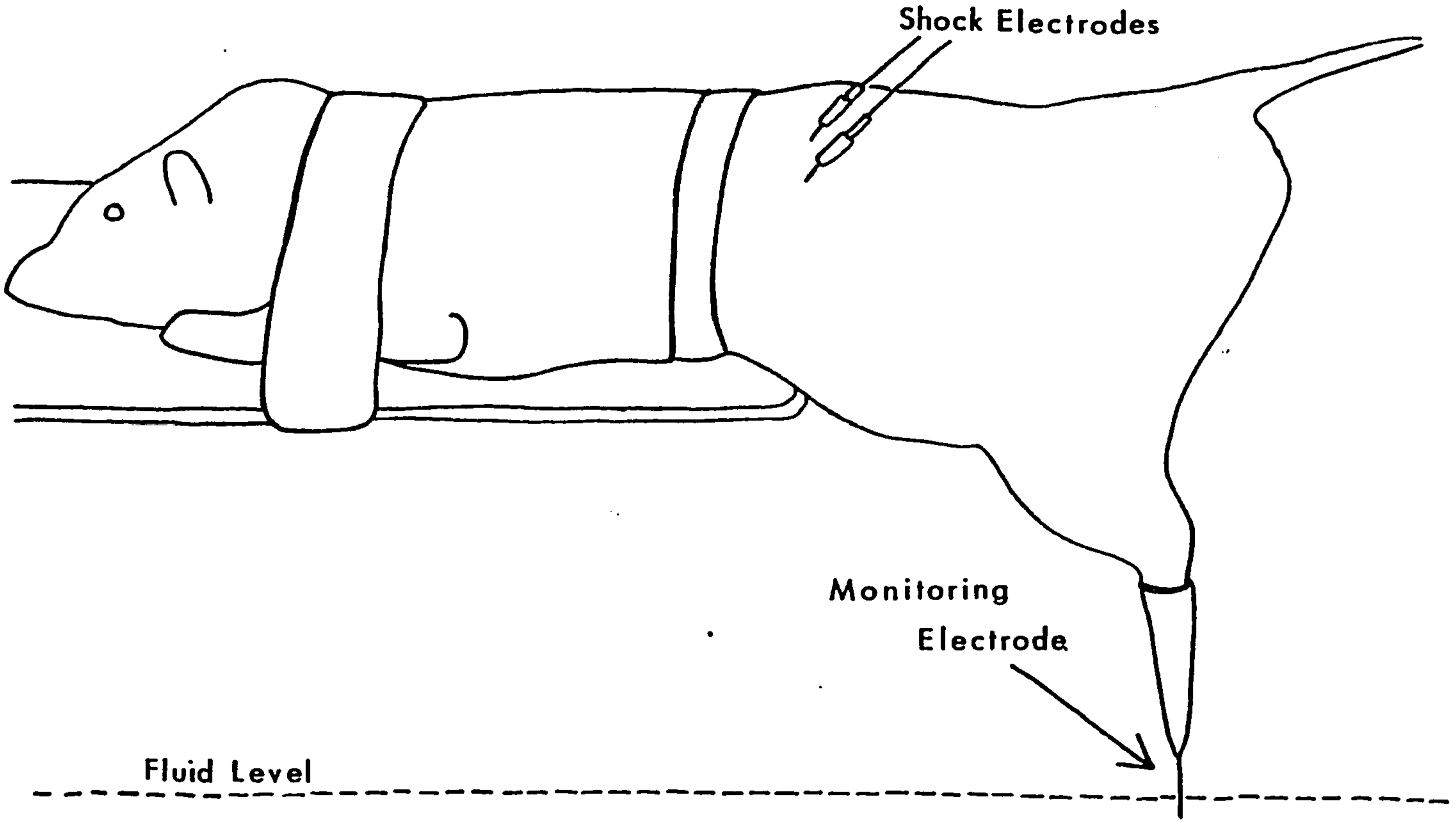


Figure 1. Lateral view of animal in apparatus.

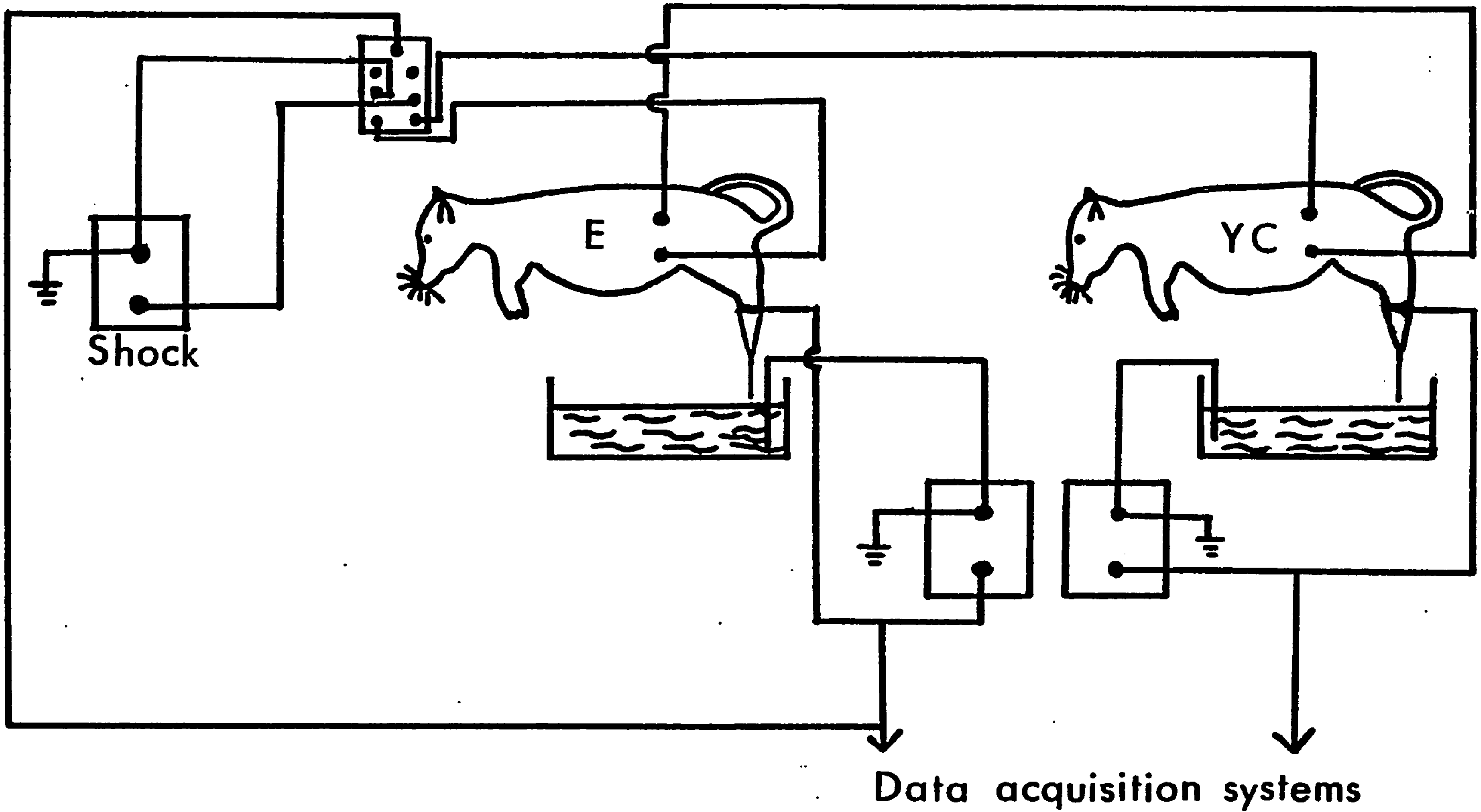


Figure 2. Wiring diagram - experimental and yoked control animals.

Procedure

Surgery and postoperative care. All surgery was performed under sodium pentobarbital anesthesia (45-50 mg/kg). Innervation of the hind limbs in rats arises from spinal segments T13-L6 (Hebel & Stromberg, 1976; Jankowska, 1959), corresponding, according to Gelderd and Chopin (1977), the vertebrae T11-L1. The prominent T2 spinous process served as an identifying landmark, and a longitudinal incision was made along the dorsal midline, exposing vertebrae T9-L3. The dorsal aspect of vertebrae T11-L1 was cleaned and separated from surrounding muscle, and a dorsal laminectomy was performed. Care was taken to remove approximately the same amount of bone bilaterally. Under 16x magnification, the dura was incised longitudinally and reflected laterally. Care was taken to avoid injury to the posterior spinal artery. Ether was then administered to insure muscular relaxation. Each of the seven dorsal roots T13-L6 on the left side was carefully lifted with a nerve hook so as to avoid tension at the dorsal root:spinal cord junction, was severed with a microscissors, and reflected, and a small section of each root was removed. This procedure precluded hemorrhage on the dorsal surface of the spinal cord. The cord was then reexamined under 40x magnification to verify that the appropriate roots had been severed completely. The exposed spinal cord was covered with Gelfoam, and the muscle and skin closed in layers. Penicillin (100,000 I.U.) was administered at the conclusion of the procedure.

When dorsal rhizotomy included body parts surrounding the limb, surgery involved removing vertebrae T10-L2, and severing dorsal roots T11-S4 on the left side. For both T13-L6 and T11-S4 dorsal rhizotomy, the clearly distinguishable components of the sciatic nerve (L4-L6) were used for anatomic orientation.

Animals were allowed to recover for four weeks before training was initiated. During the postoperative period (and for one week prior to surgery), they were paired with unoperated females in plastic cages (47.0 x 25.4 x 20.3cm) that contained bedding material in quantities sufficient to permit burrowing behavior. This arrangement appeared to optimize recovery and to guarantee that animals did not mutilate DR limbs (Rodin, Berman & Niznik, Note 4).

Throughout the period of recovery and conditioning, animals were checked semiweekly for motor performance in the free situation (ambulatory patterns, posture) and for sensation (responsivity to pin prick, pressure) in hind limbs.

<u>Adaptation, baseline and conditioning</u>. During all sessions, standardized placement of animals in the apparatus was accomplished by aligning specific parts of the trunk, labelled with indelible ink, with the edge of the platform. In addition, the hind limb not being trained and the tail were secured in unvarying positions on the apparatus. All sessions, adaptation, baseline or conditioning, were conducted at 48 hr. intervals.

Animals were adapted to restraint for a minimum of three 30 min. sessions (usually 4-8 sessions), until they lay quietly in the apparatus for two consecutive sessions.

Following adaptation, resting position of hind limbs was determined for each animal. Saline level was adjusted so that the monitoring electrode, attached to the animal's paw, was submerged 6-8mm but the animal's paw never entered the fluid. Insertions and time in fluid for each limb were determined in at least three 20 min. baseline sessions. This permitted determination of variability in resting position of the limb and verification that the selected fluid level insured submersion of monitoring electrodes. Saline level for each animal was recorded and used throughout training.

Successful performance, during training sessions, required that the monitoring electrode be lifted from the saline and maintained above the fluid surface. Animals were trained under several conditions (summarized in Table 1). Two groups of experimental animals, subjected to left T13-L6 dorsal rhizotomy, were allowed a maximum 15 sessions of training with DR limbs. Of these, one group was trained preoperatively and retrained four weeks after surgery and the other received initial training four weeks postoperatively. In both groups, hind limbs were trained sequentially with the same order used before and after surgery; the left limb was trained first for half the animals; the right, for the other half. Yoked controls were assigned to a subsample of animals in both experimental groups; they matched their experimental partners in surgical condition and in number of sessions with either limb.

Two groups of experimental animals with T13-L6 dorsal rhizotomy either were trained preoperatively and retrained after surgery or were initially trained postoperatively. Animals in these groups all were trained with the left limb first and were allowed a maximum 45 (rather than 15) sessions of training with DR limbs. One group of experimental animals was trained for the first time after T11-S4 dorsal rhizotomy. In this group, right limbs were trained first and training with DR limbs was continued for a maximum of 15 sessions.

There were a total of three surgical deaths which occurred in groups trained both before and after surgery (T13-L6) for a maximum of 15 sessions with the DR limb. Two were experimental animals, one trained with the left limb first, and one with the right limb first. The third was a yoked control tested with the right limb first.

The contingencies of the training situation were such that, whenever the experimental animal inserted its monitoring electrode into the fluid, shock was delivered to the experimental:yoked control pair for the duration of the insertion. Yoked controls received the same intensity and pattern of shock as their experimental partners, regardless of their behavior.

Training sessions were 20 min. in duration. Electrode time in saline, and number of insertions were recorded every 20 sec. Since acquisition of a sustained response was of interest, experimental animals were trained to a criterion of ≤0.1 sec. electrode time in solution in 75% of the 20 sec. intervals in three of four successive sessions. Animals were carefully observed for the topography of any avoidance response and for the presence of movement in the limb when monitoring electrodes were held above the fluid surface.

Post-mortem examination. After the behavioral data were collected, animals were killed. The surgical wound was reopened and the spinal cord examined under 40x magnification for confirmation of the level and completeness of dorsal rhizotomy.

Results

General Observations

Post-mortem examination of the spinal cord indicated that all animals had undergone complete dorsal rhizotomy at the appropriate levels. In addition, for the entire period of postoperative observation, animals exhibited no behavioral evidence of sensation in body parts expected to be rendered anesthetic by T13-L6 or T11-S4 dorsal rhizotomy, although responses to pin-prick and pressure on the non-operated side were brisk. Figures 3 and 4, respectively, show the areas without evidence of sensation after surgery.

