

Electromyographic studies of neck muscles in the intact cat

II. Reflexes evoked by muscle nerve stimulation

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Summary. Short-latency reflexes were studied in the neck muscles of four alert cats following electrical stimulation of nerves supplying biventer cervicis (BC), splenius (SP) or rectus capitis posterior (RCP). Reflexes were assessed by comparing levels of EMG activity of muscles before and after each stimulus, as the cats lapped milk, licked their paws or walked on a treadmill. When BC or SP nerves were stimulated at 1.5–4 times threshold (T) for their motor axons, no short-latency heteronymous reflexes could be identified in most neck muscles. However, stimulation of RCP nerves produced inhibitory effects as early as 3–4 ms in the ipsilateral BC, CM, and SP muscles and 6 ms in contralateral BC. At stimulus strengths above 4xT, a more complex pattern of inhibitory or excitatory effects was observed in CM, SP and the intervertebral muscle spinalis dorsi. The reflex effects were attenuated or abolished by partial or complete C1 dorsal rhizotomy (2 cats). Cervicocollic reflex data may need to be reevaluated to consider the possible effects of disinhibition rather than excitation in short-latency reflex pathways.

Key words: Reflexes – Electromyography – Nuchal afferents – Neck muscles – Cat

Introduction

Since the time of Sherrington (1906), segmental connections from muscle afferents have been regarded as an important part of the circuitry responsible for motor control. Perhaps the most intensively studied of these connections is that from spindle afferent fibers onto homonymous motoneurons. In the limbs, where most studies of motor control have been conducted, this monosynap-

tic pathway subserves a “stretch reflex” that can be readily demonstrated under a variety of experimental conditions and anesthetic states. However, in neck muscles, it has not proven so easy to elicit a similar monosynaptic reflex. Abrahams and coworkers (1975) reported that only about 1% of motoneurons serving dorsal neck extensors could be excited to fire at monosynaptic latencies when C2 or C3 dorsal roots were stimulated in the anesthetized cat. The weakness of the reflex may be a consequence of the highly restricted distribution of Ia projections from neck muscles. Spindle afferents entering the upper cervical spinal cord at one segmental level project primarily onto homonymous motoneurons of the same segment (Brink et al. 1981; Brink 1988). Further, single spindle afferents contact only a minority of homonymous motoneurons even within the same segment at which they enter the spinal cord (Keirstead and Rose 1988). This pattern is quite different from that reported in hind-limb muscles, where single spindle afferents commonly distribute terminals to most if not all homonymous motoneurons (Henneman and Mendell 1981).

The weakness of the monosynaptic reflex in the neck leads us to question the contribution of monosynaptic reflexes to the control of head movement. In the past, some investigators have been reluctant to dismiss a role for monosynaptic input from muscle spindles, because such a mechanism could plausibly explain the cervicocollic reflexes which have been repeatedly described in the decerebrate cat (Bilotto et al. 1982; Ezure et al. 1983; Peterson et al. 1985; Peterson 1988). In these reflexes, stimulation of nuchal receptors by rotation of the body in the head-fixed cat (or rotation of the head in the labyrinthectomized cat) modulates the electromyographic (EMG) activity of neck muscles according to a pattern whose dynamics resemble those of muscle spindles. Cervicocollic reflexes can still be produced after transection of the neuraxis at the level of the spino-medullary junction, so that at least part of the circuitry responsible for the reflex is in the spinal cord. Nevertheless, the monosynaptic spindle projection is not the only pathway available to subservise segmental reflex effects. Electrical sti-

Muscle abbreviations. BC – biventer cervicis; CM – complexus; OCI – obliquus capitis inferior; RCP – rectus capitis posterior; SP – splenius

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mulation of muscle nerves at strengths sufficient to recruit afferent fibers in the group II–III range is known to evoke complex polysynaptic responses in motoneurons (Anderson 1977; Brink 1988). Further, Anderson (1977) showed that stimulation of cutaneous afferents gives rise to short-latency excitation or inhibition in motoneurons of dorsal neck muscles. These segmental pathways may contribute to reflexes such as the cervicocollic reflex in ways that have yet to be explored.

In the present study, the short-latency effects evoked by stimulating neck-muscle nerves were studied in alert, freely moving cats. By monitoring EMG changes in muscles that are used during the performance of normal behaviors such as lapping, grooming or walking, reflexes could be observed as changes in the ongoing EMG activity of normally recruited muscles. In the present experiments, inhibitory rather than excitatory effects were seen in many neck muscles. Excitatory reflexes were rare and weak.

Methods

Experiments were conducted on four cats that were implanted with arrays of chronically indwelling electrodes to record EMG activity simultaneously from up to 16 neck muscles in each animal. Details of the recording electrode designs, locations and surgical procedures are provided in the companion paper (Richmond et al. 1991). In one cat, bipolar "patch" stimulating electrodes were implanted over the rostralmost compartment of biventer cervicis (BC). In the 3 later cats, electrodes were placed over BC, splenius (SP) or rectus capitis posterior (RCP) muscle nerves so that contacts were oriented parallel to the long axis of the nerve bundles as they fan toward their entry points in their respective muscles (see Table 1, in Richmond et al. 1991).

Initial experiments in this series indicated that short-latency, heteronymous inhibition was consistently evoked following low-intensity stimulation of the RCP muscle nerve, which is supplied exclusively from the C1 segment. In order to determine the relative contribution of afferent vs efferent collateral pathways to this reflex, we attempted to remove the right C1 dorsal root ganglion without damaging the underlying ventral root in two of the later cats (C4 and C6) at the time of electrode implantation. Prior to sacrifice of the cats, the effectiveness of this lesion was assessed in an acute, terminal experiment under pentobarbital anesthesia. In this experiment, an upper cervical laminectomy was performed to expose the C1 dorsal roots, and the spinal cord was bathed in a pool of mineral oil. The full range of stimuli used to evoke reflexes in the intact animal was administered through the chronically implanted electrodes on the RCP nerve on each side. Evoked potentials were recorded both from the dorsal C1 roots placed on bipolar hook electrodes and as M-waves from the previously implanted EMG electrodes.

Reflex responses were recorded on the fourth to sixth post-operative days, while the animals performed natural, repetitive movements including grooming, lapping, eating and walking on a treadmill. Single stimulus pulses were delivered at regular intervals (700 to 1200 ms) which were timed to be asynchronous with the cyclical behavior. Trains of 3–5 pulses with 3 ms interval were tried in some sites but had no greater effect than single pulses. Symmetrical, biphasic pulses (0.1 ms/phase) were delivered by a photo-isolated, constant current stimulator (Bak Electronics BPG-1 and BSI-1); intensities are expressed in multiples of the threshold for eliciting an M-wave from the muscle innervated by the nerve. For each intensity and site, we recorded 2 to 4 min of continuous analog data consisting of all available EMG signals (50–5,000 Hz bandwidth), stimulus synchronization pulses, and time-code (IRIG-B).

Simultaneous videotape recordings were used to identify periods of uninterrupted cyclical behavior and any overt movements resulting from the stimuli. Each cat was watched for behavioral signs of confusion or distress. Although muscle twitches often could be felt through the skin, cats showed no behavioral reaction to stimuli as intense as 10xT, and continued their ongoing behavior as if no stimuli were being applied.

For selected analog tape segments, the EMG signals were rectified and integrated into 1 ms bins that were digitized by a PDP-11/73 computer. The computer collected peristimulus records from all EMG channels (usually spanning from 20 ms before to 50 ms after each of 100 stimulus presentations). In addition, 1–3 channels of continuous EMG data were used to identify the phase of the cyclical behavior during which each stimulus occurred (methods described in detail in Richmond et al. 1991). Most of the neck muscles and their reflex responses showed little or no EMG modulation during the cyclical behavior. Thus, the figures have been presented as peristimulus traces in rasters that are ordered by chronology rather than by phase. At the top of each raster, there is a peristimulus histogram to show the mean level of activity for all traces in the raster. As a guideline, inhibitory effects were identified as a diminution in firing that caused more than a 50% depression in the ongoing level of EMG activity in an active muscle; excitatory effects were identified by a 50% increase in the ongoing level of EMG firing. Vertical calibration bars show the amplitude of a 1 kHz sinusoidal waveform (referred to amplifier input), also processed in this manner. The results described here are based on inspection of approximately 15,000 traces, compiled into approximately 200 rasters.

The precise determination of latency of reflex responses from these rasters is complicated by small sampling and timing uncertainties that arise with this method. The stimulus synchronization pulse is detected by the computer with one bin accuracy (0 to +1 ms) and the clocking of the bin integrators can drift one bin with respect to reflex waveforms (± 1 ms). Also, the output of the bin integrator is always one bin behind the input EMG (-1 ms). Thus, any reflex response should be interpreted with an uncertainty of -1 to $+2$ ms additional latency over that apparent in the trace (this accounts for the fact that M-waves sometimes appear to start at or even before the stimulus marker). More precise estimates of latency and reflex waveform were made by inspecting multiple, overlapped traces of unrectified EMG on an oscilloscope synchronized to the stimulus pulse itself.