Motor performance in the free situation was similar after T13-L6 or T11-S4 dorsal rhizotomy. During the first few days following surgery, normal posture and ambulatory patterns were completely disrupted and extensor hypertonus was present in operated limbs, particularly in distal musculature. Limbs were extended behind the body when the animal was in quadripedal position, and extended forward or in adduction when the animal was sitting. Within one week following surgery, the DR limb participated in ambulation. At times, it was used to support body-weight during locomotion in a stilt-like fashion. This pattern alternated with extending the limb behind the body, stepping on the paw dorsum and flexing proximal musculature rhythmically. Recovery of motor function appeared to reach asymptote within a month following surgery. Normal ambulatory patterns appeared at times, but the limb was often placed incorrectly and dragged behind the body. Throughout the course of behavioral observation (up to four months), postural adjustments with the DR

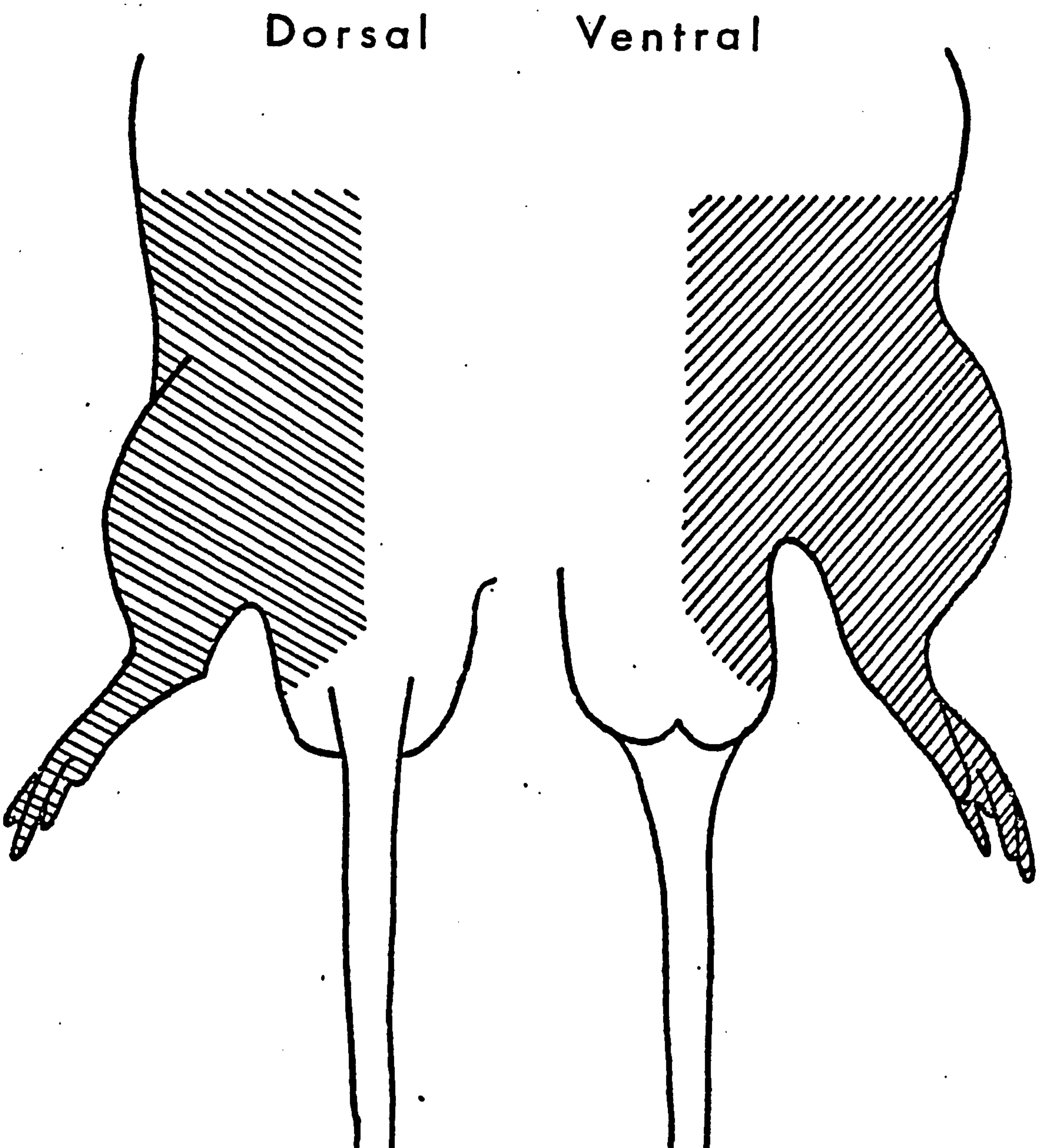


Figure 3 . Area anesthetized by T13-L6 dorsal rhizotomy.

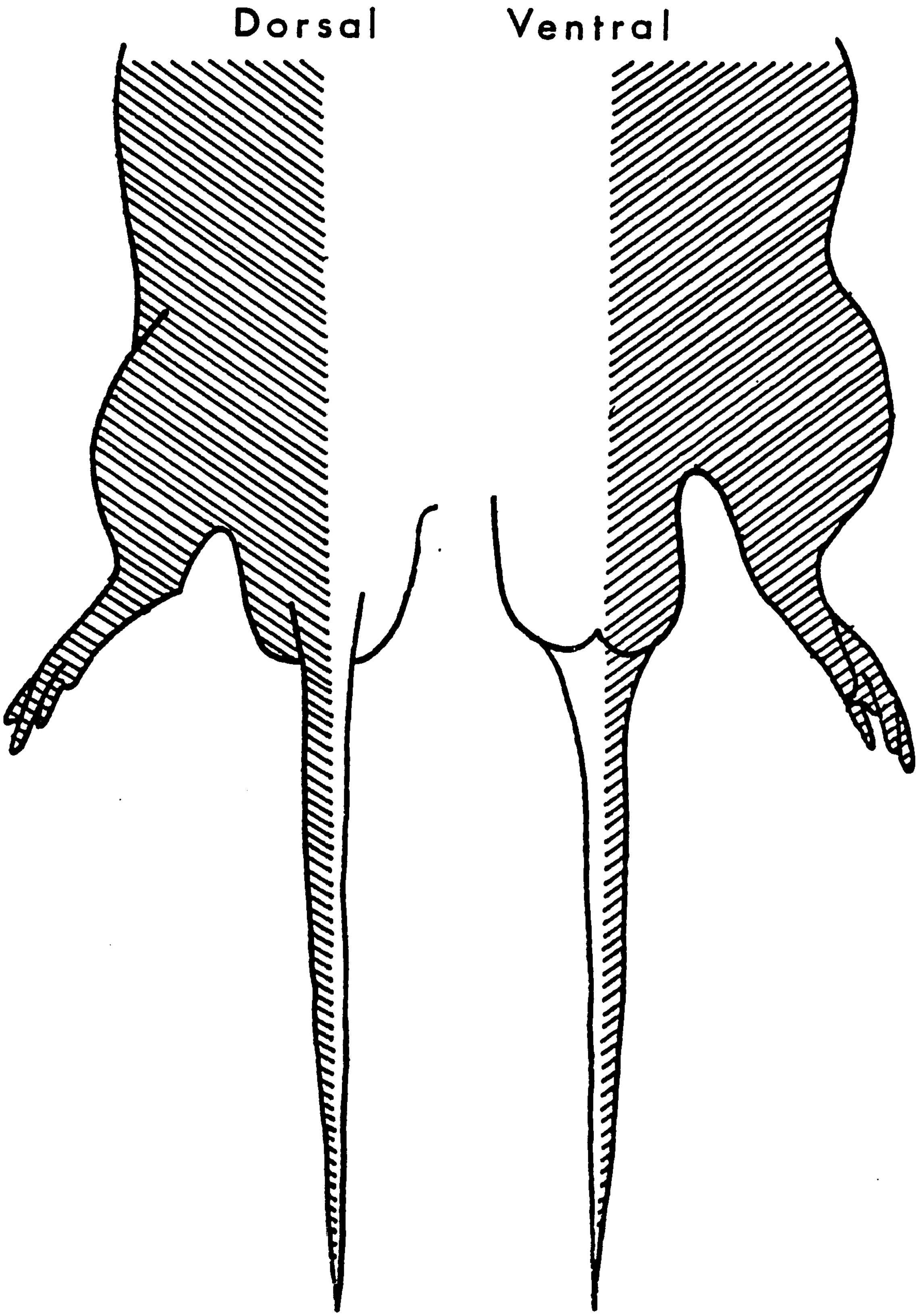


Figure 4. Area anesthetized by T11-S4 dorsal rhizotomy.

limb were crude and movement of the limb in the free situation was limited and tended to be clumsy and ballistic.

Experimental Animals

T13-L6 dorsal rhizotomy; training with DR limbs continued for a maximum of 15 sessions. During baseline sessions, both non-operated and DR limbs were kept extended so that monitoring electrodes were submerged in solution. Although alterations in limb position occurred which were sufficient to remove electrodes from the fluid, baseline positions were reachieved rapidly. Rarely (0-3% incidence) was insertion time per 20 sec. ≤0.1sec.

Table 2 summarizes mean percent insertion time[3] per baseline session for right and left limbs of non-operated and DR (not preop trained) animals. Two-way Analysis of Variance (Table 3) indicated that, before training was initiated, there were no significant insertion time differences between non-operated and DR animals, or between the right and left limbs of animals in either group.

Since dorsal rhizotomy was always on the left side, performance with left limbs, under different conditions of training, will be described first. Table 4 summarizes percent animals in each experimental condition that reached final and/or less stringent criteria[4] with left limbs, within the limits of training.

[3] Insertion time = electrode time in fluid.

[4] Criteria specified percent of 20 sec. intervals per session with ≤0.1 sec. electrode time in fluid. Final criterion: 75%; less stringent criteria: 50, 25, 10%. Less stringent criteria were considered achieved when an animal consistently performed at or above the prescribed level for the duration of training.

Table 2

Mean and Standard Error Percent Insertion Time Per Session Before Training

Group	n	Limb Right	 Left
Preop	10	93.0 ± 3.1	94.9 ± 2.8
Postop: not preop trained	10	90.6 ± 2.6	96.2 ± 1.0*

*DR

Table 3

Summary of Two-Way ANOVA
Baseline Percent Insertion Time:
Non-operated vs. DR (Not Preop Trained) Animals;
Right vs. Left Limbs

Source of Variation	SS	df	MS	F	p
Between Subjects					
Non-operated vs. DR (not preop trained)	63.50	1	63.50	0.62	N.S.
Error	1,833.43	18	101.86		
Within Subjects					
Right vs. left limbs	331.78	1	331.78	0.58	N.S.
Interaction	149.00	1	149.00	.26	N.S.
Error	10,230.83	18	568.38		

Table 4

Percent Subjects in Each Experimental Condition That Attained Successive Criteria with Left Limbs Before and After Left Dorsal Rhizotomy

Group	n	Successive Criteria: Intervals Per Session with ≤.1 sec. Electrode Time in Fluid			
		10%	25%	50%	75% (Final)
Right limb trained first					
*Preop	5	100	100	100	100
*Postop: preop trained	4	100	100	100	100
Postop: not preop trained	5	100	100	100	100
Left limb trained first					
**Preop	5	100	100	100	100
**Postop: preop trained	4	0	0	0	0
Postop: not preop trained	5	0	0	0	0

*Include same subjects; one subject did not survive surgery.

**Include same subjects; one subject did not survive surgery.

Non-operated animals reached final criterion with left limbs whether or not right limbs were previously trained. Attainment of criterion with DR left limbs, on the other hand, critically depended upon whether, after surgery, the contralateral right limb had already been trained. Even the least stringent criterion was not achieved with DR limbs unless the order of postoperative training was sensate (right) followed by DR (left) limb. When this order prevailed, however, animals achieved final criterion with DR limbs regardless of whether or not they had been trained preoperatively. Thus, the occurrence of preoperative acquisition was neither a necessary nor a sufficient condition for the occurrence of postoperative acquisition with DR limbs.

Under the condition where criteria could be attained, animals required many more sessions of training to do so with DR than with non-operated limbs and the topography of the response differed in the two cases. Responses were always such that monitoring electrodes hovered a few millimeters above the fluid surface but this was accomplished with non-operated limbs by <u>sustained</u> flexion of distal joints, whereas with DR limbs this was accomplished by <u>sustained</u> flexion of the hip (adduction of the limb) and extension of distal joints. In neither case was there visible evidence that monitoring electrodes were maintained above the fluid surface via a series of discrete changes in limb position.

Melton curves (Woodworth & Schlosberg, 1954) were constructed and studied to determine relative performance with left limbs, trained under different experimental conditions, at prescribed points in the acquisition process. Figure 5 shows mean number of sessions to successive learning criteria for each condition of training. The performance of animals that did not reach criteria with DR limbs is not represented.

Animals performed at final criterion with non-operated left limbs within two sessions of training. Acquisition was slightly more rapid when the right than when the left limb was trained first, but this advantage was not significant at any criterion ($\underline{t}$ $(8) < 1$ at each criterion, $\underline{p} > .05$). In comparison, animals that acquired the sustained response with DR limbs required 7-12 sessions of training to achieve criteria. Two-way Analysis of Variance (Table 5) indicated that acquisition differences between non-operated limbs and DR limbs that were not trained preoperatively were significant at all criteria ($\underline{F}$ $(1,8) = 197.04$, $\underline{p} < .001$), and that, as expected, animals required significantly more training to achieve successively more stringent criteria with both DR and non-operated limbs ($\underline{F}$ $(3,24) = 10.59$, $\underline{p} < .01$).