Results

Effects of stimulating C2 nerves running to or through rostral BC

In the first cat, the feasibility of recording reflexes in neck muscles was explored by applying current through an electrode pair implanted over the rostralmost compartment of BC. Such stimulation would be expected to activate not only the muscle nerves serving rostral BC but also a large mixed nerve that passes through BC and supplies the muscles and skin of the pinna (Reighard and Jennings 1963). Because the stimulating electrodes were not oriented specifically over identified nerve bundles (as they were in later experiments), larger currents (up to 4 mA at 0.1 ms duration) were required to produce clear M-waves, and recruitment of nerve axons probably depended as much on the proximity of the nerves to the electrodes as it did on their axonal diameters. Further, strong stimuli may have excited a variety of muscle afferents on the dorsal surface of BC. Thus, the measure of current as a function of threshold was not as useful as it was in subsequent experiments. However, as a guide,

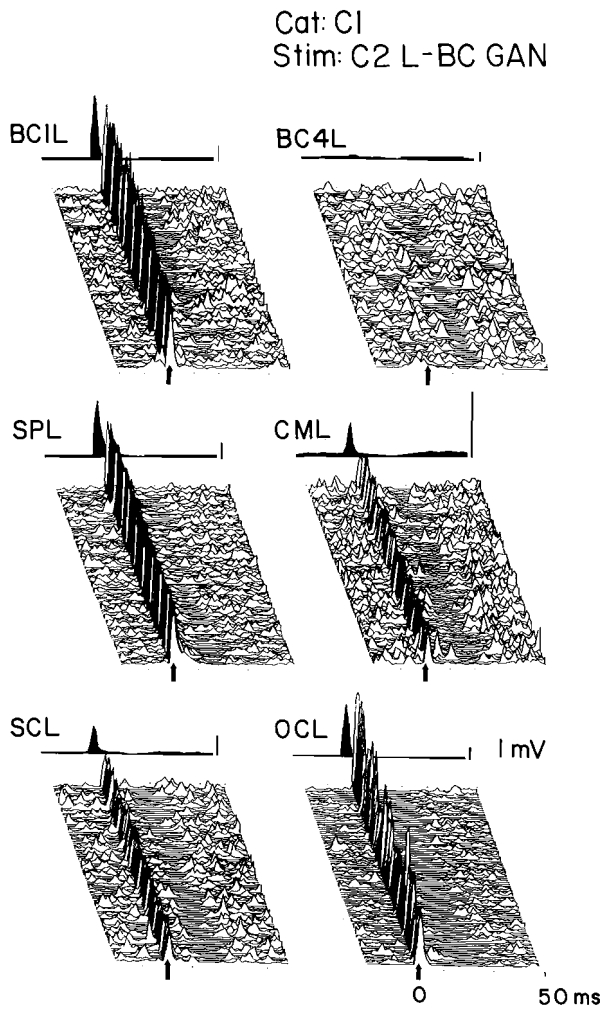


Fig. 1. Effects of stimulating the C2 nerves serving the most rostral compartment of BC and the pinna (BC GAN) on EMG activity in ipsilateral neck muscles while the cat lapped milk. Arrow shows the stimulus marker, subject to the errors pointed out in methods. Rasters of 120 stimulus trials are compared. Note the large M-wave in the most rostral compartment of BC (BC1), which is not present in the caudal compartment of BC (BC4). The M-waves in other muscles represent cross-talk in this initial cat whose stimulating electrodes around BC were poorly shielded. In all of these muscles, EMG activity was inhibited following stimulation

the effects described here were all produced at currents 2–3x those required to elicit detectable M-waves.

The most obvious effect of nonspecific BC stimulation was an inhibition of ongoing muscle activity in a range of dorsal and deep neck muscles including BC, complexus (CM), obliquus capitis inferior (OCI), semi-spinalis cervicis, splenius (SP) and rectus capitis posterior (RCP). The nature of the inhibition can be seen in Fig. 1. It could be detected within 10 ms after stimulation of ipsilateral or contralateral nerves. The trough of inhibition lasted 10–25 ms in most traces and was sometimes followed by a short period of heightened EMG activity above the prestimulus (control) levels. However, two muscles that insert on the shoulder girdle, clavotrapezius and occipitoscapularis, showed a reflex excitation, with a latency of 8–10 ms (Fig. 2).

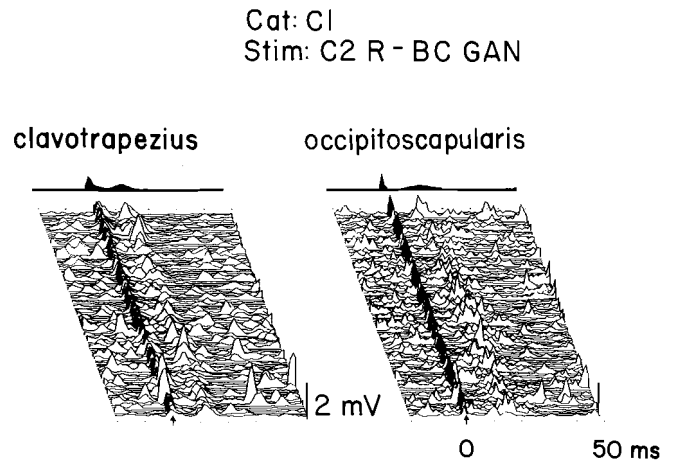


Fig. 2. Excitatory reflexes in clavotrapezius and occipitoscapularis evoked by stimulating C2 nerves to BC and the pinna on the right side (C2R-BC GAN). Note the consistent augmentation of discharge following the M-waves

Effects of stimulating nerves supplying rectus capitis posterior

In the subsequent three cats, electrical stimulation was applied directly to the C1 nerves supplying RCP close to the site at which they leave the dorsal ramus of C1. This more selective placement resulted in lower threshold (0.3–0.8 mA) and more selective and complete activation of RCP as evidenced by its evoked EMG activity. The size of this “M-wave” increased rapidly as the stimulus current was raised to 2xT, and reached a maximum at stimulus intensities approaching 3xT. In 2 cats, stimulus strengths in excess of 3xT also activated nerve branches supplying the adjacent muscle, CM, so that M-waves were also recorded in CM. Although most examinations of reflexes were carried out with stimulus strengths no higher than 4xT, strengths of up to 10xT were used in one cat (Fig. 3). At these high stimulus intensities, it was not possible to ensure that stimulation did not recruit afferent fibers entering the C1 dorsal root from sources other than RCP or CM muscles. However, no additional M-wave activity was detected in muscles innervated by other cervical segments.

Stimulation of RCP nerves at 2–4xT changed the EMG activity in only a few muscles. The most consistent effect was inhibition in ipsilateral BC with latencies as short as 4 ms. In every cat, every compartment of ipsilateral BC from which records were obtained showed an inhibitory trough of EMG activity at stimulus strengths as low as 2xT, which was the lowest strength at which testing was conducted. The trough of suppressed activity became wider and deeper as stimulus strength increased (Fig. 3) and was sometimes followed by a 10–20 ms period in which EMG amplitude increased slightly over prestimulus levels. Contralateral BC showed more modest inhibitory responses that had latencies of approximately 6–10 ms. No initially excitatory responses could be detected in ipsilateral or contralateral BC.

EMG activity in CM and SP was also inhibited by stimulation of RCP nerves. At stimulus strengths of

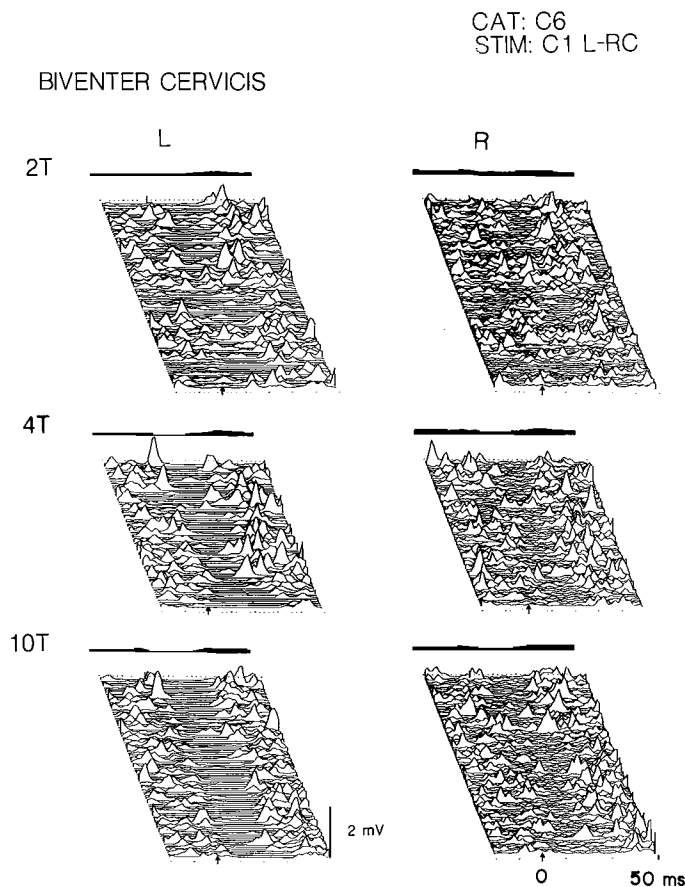


Fig. 3. Inhibitory effects in left (L) and right (R) biventer cervicis following stimulation of C1 nerves supplying left rectus capitis posterior (L-RC) as the cat lapped milk. Note that the ipsilateral side is more strongly inhibited. This inhibition is followed by a period of marginally increased excitability. The inhibition is less clear at 2x threshold (2T) than at 4-10x threshold (4T, 10T). Note the absence of M-waves in this better-shielded cat

3-4xT, inhibition commencing at latencies of approximately 6-10 ms was observed in ipsilateral muscles, but the degree of inhibition appeared to vary from cat to cat. In two cats, (cat 3, Fig. 4; cat 4, not shown), the trough of suppressed activity was clearly apparent in both CM and SP. In a third cat (C6), only a small amount of inhibition could be detected in CM, and no inhibition was apparent in SP. However, assessment of inhibitory changes in muscles like CM and SP was often difficult because the muscles were used phasically and had little or no baseline activity during many stimulus trials (e.g., Fig. 5). No major difference was seen in the nature of EMG changes when animals were tested during different forms of behavior (e.g., lapping, Fig. 3, 5, 6; walking, Fig. 4; grooming, Fig. 6), although the depth of the inhibition could vary slightly from one set of trials to another. Contralateral effects in SP and CM were difficult to detect during any stimulus trials using stimulus intensities up to 4xT.