To evaluate the postoperative deficit in DR limbs that were trained before surgery, $\underline{t}$-tests (correlated scores) were performed on preoperative:postoperative acquisition differences. Table 6 shows the average number of additional sessions of training that were required to achieve successive criteria after dorsal rhizotomy than were required preoperatively, and summarizes the statistical analysis. It is evident that reacquisition of the sustained response after dorsal rhizotomy was significantly slower than initial preoperative acquisition. It should be noted from Table 6, however,

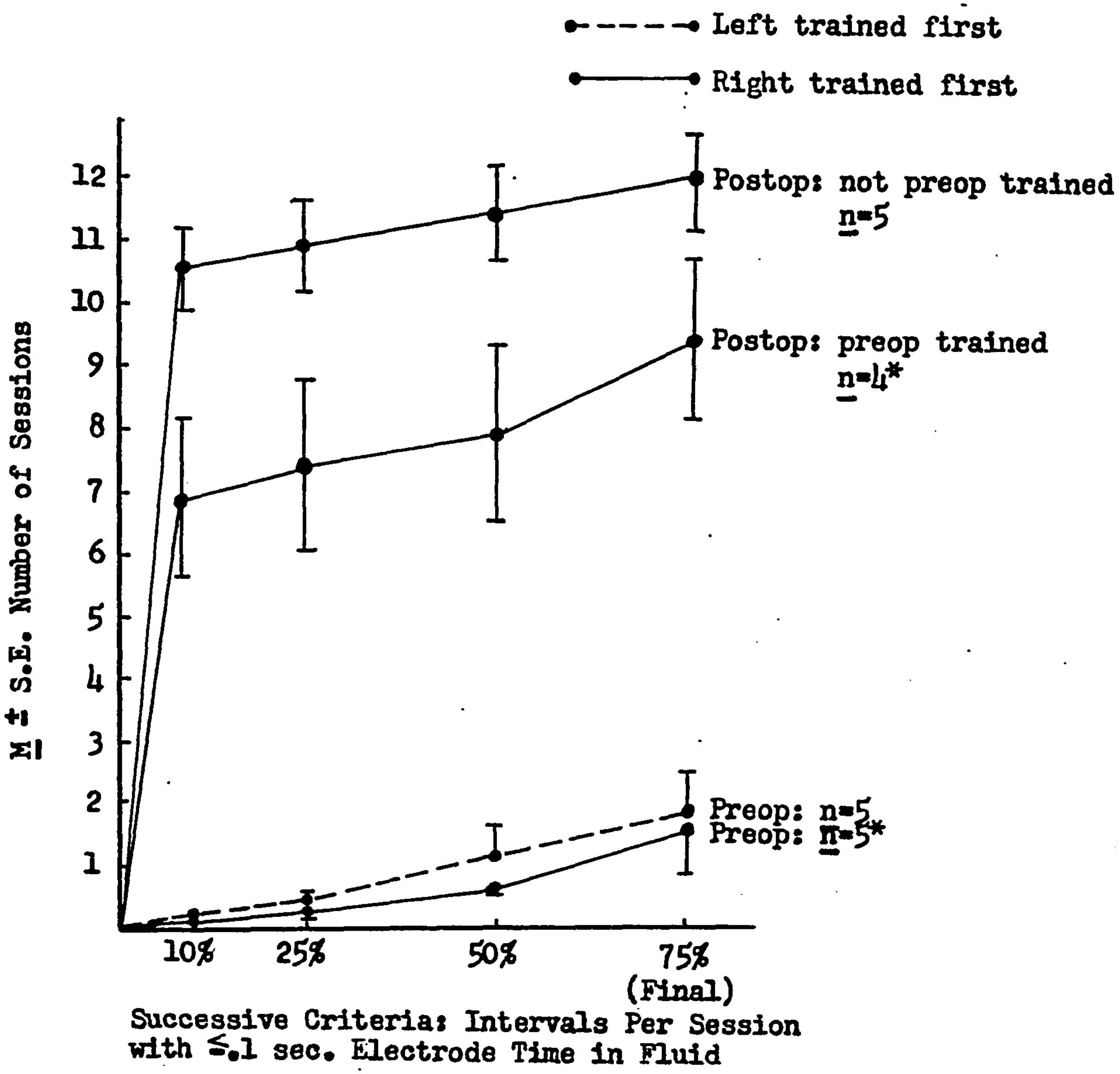


Figure 5. Melton curves depicting left limb performance before and after T13-L6 dorsal rhizotomy: group mean sessions to successive criteria.

N.B. Performance with DR limbs in the absence of postoperative training with contralateral sensate limbs is not depicted, since criteria were not attained within 15 sessions of training.

*Same subjects; one subject did not survive surgery.

Table 5

Summary of Two-Way ANOVA
Acquisition with Left Limbs, Right Limbs Trained First: Sessions to Criteria Preop vs. Postop (Not Preop Trained) and Sessions to Different Criteria Within Animals

Source of Variation	SS	df	MS	F	p
Between Subjects					
Preop vs. postop: not preop trained	1,103.44	1	1,103.44	197.04	<.001
Error	44.79	8	5.60		
Within Subjects					
Criteria (10% vs. 25% vs. 50% vs. 75%)	10.80	3	3.60	10.59	<.01
Interaction	0.32	3	0.11	0.32	N.S.
Error	8.06	24	0.34		

Table 6

Postoperative Increase in Number of Sessions to Successive Criteria, Relative to Preoperative Performance, with DR Limbs Trained After Intact Limbs

	Successive Criteria: Intervals Per Session with $\leq .1$ sec. Electrode Time in Fluid			
	10%	25%	50%	75% (Final)
M increase	6.73	7.14	7.24	7.61
t (*df*=3)*	5.34	5.05	4.89	3.62
p	<.02	<.02	<.02	<.05

*Correlated data

that the postoperative deficit in acquisition with DR limbs was in number of sessions to attain the 10% criterion. Once animals progressed beyond the 10% criterion, acquisition with DR limbs occurred at the same rate as with non-operated limbs. This was indicated by the fact that the preoperative:postoperative acquisition difference did not increase substantially with successive criteria. This was also true for performance with DR limbs that were not trained preoperatively (Figure 5).

Although preoperative training was not sufficient to insure acquisition with DR limbs, when animals were trained preoperatively and initially trained with contralateral sensate limbs postoperatively, acquisition with DR limbs was more rapid than when only the latter condition prevailed. Two-way Analysis of Variance (Table 7) indicated that acquisition was significantly more rapid with DR limbs that were trained preoperatively than with those that were not (F (1,7) = 15.32, $p < .01$) and, in either case, animals required significantly more training to achieve successive criteria (F (3,21) = 19.93, $p < .01$).

The possibility was considered that, when criterion was not achieved with DR limbs, animals nevertheless exhibited performance changes across training which were indicative of acquisition. For example, if monitoring electrodes came to be maintained above the fluid surface for 18 sec. of every 20 sec. interval, the criterion chosen in the present study never would have been achieved, in spite of the fact that insertion time per session would have been reduced significantly.

Table 7

Summary of Two-Way ANOVA Acquisition with DR Left Limbs, Right Limbs Trained First: Sessions to Criteria Preop Training vs. No Preop Training and Sessions to Different Criteria Within Animals

Source of Variation	SS	df	MS	F	p
Between Subjects					
Postop: preop trained vs. not preop trained	266.18	1	266.18	15.32	<.01
Error	121.60	7	17.37		
Within Subjects					
Criteria (10% vs 25% vs. 50% vs. 75%)	16.74	3	5.58	19.93	<.01
Interaction	0.89	3	0.30	1.07	N.S.
Error	5.96	21	0.28		

Figure 6 depicts mean percent insertion time per session for animals that did not achieve criterion with DR limbs. Since changes in insertion time can be more clearly interpreted by examining concomitant changes in insertion rate, mean number of insertions per session also is depicted. During baseline sessions, high insertion times and few insertions indicated that electrodes were submerged in solution. When final criterion was achieved, before surgery, electrodes were maintained above the fluid surface; insertion time per session was minimal, and insertions were relatively few. When animals did not achieve criterion with DR limbs, however, they escaped shock with a rapid series of discrete changes in limb position; number of insertions per session was elevated but insertion time was only slightly reduced. This was particularly true when there had been preoperative training, but it also occurred frequently when animals had not been trained preoperatively. Unless contralateral sensate limbs were trained first after surgery, therefore, animals did not sustain changes in the position of DR limbs for even short periods of time. Rather, punishment was reduced slightly with a rapid series of non-sustained movements.

Performance with right limbs, before and after contralateral dorsal rhizotomy, was studied to provide a baseline from which to assess deficits in DR limbs. Also, examination of right limb performance, when training was initiated following unsuccessful training with DR limbs, could provide information concerning the possible debilitating effects of unsuccessful training on subsequent learning.

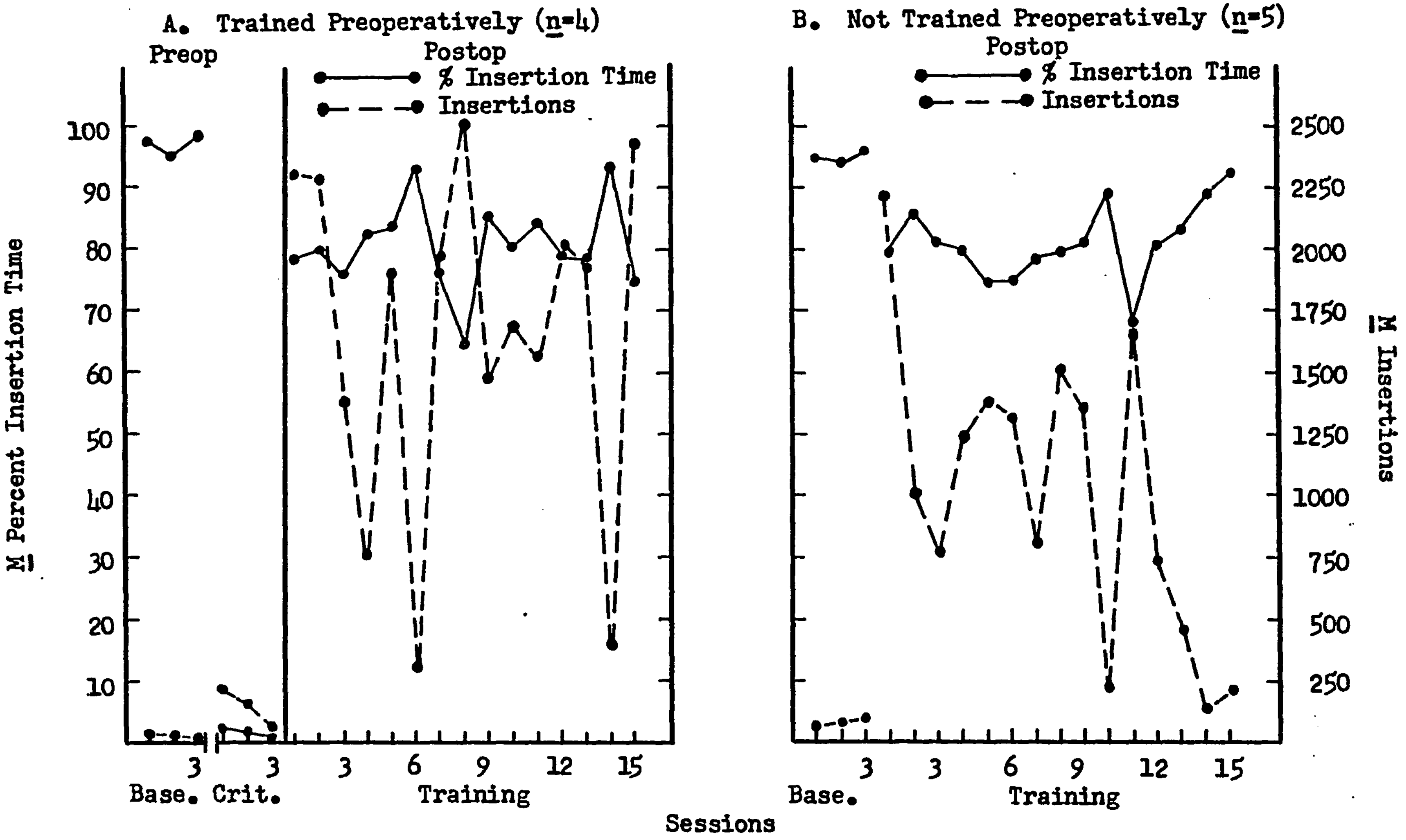


Figure 6. Performance with DR limbs in the absence of postoperative training with contralateral sensate limbs, when training continued for 15 sessions: group mean percent insertion time or insertions per session.

Base.: Performance before conditioning initiated.

Crit.: Performance during the three conditioning sessions that preceded dorsal rhizotomy (T13-L6).

Table 8 shows percent subjects in each experimental condition that achieved successive criteria with right limbs. Before contralateral dorsal rhizotomy, not every animal achieved final criterion with the right limb within 15 sessions, if the left limb had been trained first. This contrasted with preoperative performance with left limbs (Table 4); in this case, final criterion was invariably achieved. Examination of the pattern of insertion time across training for animals that did not achieve final criterion with right limbs, however, revealed evidence for acquisition (Figures 7A, 8A). Insertion time was considerably less than during baseline sessions, and was substantially below the insertion time of animals that did not achieve criterion with DR limbs (Figure 6).

After contralateral dorsal rhizotomy, performance with right limbs did not deteriorate. All animals that achieved criterion before surgery did so postoperatively. In addition, the performance of animals that did not achieve final criterion preoperatively improved after surgery; time in fluid per session decreased and, in one case, final criterion was achieved (Figures 7B, 8B).

Melton curves depicting the course of acquisition for right limbs are presented in Figures 9 (preop trained) and 10 (not preop trained). For the purpose of grouping data, animals that did not achieve a specific criterion within the limits of training were considered to have done so in 15 sessions.

Striking differences emerged in preoperative performance with right and left limbs. First, animals achieved criterion with left limbs with ease, whether or not they were trained previously

Table 8

Percent Subjects in Each Experimental Condition That Attained Successive Criteria with Right Limbs Before and After Left Dorsal Rhizotomy

Group	n	Successive Criteria: Intervals Per Session with ≤.1 sec. Electrode Time in Fluid			
		10%	25%	50%	75% (Final)
Right limb trained first					
*Preop	5	100	100	100	100
*Postop: preop trained	4	100	100	100	100
Postop: not preop trained	5	100	100	100	100
Left limb trained first					
**Preop	5	80	80	60	60
**Postop:preop trained	4	100	100	75	75
Postop: not preop trained	5	100	100	100	100

*Include same subjects; one subject did not survive surgery.