In a single cat, EMG responses were also analyzed when stimulus currents were increased from 4xT to 10xT (Fig. 5). The inhibitory responses evoked in BC showed no obvious changes, but there were changes in the re-

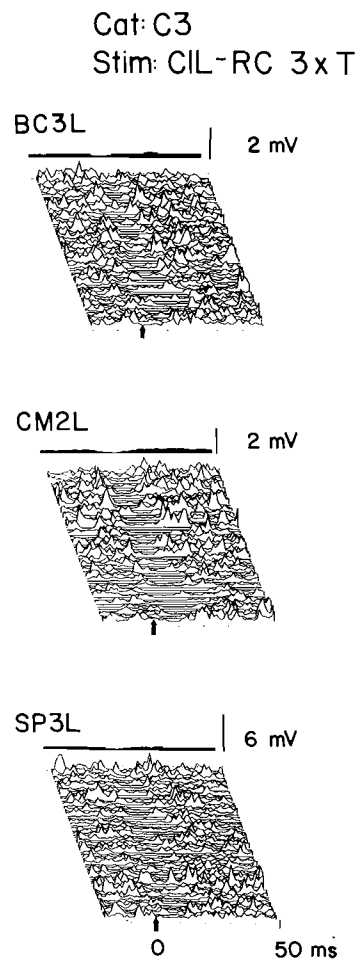


Fig. 4. Inhibitory effects of stimulating rectus capitis posterior (RC) nerves on ipsilateral biventer cervicis (BC3L), splenius (SP3L) and complexus (CM2L) during locomotion

sponses of SP and CM. On the side ipsilateral to nerve stimulation, SP continued to be inhibited, but contralaterally, there was a modest excitatory response with a latency of about 10 ms (Fig. 5). CM had an inverse pattern; the ipsilateral CM had a small excitatory response with a latency of about 20 ms, whereas the contralateral CM was inhibited (not shown). A modest excitatory response was also seen bilaterally in the intervertebral muscle spinalis dorsalis at 10xT (Fig. 5), although this muscle showed no consistent reflex responses at lower stimulus intensities. Reflexes were also investigated by stimulating deep muscles directly through surface EMG electrodes overlying the fascia but not muscle nerves. No reflex changes could be observed with narrow (0.1 ms) pulses up to 8 mA in strength.

In two cats, RCP nerves on the right (contralateral) side were also stimulated following C1 dorsal root ganglionectomy. In one cat (C4), the ganglion could not be removed completely because of surgical difficulties; in the acute experiment to ascertain the success of the ganglionectomy, an afferent volley much smaller than that on the non-operated side could still be recorded in the dorsal roots. In this cat, inhibitory reflexes were reduced compared to those seen on the intact left side, but they were not abolished. In the other cat (C6), the ganglionectomy was judged to be successful because no dorsal root volley could be recorded subsequently. Stimulation of