**Include same subjects; one subject did not survive surgery.

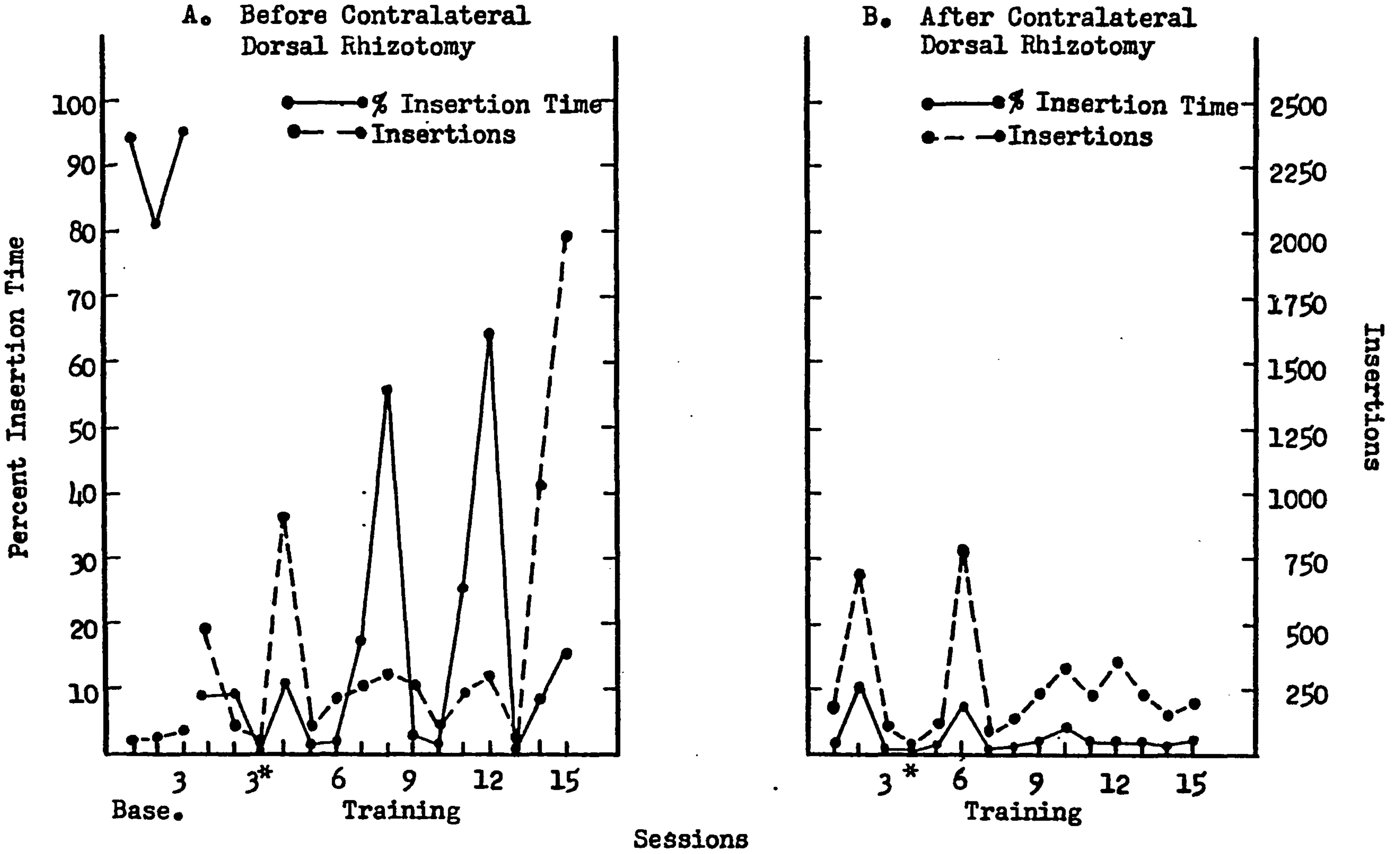
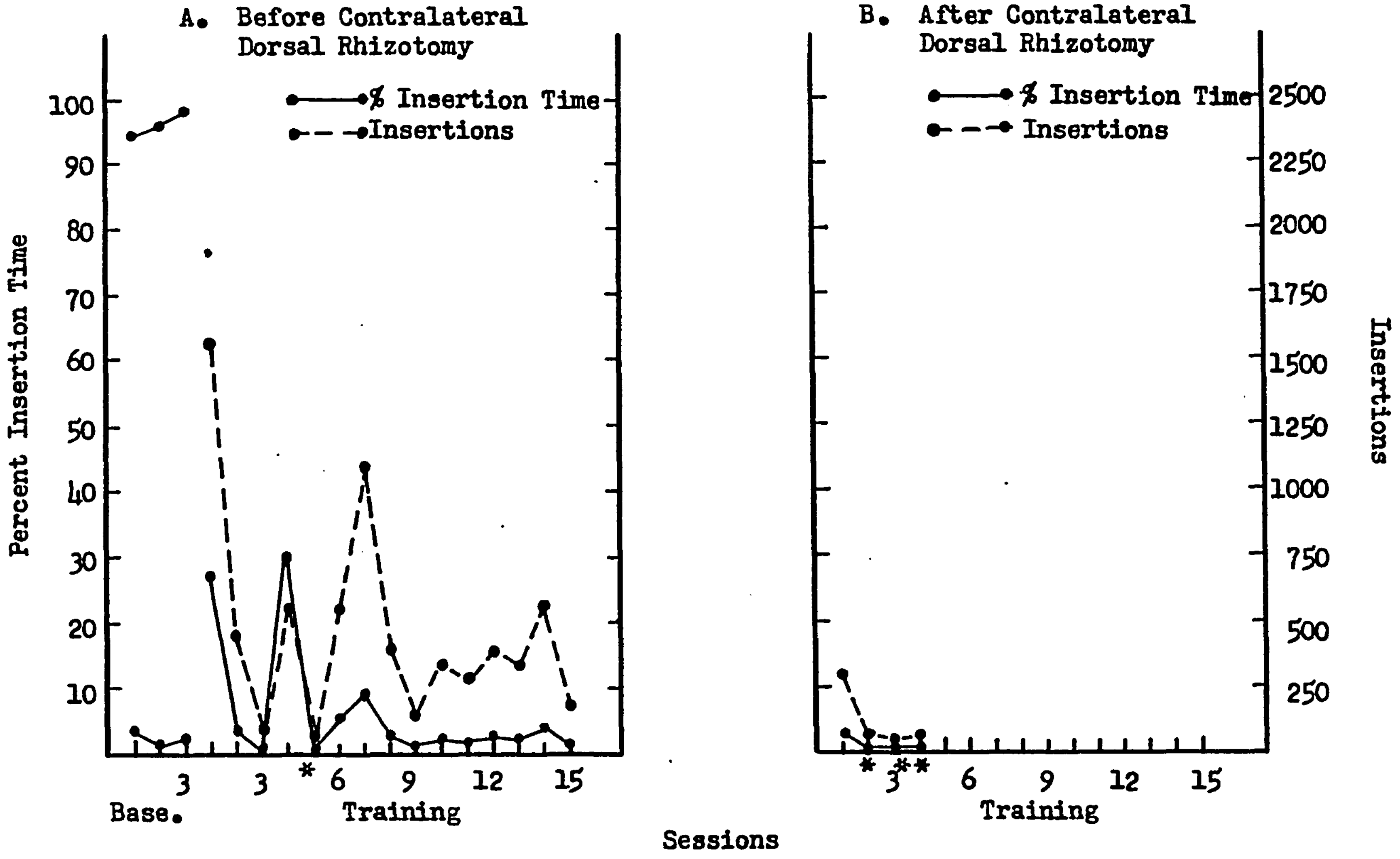


Figure 7. Preoperative:postoperative performance with right limb of subject (#3) that did not reach final criterion with right limb before contralateral dorsal rhizotomy (T13-L6): percent insertion time and insertions per session. (Training with right limb initiated after animal either achieved final criterion or received maximum 15 sessions of training with left limb.)

Base.: Performance before conditioning initiated.

*≥75% 20 sec. intervals with ≤.1sec. in fluid



A. Before Contralateral Dorsal Rhizotomy

B. After Contralateral Dorsal Rhizotomy

Figure 8. Preoperative:postoperative performance with <u>right</u> limb of subject (#13) that did not reach final criterion with right limb before contralateral dorsal rhizotomy (T13-L6): percent insertion time and insertions per session. (Training with right limb initiated after animal either achieved final criterion or received maximum 15 sessions of training with left limb.)

Base.: Performance before conditioning initiated.
*≥75% 20 sec. intervals with ≤.1sec. in fluid

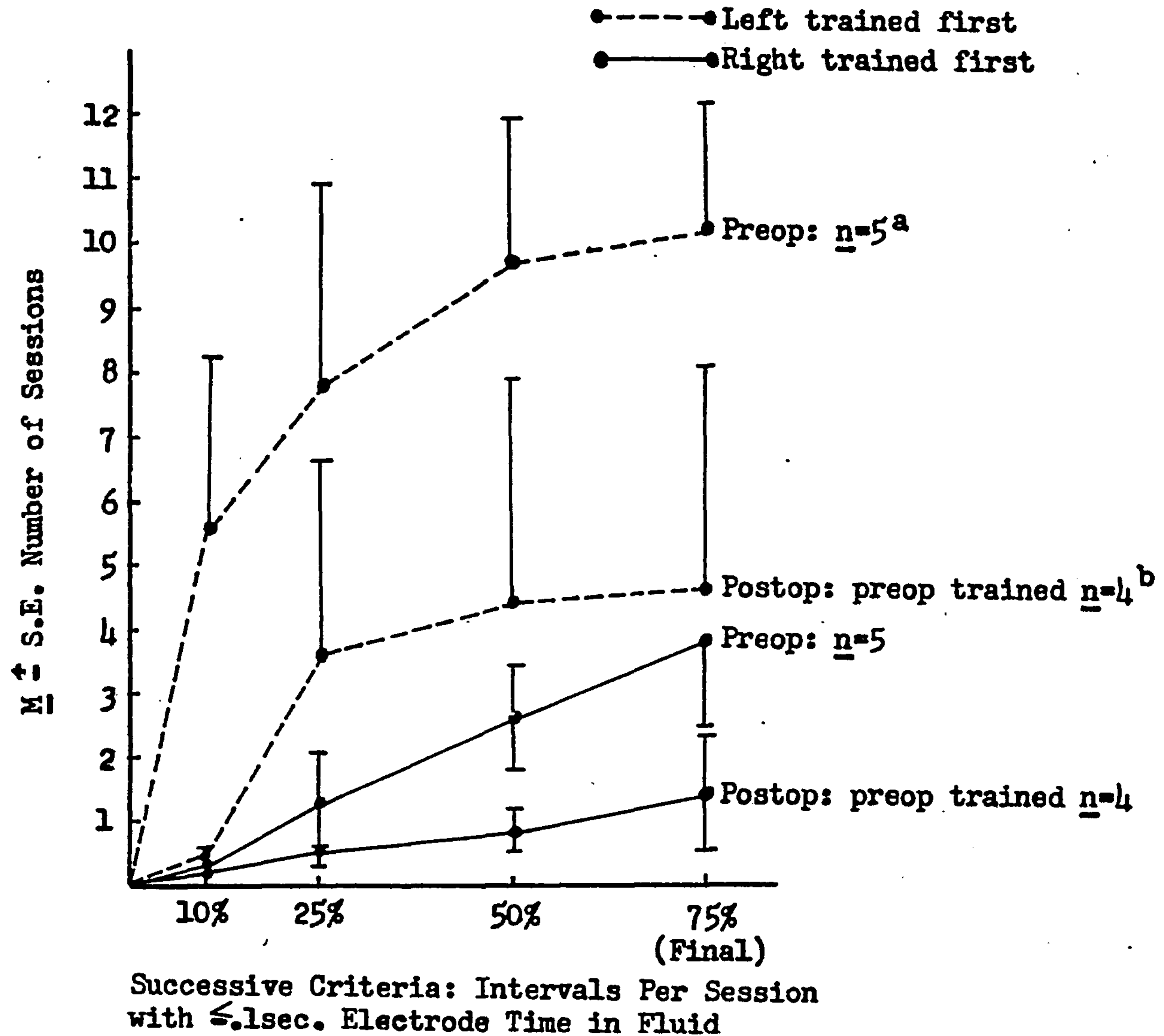


Figure 9. Melton curves depicting performance with right limbs before and after contralateral dorsal rhizotomy (T13-L6): group mean sessions to successive criteria. (Both postop groups contain same subjects as corresponding preop group; in each case, one subject did not survive surgery.)

a. Number of sessions for two subjects that did not reach criteria within 15 sessions was taken to be 15 for the purpose of analysis.

b. Number of sessions for one subject that did not reach criteria within 15 sessions was taken to be 15 for the purpose of analysis.

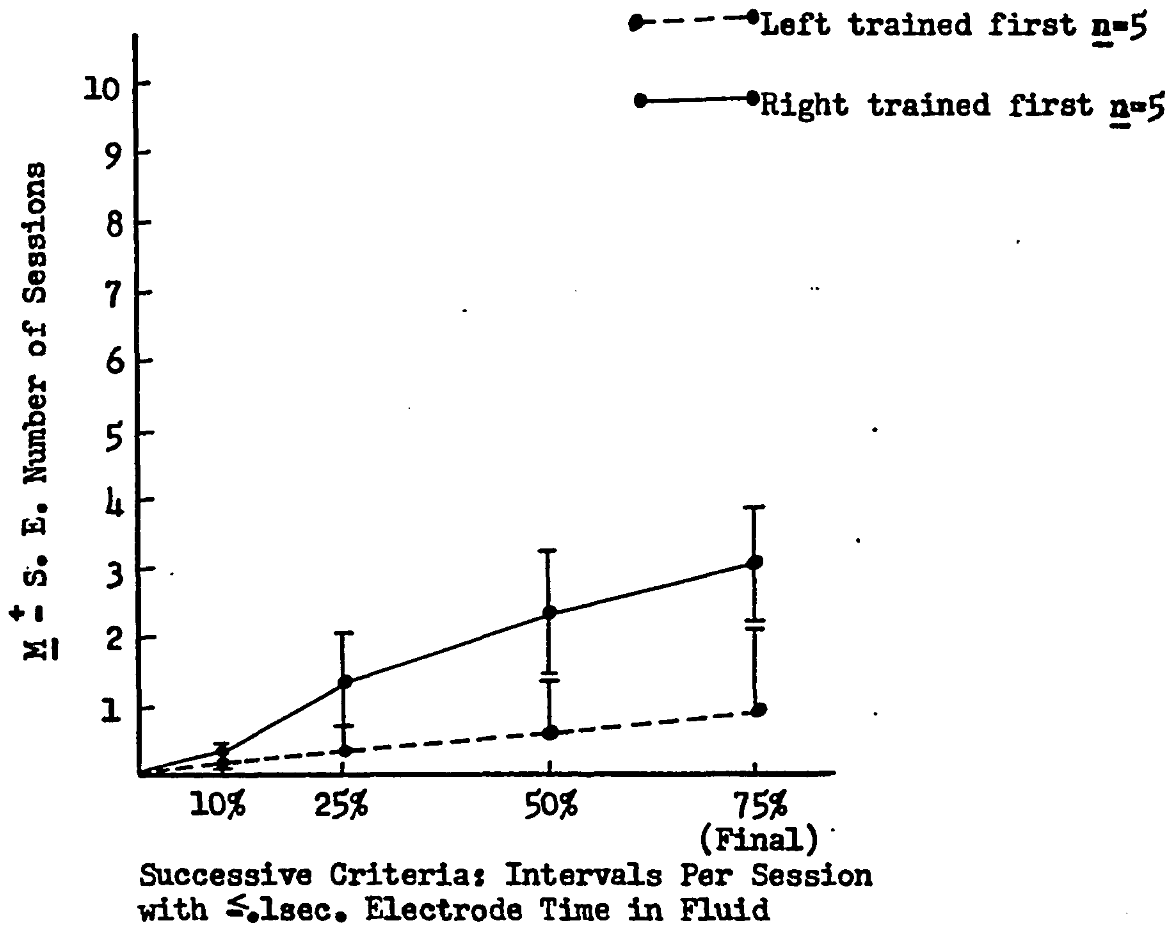


Figure 10. Melton curves depicting performance with right limbs initially trained after contralateral dorsal rhizotomy (T13-L6): mean sessions to successive criteria for groups trained with right vs. left (DR) limbs first.

with right limbs (Figure 5). This was not the case with right limbs; acquisition was slower if left limbs had been trained first. Two-way Analysis of Variance (Table 9) indicated that acquisition differences between right limbs trained before vs. after left limbs were significant at all criteria ($\underline{F}$ (1,8) = 6.53, $\underline{p} < .05$) and, in either case, animals required additional training to achieve successive criteria ($\underline{F}$ (3,24) = 9.04, $\underline{p} < .01$). Second, acquisition was slower with right than with left limbs, regardless of order of training. Table 10 shows the frequency (number of subjects per group) with which animals required more training with right than left limbs to achieve specific criteria. When data from animals that were trained with right vs. left limbs first were grouped for statistical analysis, Sign Tests for Matched Pairs at each criterion indicated that the incidence of poorer performance with right than left limbs was significantly above chance level. However, when animals trained with the right limb first were considered separately from animals trained with the left limb first, Sign Tests for Matched Pairs indicated that the performance difference between the two hind limbs was not significant at any criterion.

Performance with right limbs that were trained before contralateral dorsal rhizotomy improved after surgery (Figure 9). Table 11 summarizes average postoperative "savings" in sessions to each criterion with right limbs when animals were trained with right vs. left limbs first. The postoperative improvement in right limb performance was more marked when right limbs were trained after than before left limbs but, in neither case, did the improvement

Table 9

Summary of Two-Way ANOVA
Preoperative Acquisition with Right Limbs: Sessions to Criteria Right vs. Left Limb Trained First and Sessions to Different Criteria Within Animals

Source of Variation	SS	df	MS	F	p
Between Subjects					
Right vs. left first	397.09	1	397.09	6.53	<.05
Error	486.29	8	60.79		
Within Subjects					
Criteria (10% vs. 25% vs. 50% vs. 75%)	98.20	3	32.73	9.04	<.01
Interaction	4.97	3	1.66	0.46	N.S.
Error	86.78	24	3.62		

Table 10

Non-operated Subjects Requiring More Training With Right Than With Left Limbs To Achieve Successive Criteria

		Successive Criteria: Intervals Per Session with ≤.1 sec. Electrode Time in Fluid			
Group	n	10%	25%	50%	75% (Final)
Right limb trained first	5	5	5	5	4
Left limb trained first	5	5	5	5	5
Percent subjects requiring more training with right than left		100%	100%	100%	90%
Sign Test (z) p		2.85, <.01	2.85, <.01	2.85, <.01	2.22, <.05

Table 11

Mean Postoperative "Savings" In Sessions To Each Criterion With Right Limbs Trained Before Contralateral Dorsal Rhizotomy

	Successive Criteria: Intervals Per Session with $\leq .1$ sec. Electrode Time in Fluid			
Group	10%	25%	50%	75% (Final)
Right limb trained first	-0.05	0.01	1.14	1.15
t (*df*=3)	0.40	0.07	2.04	2.88
p	N.S.	N.S.	N.S.	N.S.
Left limb trained first	6.36	5.91	6.13	6.37
t (*df*=3)	2.17	2.05	2.15	2.36
p	N.S.	N.S.	N.S.	N.S.

attain statistical significance (t tests, correlated scores). This can be accounted for by the large variability contributed by subjects who did not achieve criteria.

Criteria were achieved with ease with right limbs when training was initiated after contralateral dorsal rhizotomy (Figure 10). Although average performance was slightly better when the left (DR) limb was trained first than when it was not, performance differences under the two training conditions were not statistically significant (Table 12). In this regard, it is noteworthy that acquisition with right limbs was considerably more rapid when previous training was with a DR than with a non-operated left limb (Figure 9).

T13-L6 dorsal rhizotomy; training with DR limbs continued for a maximum of 45 sessions. It was conceivable that, if training was extended beyond the 15 session limit, animals might have acquired the sustained response with DR limbs, even when there had not been previous postoperative training with contralateral sensate limbs. Performance with DR limbs under such training circumstances was examined, therefore, when the training limit was extended to 45 sessions.

Animals did not achieve criteria with DR limbs, even after 45 sessions of training. Figure 11 shows that electrode time in fluid and number of insertions per session remained elevated throughout training, regardless of whether animals were trained preoperatively (11A) or received initial training postoperatively (11B). Although punishment was escaped with a rapid series of non-sustained movements, it was not avoided with sustained alterations in limb posi-

Table 12

Summary of Two-Way ANOVA Postoperative Acquisition with Right Limbs (Not Preop Trained): Sessions to Criteria Right vs. Left (DR) Limb Trained First and Sessions to Different Criteria Within Animals

Source of Variation	SS	df	MS	*F*	*p*
Between Subjects					
Right vs. left (DR) limb first	16.19	1	16.19	5.00	N.S.
Error	25.88	8	3.24		
Within Subjects					
Criteria (10% vs. 25% vs. 50% vs. 75%)	17.16	3	5.72	11.00	<.01
Interaction	5.29	3	1.76	3.38	<.05
Error	12.38	24	0.52		

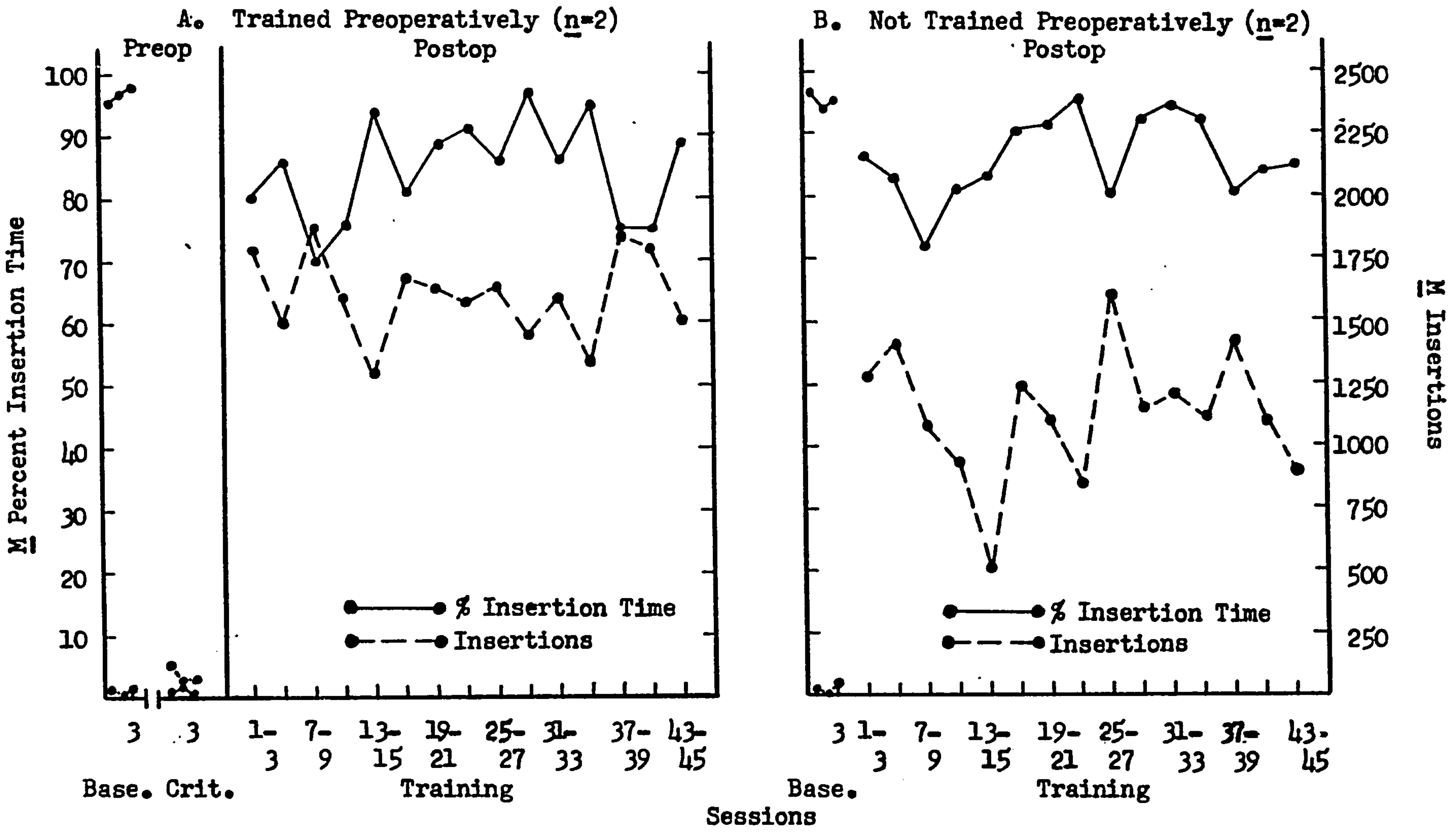


Figure 11. Performance with DR limbs in the absence of postoperative training with contralateral sensate limbs, when training continued for 45 sessions: group mean percent insertion time or insertions per session block.

Base.: Performance before conditioning initiated.

Crit.: Performance during the three conditioning sessions that preceded dorsal rhizotomy (T13-L6).

tion.

It might have been the case that prolonged unsuccessful training had an effect on the animal such that the response could no longer be acquired with either limb, treated or intact. To explore this possibility, relative performance with right limbs was examined after 15 or 45 unsuccessful sessions of training with DR limbs. Following 45 sessions of training with DR limbs, both average insertion time for the first session of training (Figure 12) and number of training sessions required to achieve the 10% criterion (Figure 13) with right limbs were significantly greater than when DR limbs had been trained for only 15 sessions (insertion time difference; $\underline{t}$ (5) = 6.59, $\underline{p} < .01$; difference in sessions to the 10% criterion; $\underline{t}$ (5) = 3.6, $\underline{p} < .05$). Although unsuccessful training with DR limbs impeded subsequent performance with right (sensate) limbs, particularly during initial training, all animals performed at final criterion with right limbs within an average of three sessions.

T11-S4 dorsal rhizotomy; training with DR limbs continued for a maximum of 15 sessions. Figure 14 depicts relative performance (mean session to successive criteria) with DR limbs when animals were trained for the first time after T13-L6 or T11-S4 dorsal rhizotomy. In both cases, contralateral sensate limbs were trained first. All animals acquired the sustained response but acquisition was slower, on the average, after T11-S4 than after T13-L6 dorsal rhizotomy. Performance differences between the two groups at any criterion, however, did not reach statistical signifi-

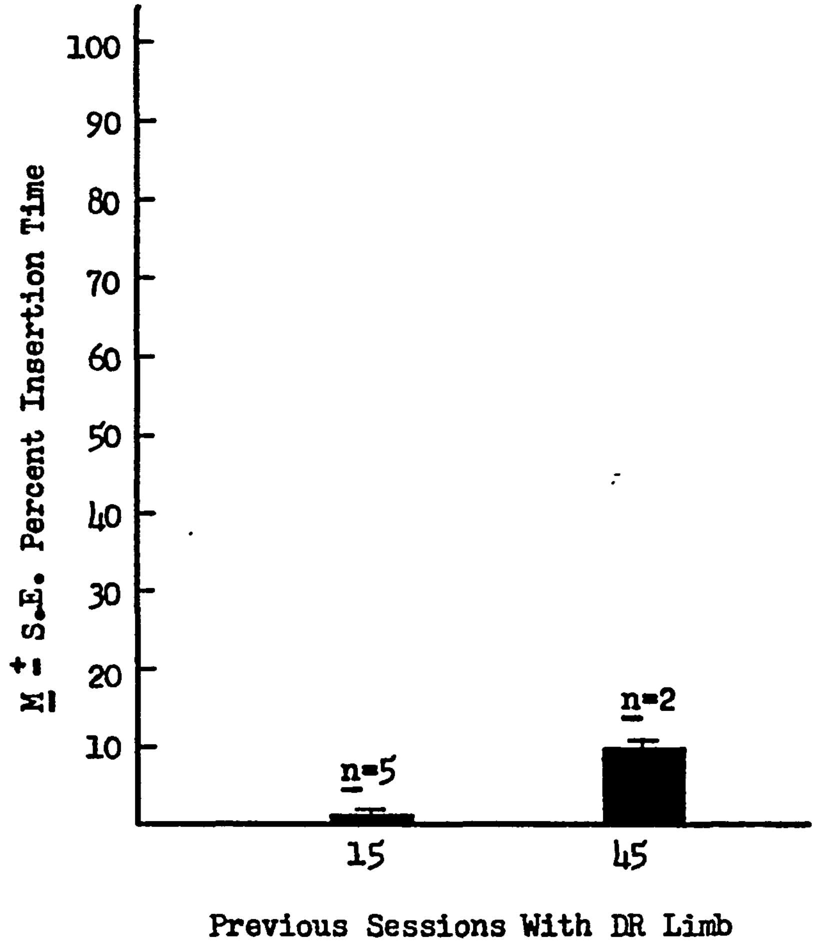


Figure 12. Group mean percent insertion time for right limbs (no preop training) during first training session following unsuccessful training with contralateral DR limbs (T13-L6).