Cat: C6
Stim: CIL-RC 10xT

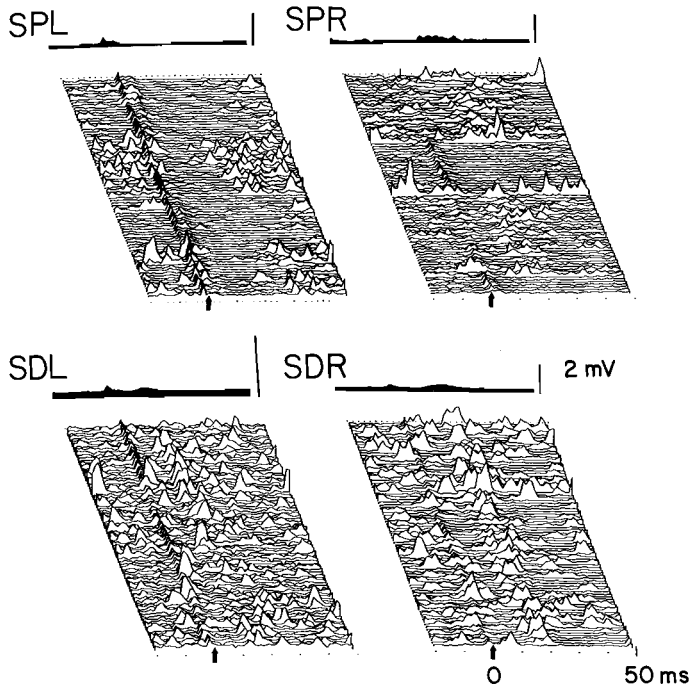


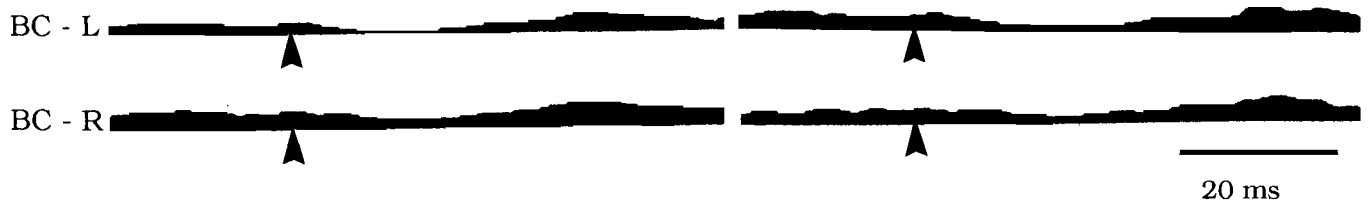
Fig. 5. Reflex patterns in splenius (SP) and spinalis dorsi (SD) when left nerves supplying rectus capitis posterior were stimulated at 10xT as the cat lapped milk. Ipsilateral SP shows a modest inhibition with a latency of about 6 ms, whereas contralateral SP shows a modest excitation. Spinalis dorsi shows small excitatory reflex bilaterally

RCP nerves on the operated side of this cat did not produce detectable reflex responses in any of the neck muscles under study (Fig. 6). In both cats, ventral roots were judged to be largely if not entirely undamaged because the RCP muscle showed seemingly appropriate EMG activity during natural head movements, matching that in RCP on the intact left side.

Stimulation of muscle nerves serving BC or SP

As extensive a series of stimulus trials were conducted by stimulating SP or BC muscle nerves at strengths of 2–4xT. However, these trials did not produce detectable inhibitory or excitatory effects in any of the dorsal neck muscles recorded in 3 cats. This is apparent from the ongoing records of stable EMG activity after the M-waves in Fig. 7. Stimulation of nerves serving dorsal neck muscles caused large M-waves resulting from the synchronous efferent activation of large sheets of muscle fibers. These were more difficult to shield from recording electrodes on nearby muscles. Thus, we cannot exclude the possibility that excitatory reflexes with latencies of less than 5 ms were masked within the large M-waves recorded homonymously and as cross-talk in some adjacent muscles (Fig. 7). However, examination of unprocessed analog EMG signals as stimulus-triggered oscilloscope traces showed no deviations from the simple biphasic waveform expected for an M-wave alone. The inhibitory changes evoked consistently by stimulation of C1 nerves were never observed following stimulation of SP or BC nerves supplied from C3. A small and inconsistent increase in EMG activity was recorded in the deep

Stim: L - RC (control)



Stim: R - RC (deafferented)

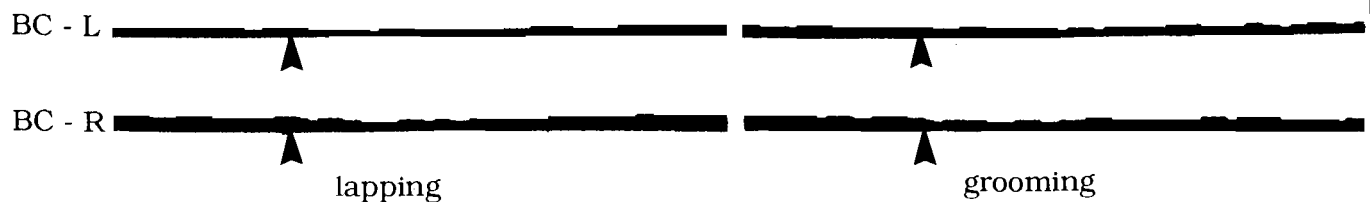


Fig. 6. Reflex effects evoked by stimulating nerves to rectus capitis posterior (RCP) with and without deafferentation. Each averaged record was derived from 50 stimulus trials such as those shown in Fig. 3. The arrows mark the point at which stimuli were delivered. Upper traces: intact nerves were stimulated at 4xT; inhibition is

present bilaterally in biventer cervicis (BC-L, BC-R). Lower traces: nerves stimulated contralaterally after deafferentation evoke no similar reflex effects. Averages in the left column were taken from episodes in which the cat lapped milk; those on the right were recorded during grooming. Vertical scale = 1 mV

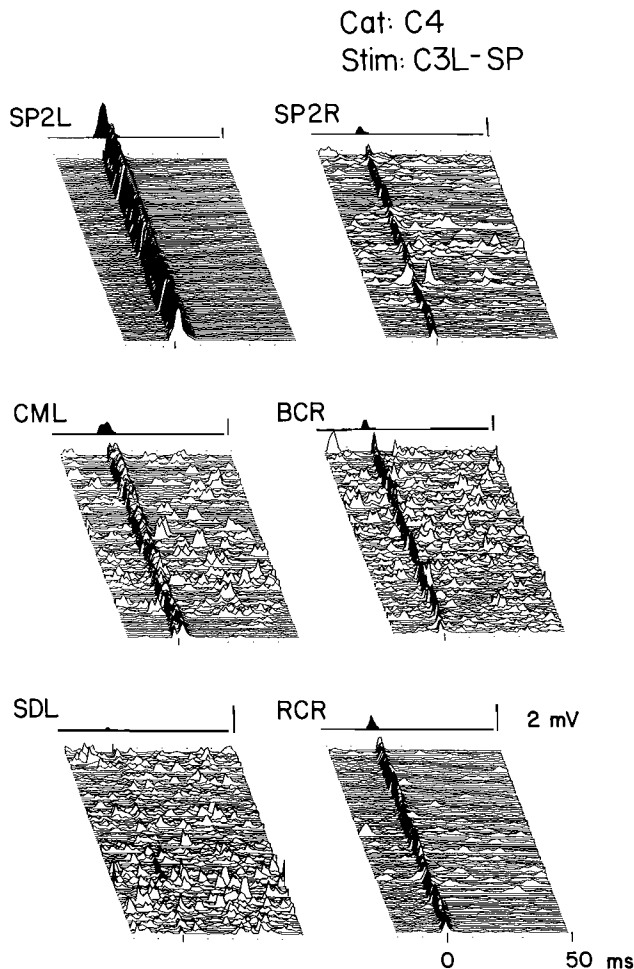


Fig. 7. Absence of detectable reflexes in selected neck muscles following stimulation of nerves serving splenius (SP) from C3. Stimuli were delivered at $4\times T$. Strong M-waves are evident in the EMG record on the corresponding side. Apart from smaller M-wave cross-talk in the other nearby muscles, little deviation can be seen in the ongoing EMG records of other muscles. CM: complexus, BC: biventer cervicis, SD: spinalis dorsi, RC: rectus capitis posterior

layers of contralateral OCI following stimulation of SP muscle nerves in a single cat.

Discussion

The present studies in alert cats suggest that reflexes evoked from neck-muscle afferents are organized according to different rules than they are in the well-studied limb muscles. Two differences were particularly obvious. First, few reflexes could be produced by stimulating some of the neck-muscle nerves. Second, these reflex actions were primarily inhibitory in nature.

Sensitivity of the methods to reveal reflexes

Can the paucity of reflexes, and particularly excitatory reflexes, be ascribed to an insufficiency of the method to

demonstrate such connections? The methods employed in this study were chosen because they have been particularly effective in revealing both excitatory and inhibitory reflexes elsewhere. Many motoneurons supplying muscles that participate in phasic behaviors (such as the lapping and eating behaviors studied here) will be close to their firing thresholds and thus will be more likely to respond to excitatory inputs. Further, the use of synchronous electrical stimuli to excite many nerve fibers should reduce the need for long periods of temporal summation such as might be required by natural stimuli. By using the same approach to study reflexes in the cat hindlimb, Loeb and co-workers (Abraham et al. 1985; Duysens and Loeb 1990; Pratt et al. 1991) have previously demonstrated excitatory reflexes so large that they were found to overwhelm the background EMG activity; gains in most raster displays had to be reduced until the ongoing EMG could no longer be discerned in the active traces. These observations suggest that the methods used here should be sufficiently sensitive to demonstrate any substantial excitatory connection. The methods are also clearly useful to demonstrate inhibitory connections because inhibitory effects can be detected by the diminution of background EMG activity which is present in the alert moving cat but not in the anesthetized preparation.

Studies of hindlimb reflexes have conditioned us to expect that muscle afferents should have excitatory actions on at least some muscle groups: through stretch reflexes onto homonymous motoneurons, flexion reflexes onto ipsilateral flexors, and crossed extension reflexes onto contralateral extensors. However, it was never possible to demonstrate excitatory actions in any of the large dorsal neck muscles when nerves containing only muscle afferents were stimulated at current strengths up to $4\times T$. In making this statement, it is important to recognize that one potentially important pathway, the monosynaptic pathway from spindle afferents onto their homonymous motoneurons, is impossible to study with the present method because any reflex activation of the homonymous muscle would be masked within the "M-wave" produced by direct stimulation of motor axons in the muscle nerve. It is probably unwise to draw inferences about the homonymous pathways from the apparent absence of significant monosynaptic effects in heteronymous muscles or other compartments of the same muscle. Previous electrophysiological observations in anesthetized cats have shown that afferents in neck muscles generally make weaker monosynaptic connections with motoneurons supplying other muscles and send fewer collaterals to homonymous motoneurons in other segments, particularly more caudal segments (Brink et al. 1981).