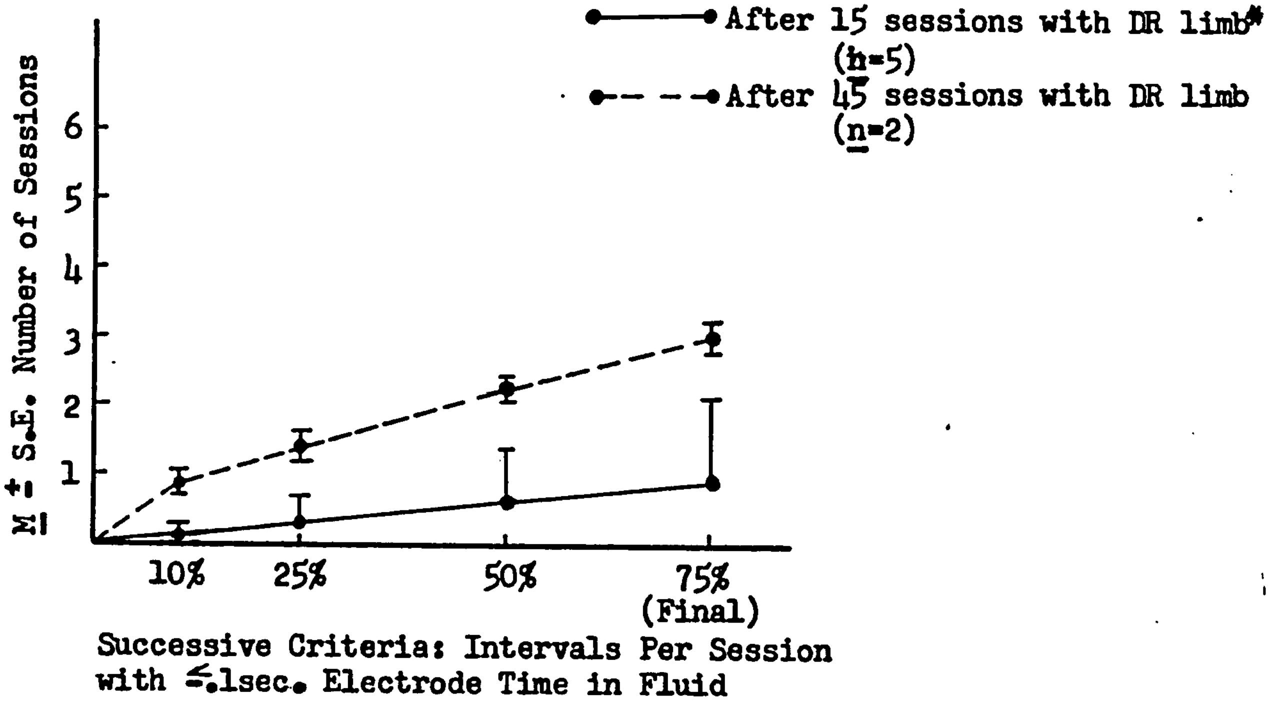


Figure 13. Melton curves depicting performance with right limbs initially trained after 15 or 45 unsuccessful sessions of training with contralateral DR (T13-L6) limbs: group mean sessions to successive criteria.

*Data also appear in Figure 10.

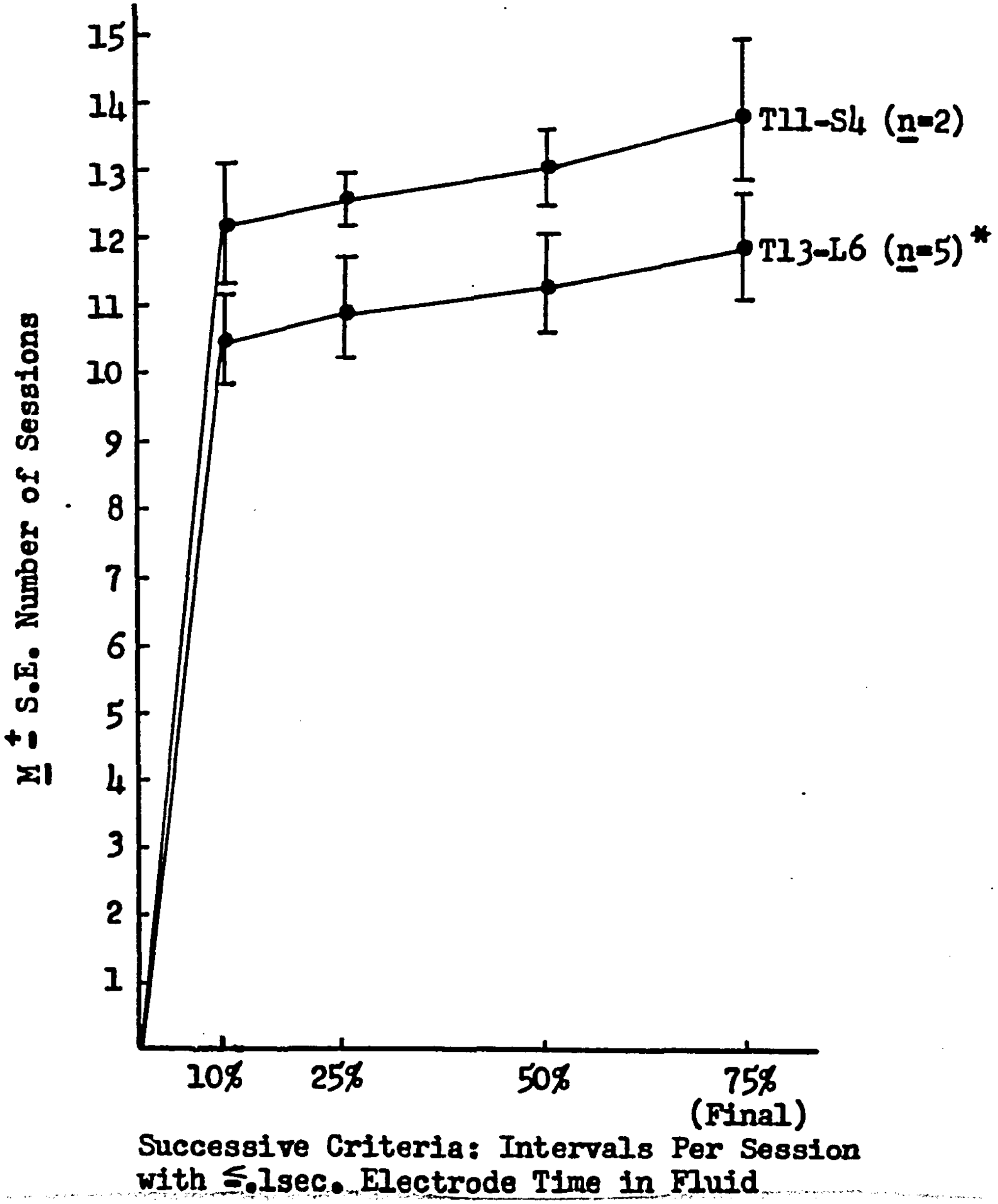


Figure 14. Melton curves depicting acquisition with DR left limbs following T13-L6 or T11-S4 dorsal rhizotomy. [In all cases, training initiated after surgery, and right (sensate) limbs trained first.]

*Data also appear in Figure 5.

cance (independent groups t-tests). In addition, the topography of the avoidance response was the same after either T13-L6 or T11-S4 rhizotomy.

Yoked Control Animals

During baseline sessions, yoked control animals, like their experimental partners, kept monitoring electrodes submerged in the electrolyte solution. In fact, there were no significant experimental:yoked control differences in mean insertion time per baseline session with sensate or DR limbs (Table 13) (independent groups t-tests).

The relative performance of experimental:yoked control pairs, before and after dorsal rhizotomy, was examined for the sessions in which experimental animals achieved criterion. Figure 15 depicts average insertion time differences between experimental and yoked control animals under different conditions of training. Since the preoperative performance of groups trained with right vs. left limbs first did not differ substantially during criterion sessions, their insertion times are not depicted separately.

During criterion sessions, experimental animals maintained monitoring electrodes above the fluid surface; their yoked partners, on the other hand, kept monitoring electrodes submerged. Insertion time differences between experimental and yoked control animals were significant under all conditions of training with both hind limbs (independent groups t-tests; in all cases $p < .001$).

Figure 16 shows the relative performance (percent insertion time per session) of typical experimental:yoked control pairs

Table 13

Mean and Standard Error Percent Insertion Time Per Session for Experimental Animals and Their Yoked Controls Before Training

Group	n	Limb Right	 Left
Experimental			
Preop	5	94.6 ± 2.2	95.7 ± 1.9
Postop: not preop trained	4	91.2 ± 3.1	96.4 ± 1.7*
Yoked Control			
Preop	5	95.2 ± 0.6	95.4 ± 2.1
Postop: not preop trained	4	93.5 ± 2.1	95.9 ± 0.8*

*DR

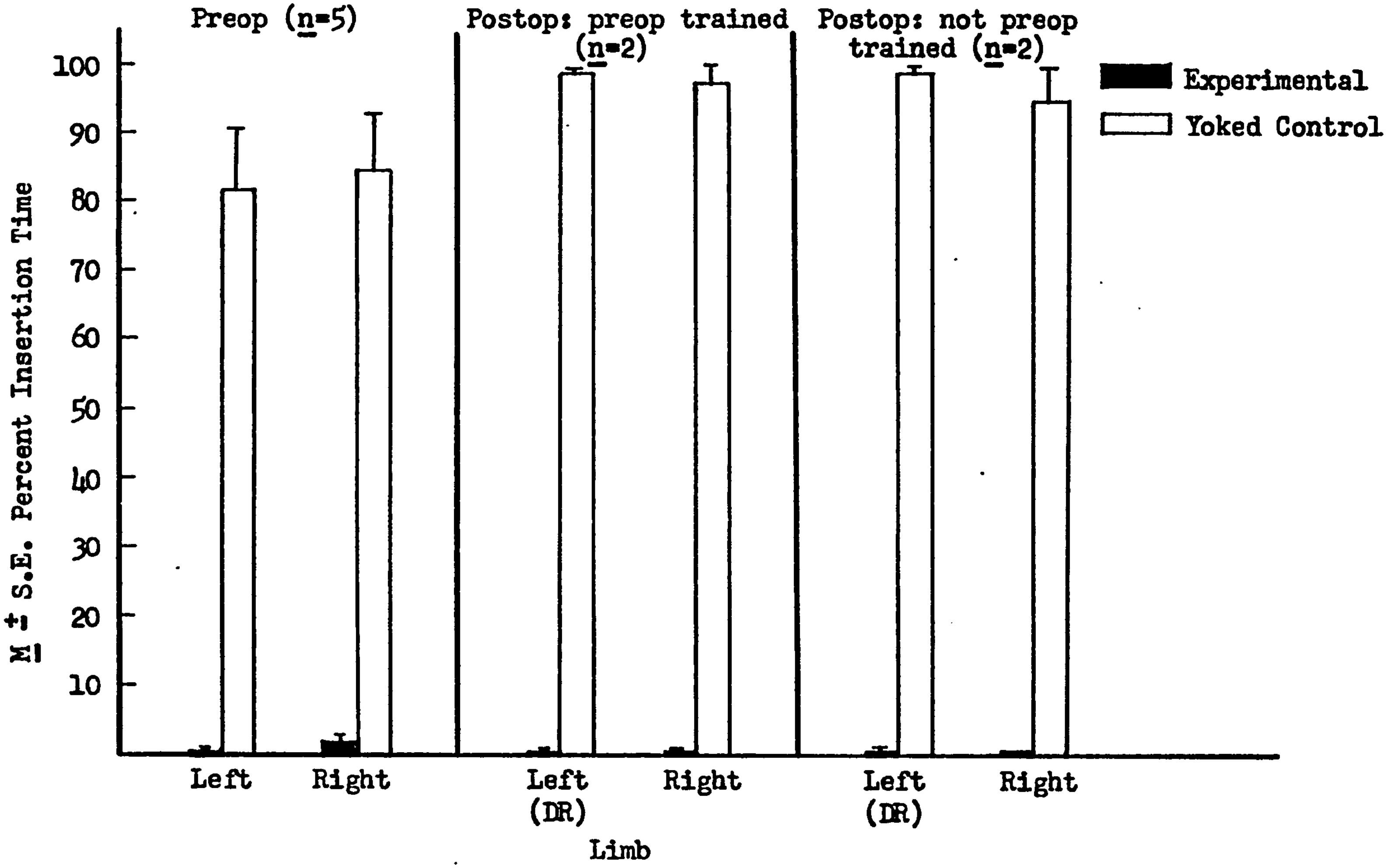


Figure 15. Group mean percent insertion time per session for experimental and yoked control animals during the three sessions in which final criterion achieved by experimental animals. [Only experimental animals which achieved final criterion with DR limbs are included. Order of postoperative training, right (sensate) followed by left (DR) limb.]

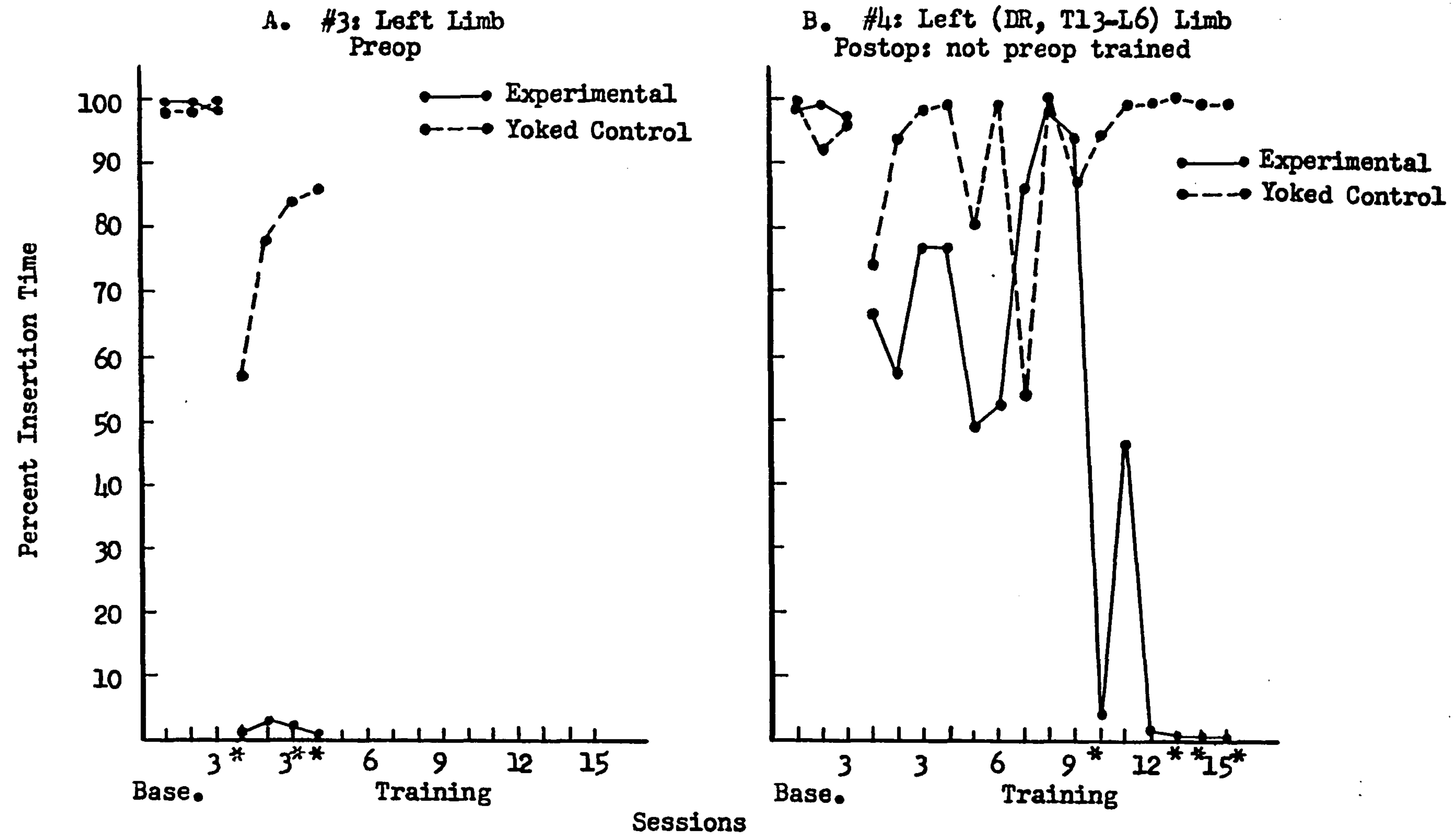


Figure 16. Typical experimental:yoked control performance across training with non-operated and DR limbs.

Base.: Performance before conditioning initiated.
*≥75% 20 sec. intervals with ≤.1sec. in fluid

across sessions of training, before (16A) and after (16B) dorsal rhizotomy. Although insertion times were equally high for experimental and yoked control animals during baseline sessions, their performance diverged as training progressed; experimental animals came to maintain monitoring electrodes above the fluid surface, while yoked controls submerged monitoring electrodes for progressively greater periods of time.

The postoperative performance of experimental:yoked control pairs also was examined when experimental animals that had yoked partners did not achieve criterion with DR limbs (Figure 17). Regardless of whether or not there had been preoperative training, the average insertion time of experimental animals during the final three sessions of training with DR limbs was less than the average insertion time of yoked animals, although differences were not significant (independent groups *t*-tests). Decreased insertion times for experimental animals reflected the fact that, throughout training, they escaped shock. After a number of sessions of noncontingent shock, yoked control animals, on the other hand, left monitoring electrodes submerged and only occasionally removed them from the fluid.

It should be noted from Figure 17 that experimental:yoked control insertion time differences with right limbs during criterion sessions were in the expected direction (independent groups *t*-tests, $p < .001$), even though right limbs, in this instance, were tested following 15 punishing sessions of training with DR limbs.

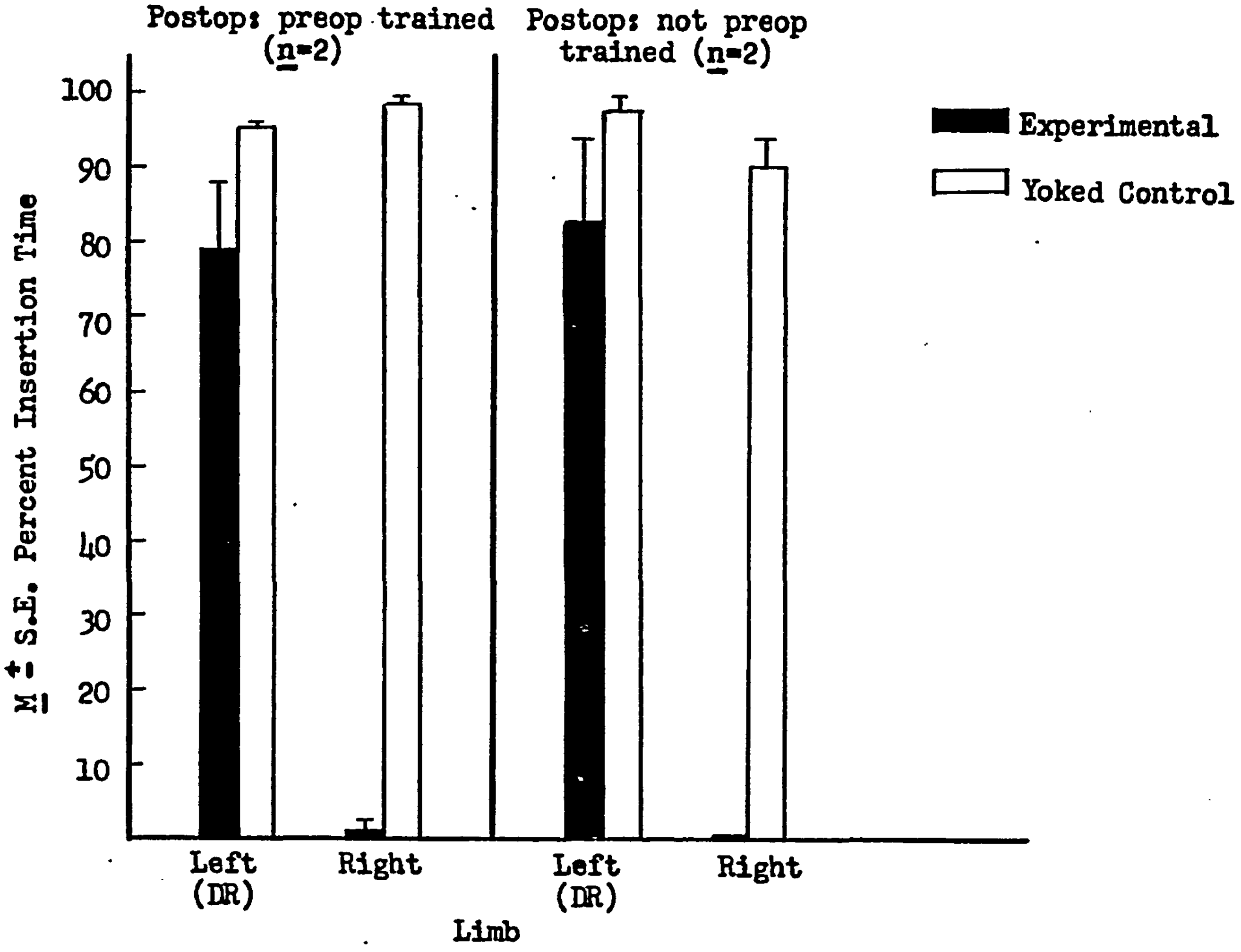


Figure 17. Postoperative performance of experimental:yoked control pairs, when experimental animals did not reach final criterion with DR limbs: DR limbs, mean percent insertion time during the last three sessions of training; sensate limbs, mean percent insertion time during criterion sessions. [Order of postoperative training, left (DR) followed by right (sensate) limb.]

Discussion

The aim of the present study was to determine whether rats would acquire a sustained response in the absence of somatosensory and visual feedback concerning position and movement of responding body parts. This acquisition was not observed except when sensate limbs were trained postoperatively before DR limbs. Only then did animals acquire the sustained response with DR limbs. In the following discussion, an attempt will be made to explain the failure of acquisition with DR limbs and to propose the mechanisms by which acquisition occurred when sensate limbs were trained first. Next, the finding that non-operated animals acquired the sustained response more rapidly with the left than right limb will be discussed within the theoretical framework of functional asymmetry of the two cerebral hemispheres.

Two questions must be addressed before an interpretation can be placed upon the major findings of the present study. The questions are: was the dorsal rhizotomy in fact complete, and was the avoidance response in fact sustained. In regard to the completeness of rhizotomy, histological verification of the lesion was not feasible because intact rootlets might have been detached from spinal cord during the course of necropsy. Also, since no single tract in rat spinal cord transmits all afferent information from one hind limb alone, the presence of intact fibers in such a tract could not have been used as a criterion for incomplete dorsal rhizotomy. However, gross post-mortem examination of the spinal cords indicated that the appropriate dorsal roots were severed completely in all animals.

Completeness of lesion was also suggested by the fact that the sensori-motor effects of hind limb dorsal rhizotomy observed in the present study are in accord with the observations of previous investigators (Jankowska, 1959; Lombard, Nashold, Albe-Fessard, Salman & Sakr, 1979). Of course, this reasoning is valid only to the extent that lesions were complete in the earlier studies.

As far as the temporal characteristics of the avoidance response in DR and sensate limbs, electromyographic recordings in responding muscles surely would have indicated the presence of small adjustments which were not detectable to the naked eye. However, for the purposes of the present study, a response was considered sustained when the limb was maintained above the fluid surface and drift in limb position could not be detected with the naked eye. When defined in this way, there can be no doubt that responses were truly sustained. Even though animals could have avoided shock by continually changing the position of the limb, as long as the monitoring electrode was above the fluid surface, this was not observed. The electrode was maintained in a specific position close to the fluid surface and even the smallest amount of drift in limb position would have resulted in insertion of the monitoring electrode. These considerations lead to the conclusion that the response was in fact sustained.

Failure of Acquisition When DR Limb Was Trained Before Sensate Limb

For conditioning to be successful, there is both an information processing requirement and a performance requirement; the response requirement must be determined by the animal, and the animal must be able to execute the response. When there was failure of acquisition with DR limbs, this probably reflected an inability of animals to determine the response requirement on the basis of available feedback, central and/or residual peripheral, rather than an inability to execute the sustained response. This was indicated by the fact that when animals could obtain information regarding the response requirement via postoperative training with the contralateral sensate limb, acquisition with DR limbs ensued. This finding of course points to the importance of somatosensory and/or visual feedback concerning movement for the information processing rather than the performance requirements of the sustained avoidance task.

Any explanation for failure of acquisition involving a supposition that animals could not perform the sustained response does not apply. One such explanation might have been that dorsal rhizotomy resulted in loss of facilitation of alpha motoneurons, rendering them incapable of discharging effectively. In this regard, however, it has been demonstrated that the excitability of the efferent part of the reflex arc is not diminished after dorsal rhizotomy (Lassek, 1953a; Teasdall & Stavraky, 1953). A second explanation, that extensor hypertonus in distal musculature of DR limbs prevented execution of the sustained response, again does not apply. Animals easily removed DR limbs from solution via contraction of proximal flexor muscles (e.g., pectineus muscle) which resulted in flexion of the hip and adduction of the limb. This same response has also been used by myelencephalic (Peters & Wirth, 1976) and spinal (Farel & Buerger, 1972) frogs to solve the problem embodied in the Horridge paradigm.

It should be mentioned that, even if DR limbs were tied so that escape was accomplished by flexion of the limb, sustained responses still were not acquired, unless the contralateral sensate limb was trained first (pilot data).

Since postoperative training with the contralateral sensate limb apparently informed animals of the response requirement, it was surprising that preoperative training, by itself, did not serve the same function. Perhaps the amount of preoperative training given was not sufficient for retention of the sustained response requirement postoperatively. This view is supported by the fact that, even in sensate limbs, preoperative:postoperative "savings" averaged only fifty percent (Figure 9).

If animals had undergone some critical amount of overtraining preoperatively, postoperative retention of the response requirement might have been sufficient to insure performance with the DR limb. It is noteworthy that the amount of preoperative training given was not without effect on postoperative performance. When animals were trained preoperatively and then with the sensate limb first postoperatively, acquisition with the DR limb occurred more rapidly than when only the latter condition prevailed. The present findings indicate that the success or failure of acquisition with DR limbs was not necessarily related to the number of previous training sessions with sensate limbs, given only that such training had occurred. Rather, all that was required for acquisition with DR limbs was that one previous training experience (to criterion) with a sensate limb be recent. On the other hand, once this condition was satisfied, rate of acquisition with DR limbs varied directly with number of previous training sessions with sensate limbs. It is possible, of course, that, when previous training with a sensate limb is not recent, the success or failure of acquisition with DR limbs is related to the number of previous training sessions with sensate limbs. This cannot be determined from the results of the present study, since preoperative training was not extended beyond attainment of criterion and this many sessions were inadequate for postoperative performance with DR limbs.

We considered the possible interpretation that, when criterion was not achieved with DR limbs, the higher insertion rate by animals that were trained preoperatively than by animals that received initial training after surgery (Figure 6) represented a "savings" from preoperative training. This "savings" might have involved the phasic:escape component as opposed to the tonic:avoidance component of the response. This seemed unlikely, however, since the number of insertions by animals that were initially trained postoperatively was often as high as by animals that were trained before surgery, and the topography of the escape response was the same in both groups.

Several explanations for failure of acquisition with DR limbs have been ruled out by the results of the present study. The possibility that there was insufficient training with DR limbs was excluded by the fact that performance did not improve when training was extended from 15 to 45 sessions. Another possibility that failure of acquisition with DR limbs reflected a nonspecific effect of surgery, such as spinal shock or edema, was ruled out since all animals performed successfully with contralateral sensate limbs after surgery. Still another explanation was that animals developed "learned helplessness" (Seligman & Maier, 1967) after a few sessions of unsuccessful training with DR limbs. Recent evidence indicates, however, that "learned helplessness" diminishes within 48 hrs. (Weiss & Glazer, 1975; Weiss, Stone & Harrel, 1970). Since training sessions were separated by 48 hrs. in the present study, "learned helplessness" was an unlikely explanation for poor performance with DR limbs. Furthermore, it cannot be argued that a general cognitive deficit developed as a result of many punishing sessions of training with the DR limb since animals easily acquired the sustained response with the contralateral sensate limb immediately thereafter.

Another possibility, that failure of acquisition with DR limbs reflected insufficient recovery from the general effects of surgery, is also unlikely. The four week recovery period allowed in the present study was sufficient for asymptotic recovery of motor function in the free situation. In addition, there were animals that were trained with DR limbs for 45 sessions (extending 16 weeks into the postoperative period), and even these did not acquire the response. In those cases when animals acquired the response with the DR limb, training was initiated within five weeks and was completed within nine weeks of surgery.

A further point is that attainment of criterion with DR limbs under specified training circumstances precluded the possibility that failure of acquisition, when it occurred, was due to training parameters which were inappropriate for conditioning. Such parameters as shock-frequency and duration, the length of training sessions and the intersession interval were standarized for all groups of animals.

The finding that a sustained response was not acquired with a DR limb, unless the contralateral sensate limb was trained first, should be placed in perspective. In this regard, all previous research concerned with movement acquisition after dorsal rhizotomy has indicated that central feedback and/or putative residual peripheral feedback concerning limb movement can substitute for somatosensory feedback from the responding limb in mediating response acquisition. The findings of the present study are thus the first to indicate that feedback alleged to survive dorsal rhizotomy has its limitations. Whatever information may have been available through central feedback pathways, or ventral roots, or movement produced changes in non-deafferented body parts (e.g., vibration, changes in the visual field, etc.) was not sufficient to mediate acquisition of the sustained response. This indicates that, at least in terms of sustained responses, an explanation of motor learning which stresses the necessity of somatosensory and/or visual feedback concerning movement in responding body parts applies (e .g., Adams, 1971). This is true even though knowledge of results, provided by the reinforcement contingencies, and central monitoring of efference may be sufficient for the acquisition of discrete responses (Schmidt, 1975). Of course, the generality of the present findings must be determined, since they may be specific for the species, limb and task used in the present study.

It should be emphasized that the present study is one of the first to investigate response acquisition in rats after dorsal rhizotomy, in the absence of visual feedback. It was therefore necessary to establish that some response, other than the one tested, could be acquired with a DR limb. This was indicated by the observation that, when rats were required to remove the monitoring electrode from solution within four seconds of an exteroceptive stimulus (click that could not be response-terminated) to avoid shock, a discrete response was acquired (pilot data).

Acquisition with DR Limbs When Contralateral Sensate Limb Was Trained First

It was important to determine whether attainment of criterion with DR limbs reflected learning or was due to sensitization. If sustained changes in limb position could be attributed to some effect of repeated shock that was independent of the shock:limb-position contingency, then the results of the present study would have no significance for theories concerned with the role of peripheral feedback in movement acquisition.

It is unlikely that sensitization was operative, for two reasons: animals in some experimental groups did not develop sustained changes in limb position in spite of the fact that they were exposed to considerable amounts of shock, and yoked controls, that received the same pattern and intensity of shock as their experimental partners, did not maintain monitoring electrodes above the fluid surface.

It should be pointed out that the use of yoked animals as a control for sensitization has been criticized (Church, 1963, 1964, 1975; Church & Getty, 1972; Church & Lerner, 1976). Church and Lerner (1976) have posited that insertion time differences between experimental and yoked control animals might reflect differences in reactivity to shock of the two animals. However, they have not explained why animals assigned to yoked control groups should consistently be less sensitive to shock. A large number of yoked controls have been tested in this paradigm by many investigators over the years and it is improbable that, in all cases, experimental animals happened to be more sensitive to shock than their yoked controls. Evidence for this can be found in the fact that, when individual subjects served both as experimental and yoked control animals in successive phases of an experiment, typical insertion time differences between experimental animals and their yoked controls were not altered (Chopin & Buerger, 1975). In addition, minimum effective shock level for yoked controls in the present study was approximately the same as for their experimental partners, and both animals continued to exhibit the same behavioral response to shock throughout training.

A further criticism of the use of yoked controls in the Horridge task has been that the design of the paradigm insures greater insertion times by yoked control than experimental animals (Horridge, 1962; Church & Lerner, 1976). This occurs because experimental animals inevitably receive shock upon insertion of their monitoring electrode into the fluid, while shock delivery to yoked controls, after they have made an insertion, must await an insertion by their experimental partners. In this regard, Church and Lerner have constructed a statistical model which predicts that, even in the absence of associative learning in experimental animals, yoked controls can spend 40% more time per session with monitoring electrodes submerged than their experimental partners. In the present study, the differences in performance between an experimental animal and its yoked partner did not remain constant across training, as would be expected from the Church and Lerner model, but rather increased as a function of training: yoked animals spent progressively more time with monitoring electrodes submerged, while their experimental partners came to maintain monitoring electrodes above the fluid surface. During criterion sessions, the difference in percent insertion time between the two groups of animals was approximately 90% (Figure 15) whereas, when experimental animals did not acquire the sustained response, difference in percent insertion time during the last three sessions of training was only 15% (Figure 17), far below the 40% difference predicted by the statistical model.

There is other evidence which indicates that successful performance in the Horridge paradigm is not due to sensitization. When periods of unavoidable shock have preceded training, for example, acquisition of the sustained response has been hindered, rather than accelerated (Chopin & Bennet, 1975).

Although early work with insects indicated that peripheral factors, such as alterations in the excitability of muscle during training, explained acquisition of the sustained avoidance response (Eisenstein & Cohen, 1965), this was not the case with amphibians and rodents. The sustained response was neither acquired by spinal frogs after sciatic nerve section (Farel & Buerger, 1972) nor by spinal rats after spinal tissue within the L2-S2 segments was destroyed (Chopin & Kerrigan, cited in Buerger & Chopin, 1976; Fennessy-Fields, 1973). These conflicting data may indicate significant species differences in the mechanisms underlying sustained avoidance. Even if this is the case, rats were used in the present study, so that it is safe to assume that peripheral factors did not mediate acquisition.

Finally, with regard to the present study, the fact that there was retention of the acquired response suggests that an associative process was operative (Gormezano, 1975). In this regard, the sustained response was retained with both sensate and DR limbs for at least three criterion sessions (each separated by 48 hrs.) and some preoperative:postoperative "savings" occurred in sensate limbs after a one month retention interval. This degree of retention certainly would not fit a description of sensitization.

Since it is likely that the sustained avoidance response reflected learning rather than sensitization, the processes which may have mediated acquisition with DR limbs will be discussed. In order to do this, certain factors must be taken into consideration. First, acquisition with DR limbs occurred only when there had been previous postoperative training with the contralateral sensate limb. Second, the topography of the sustained response was different in DR and sensate limbs. Together, these two facts indicate that for a sustained response to be acquired with a DR limb, the animal had to be informed of the general class of response (as opposed to the particular pattern of muscular contraction) that was required, and that this could be accomplished via previous training with a sensate limb. A third point is that even after animals were informed of the response requirement in this way, the performance requirement of the sustained avoidance task had to be satisfied. Therefore, acquisition with DR limbs, when it occurred, must have involved the development of a mechanism for executing the sustained response in the absence of peripheral topographic feedback. The slow rate of acquisition with DR limbs[5] indicated that acquisition of such a response mechanism was not easily accomplished. On the average, animals required four to five times as many training sessions to attain some minimal level of performance with DR than sensate limbs.

After dorsal rhizotomy, execution of the sustained response might have been controlled open-loop by central programming or closed-loop by a combination of central programming and residual peripheral feedback concerning movement of the limb. One can only speculate, however, as to which of these alternatives was operative and would account for the topography and/or temporal characteristics of the response.

It is probable that the topography of the response in DR limbs was controlled open-loop by execution of a motor program. Rapid phasic movements involving proximal musculature are believed to be preprogrammed and executed in open-loop fashion via cerebellar mechanisms (Kornhuber, 1974; Stetson & Bouman, 1935; Stetson & McGill, 1923) even when peripheral feedback is present. This view is bolstered by reports that large muscles which operate on proximal joints contain relatively few spindles per unit volume compared to small muscles which operate on distal joints (Barker, 1974).

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[5] The slow rate of acquisition probably could not be explained by insufficient recovery from surgery. When animals were allowed to recover for two months before postoperative training was initiated, the nature of the deficit in DR limbs was not altered (pilot observations).

In regard to the temporal characteristics of the sustained response, it is possible that they also were controlled open-loop by execution of a motor program which specified the protracted duration of the response. It is unlikely, however, that such a program was present in central nervous system before dorsal rhizotomy. This can be deduced from the fact that tonic changes in musculature involve somatosensory feedback from responding body parts, when such feedback is available (Granit & Burke, 1973). Even if the sustained response involved central programming before surgery, therefore, it must have been executed in closed-loop rather than open-loop fashion. This view, that somatosensory feedback from the limb was an integral part of preoperative performance, is upheld by the fact that, in the present study, preoperatively acquired responses were lost and could not be reacquired after dorsal rhizotomy, unless contralateral sensate limbs were trained first. On the basis of these facts, it can be assumed that postoperative acquisition of a mechanism for executing the sustained response did not involve an association between execution of an already-acquired motor program, which could control both the initial contraction and "hold" components of the response, and reinforcement. Rather, if the response was executed in open-loop fashion after surgery, postoperative acquisition must have involved the acquisition of a new motor program, or an elaboration of an already-existing program for a rapid phasic response involving proximal musculature, which specified muscular contraction for a protracted period of time.

For the purposes of the present discussion, the motor program will be defined as an organized cognitive structure which can produce sequential patterns of efferent commands and thus determine spatio-temporal patterns of muscular contraction. Acquisition of such a motor program, which can produce a sustained change in limb position, might have occurred with or without the help of any residual peripheral cues concerning movement in DR limbs. In the absence of peripheral cues, it is conceivable that the motor program was gradually shaped by the reinforcement contingencies of the training situation. For this to have occurred, central nervous system whould have had to monitor the patterning of efference to a specific body part and specific patterns of efferent discharge would have had to produce a specific delay in subsequent punishment. This mechanism for acquisition of a motor program is a distinct possibility in that central feedback mechanisms can probably monitor efference and physical factors (e.g., gravity, body position, weight of the limb) which influences passive return of the limb to resting position, and thus controlled delay in subsequent punishment, remained relatively constant throughout training.

Residual peripheral cues concerning limb movement must be considered for their role in performance of the sustained response with DR limbs. In this regard, such cues could have served one of two functions: they may have been involved in the acquisition of the motor program which, once established, could control the topography and temporal characteristics of the response without information from the periphery, or they may have been sufficient for closed-loop execution of the response. In the latter case, central programming could have specified a phasic movement with peripheral feedback triggering additional output necessary for a sustained change in limb position. Since proprioceptive feedback has been demonstrated to have an effect upon the output of pyramidal tract neurons within 25 msec. of a peripheral disturbance (Evarts, 1974), it is conceivable that a sustained response was executed in this way. It is puzzling, however, why residual peripheral cues (and cues provided by central feedback for that matter) should be ineffective in the absence of postoperative training with the contralateral sensate limb. It would seem that, if such cues are operative, they facilitate completion of the performance requirement but not the information processing requirement of the sustained avoidance task.

Several sources of residual peripheral afference are possible, although the likelihood of any particular one being involved in the sustained response varies. Proprioceptive feedback from the DR limb might have been provided by intact afferents which entered central nervous system through ventral roots. This is unlikely, however, since ventral root afferents are not believed to mediate somatic sensation in the absence of their corresponding dorsal roots.

Feedback concerning limb movement also could have been provided by afferents from body parts contiguous to the DR limb, even though all muscles actually involved in such movement were deafferented by T13-L6 dorsal rhizotomy (Hebel & Stromberg, 1976). The ballistic response in DR limbs must have created stretch in body parts surrounding the limb, thereby producing movement-related afferent volleys. When dorsal rhizotomy included these surrounding body parts, however, animals still acquired the sustained response with DR limbs if contralateral sensate limbs were trained first. Of course, this observation does not preclude the possibility that cues from areas contiguous to those denervated by either the original (T13-L6) or the extended (T11-S4) dorsal rhizotomy were involved in performance with the DR limb.

Proprioceptive feedback from body parts not affected by movement of the DR limb also might have been involved in postoperative performance. If it is assumed that nervous system emitted parallel efferent commands to sensate and non-sensate musculature, feedback from sensate musculature could have been used to monitor passive movement in the non-sensate body part. This could have occurred in the present study only if, following parallel commands, a constant temporal relationship existed between relaxation of musculature in the sensate body part and passive return of the DR limb to resting position. If this occurred and if this relationship was determined by the animal, cues from sensate musculature could have signalled additional efference to the DR limb.

It is evident from this discussion that the peripheral cues that may be available to guide movement after dorsal rhizotomy of a particular body part are numerous. It is unlikely, therefore, that peripheral mechanisms in movement can ever be completely obviated. We have shown, however, that after dorsal rhizotomy, when punishment is contingent upon the position of the affected body part and visual feedback is prevented, the combination of all possible residual peripheral and/or central sources of feedback are not sufficient to inform nervous system that a sustained response is required. Rather, initial determination of the response requirement depends upon training with a sensate limb.

Performance Differences Between Right and Left Limbs of Non-Operated Animals

Non-operated animals consistently acquired the sustained avoidance response more rapidly with left than right limbs. This finding denoted the existence of an asymmetry in rodent nervous system. This was not altogether surprising, since a large body of recent evidence has indicated that neuroanatomical, neurochemical and functional asymmetries exist in the central nervous system of a variety of non-human species. For example, hemispheric asymmetries have been reported in cortical fissure patterns in cats (Webster & Webster, 1975) and in the deoxyglucose metabolism of frontal cortex and hippocampus in rats (Glick, Meibach, Cox & Maayani, 1979). Paw-hand preferences have been reported to exist in monkeys (Warren, Abplanalp & Warren, 1967), cats (Cole, 1955; Warren, 1958) and rats (Tsai & Maurer, 1930). Spatial preferences in rats in both a bar-pressing situation (Glick & Jerussi, 1974) and in a T-maze (Glick, Zimmerberg & Jerussi, 1977; Zimmerberg, Glick & Jerussi, 1974) have been demonstrated to reflect dopaminergic asymmetries in nigrostriatal pathways. Recent evidence has also suggested that "affective" processes may be lateralized in rat brain. For example, self-stimulation thresholds are lower in the lateral hypothalamus contralateral to a rat's preferred direction of rotation (as judged by nocturnal circling behavior; Glick, Weaver & Meibach, 1980) and the effects of early handling on emotionality in rats have been demonstrated to be mediated by the right hemisphere (Denenberg, Garbanati, Sherman, Yutzey & Kaplan, 1978).

The finding of a left limb superiority in the Horridge task is consonant with the view that the right hemisphere is specialized for the processing of spatial information. If right hemisphere specialization for spatial tasks translates into an increased efficiency for monitoring the position of the left than the right hind limb in space, then acquisition of the sustained response would be expected to occur more rapidly on the left than the right side. However, two points should be considered when evaluating the left limb superiority. First, with the small number of subjects in each group (five trained with the left limb first, five with the right first), no result, not even our finding of 100% left limb superiority, will satisfy the requirement for statistical significance (Sign Test for Matched Pairs) when each group is considered separately. Second, the right-left difference in acquisition was more robust when right limbs had been trained subsequent to, rather than before, left limbs. There was thus negative transfer of training from left to right limbs (but not the converse) which confounded any laterality effect. It is important, therefore, that this study be replicated with larger numbers of subjects per group.

After these findings have been confirmed, their significance in terms of lateralization of function in non-human species should be further explored. If such lateralization exists for the processing of spatial information in rats, a similar asymmetry should be found in forelimb acquisition and in the acquisition of tasks which involve accurate localization of body parts in space. It would also be of interest to determine whether the behavioral asymmetry is mediated by a functional asymmetry at cerebral, spinal or peripheral levels.

Summary Statement

It has been demonstrated that a sustained response is not acquired with a DR limb, when vision of the limb is precluded, unless the animal is first informed of the response requirement via recent training with a sensate limb. These findings provide information, not previously available, concerning the effects of dorsal rhizotomy on the acquisition of movement. At the same time, they indicate a distinct limitation of central feedback and residual postoperative sources of peripheral feedback (e.g., ventral root afferents) in motor control. In the absence of feedback provided by dorsal root afferents from the responding body part, central feedback and/or residual peripheral feedback cannot provide the information that is necessary for the acquisition of a sustained change in limb position.

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