Mechanisms underlying inhibitory reflexes

The inhibitory effects that were seen in dorsal neck muscles were consistently produced by stimulating C1 nerves serving RCP; these appeared to be abolished by interrupting the afferent pathway by dorsal root ganglionectomy. Thus, it is likely that the inhibitory effects arose

from the actions of afferent fibers rather than from recurrent inhibition. The same inhibitory effects did not follow stimulation of C2 or C3 nerves supplying BC or SP, suggesting that receptors in the suboccipital region may have a specialized reflex role that is not shared by receptors in the longer dorsal muscles. In present studies, reflex inhibition was evoked at stimulus strengths that would probably recruit primarily the larger afferents of muscle spindles and Golgi tendon organs, known to be distributed densely throughout suboccipital muscles (Richmond and Bakker 1982). Cutaneous effects can be tentatively excluded because the C1 segmental nerves are believed to lack cutaneous afferent fibers (Reighard and Jennings 1963). However, receptors in nearby connective tissues might conceivably send axons into the RCP nerves or lie in such close proximity to the stimulating electrodes that their participation could not be ruled out.

Inhibitory effects in neck muscles were also seen following intense electrical stimulation of rostral BC. Such stimulation would undoubtedly recruit cutaneous afferents serving the pinna, as well as muscle afferents from BC itself. Because high current strengths were required to stimulate intramuscular nerves, nerve fibers supplying the adjacent intervertebral muscles might well have been recruited. Any of these afferent systems presumably could contribute to the inhibitory reflexes that were evoked. Anderson (1977) reported that stimulation of the greater auricular nerve or contralateral muscle nerves commonly produced inhibition rather than excitation of motoneurons supplying neck muscles, particularly the extensor BC. The strong inhibitory effects produced by C1 and C2 nerves in our studies are consistent with observations made nearly a century ago by Sherrington (1897) who reported in the decerebrate cat that...

"on excitation of the central end of the 2nd cervical nerve, or of a branch, even a small twig of that nerve, the high-held retracted head drops almost as if knocked down by a blow from above."

Functional implications

The absence of short-latency heteronymous excitatory reflexes in most muscles of the neck adds to our list of reflexes that the neck does not seem to have. In previous studies using intracellular recording methods, Anderson (1977) could not demonstrate crossed group I reflex actions or crossed reciprocal inhibition between long dorsal muscles. Further, Rapoport (1979) found no evidence for reciprocal inhibitory effects between muscles thought to act as functional antagonists (BC-CM versus sternomastoid) when stimulus strengths were below 1.4T, although mixed synaptic potentials or IPSPs were observed at higher thresholds. Crossed reflex interactions between BC-CM afferents and contralateral sternomastoid motoneurons were characterized by inhibitory effects in which IPSPs were followed by disinhibition. In the present studies, the reflex responses of most muscles also seemed dominated by inhibition if any activity could be detected at all. The absence of excitatory short-latency reflexes in this work is difficult to reconcile with the presence of

cervicocollic reflexes that have been thought to reflect excitatory reflex actions. From the processed records describing cervicocollic reflexes to date, it is difficult to assess the magnitude of the EMG changes and thus the strength of the reflex effects that might be required to produce such a reflex. It has been suggested that monosynaptic reflexes from Ia afferents (weak as they seem in the anesthetized or decerebrate cat) could produce some of the reported cervicocollic effects (Peterson 1988). However, such an explanation does not account for the reduced but nevertheless continued modulation of EMG activity in SP when SP is dissected from its attachments and its spindles are spared the length changes that occur during neck rotation (Ezure et al. 1983). In this situation, homonymous reflexes could not be responsible for the EMG modulations.

Our studies do not show another segmental excitatory reflex that might explain the cervicocollic effects. Perhaps the development of such reflexes depends on the simultaneous activation of receptors in several muscles. In such a case, the lack of excitatory reflexes in neck motoneurons might be attributed to the fact that electrical stimulation of one muscle nerve in isolation is not an adequate stimulus. Alternatively, reflex connections that underlie cervicocollic effects might be demonstrable in the decerebrate cat but gated out by some other inhibitory mechanism in the alert animal as has been suggested by Banovetz and others (1987). However, it is also possible that such effects do not come about through excitatory pathways at all, but rather through other mechanisms such as disinhibition. The inhibitory system revealed by this study might well provide a substrate for disinhibition due to phasic reductions in tonic afferent activity.

The differences between reflexes in the neck and the limb may highlight an important feature of segmental circuitry – that it can be specialized in ways that fit with the needs of a particular musculoskeletal system and the motor behaviors that it must generate. It might be argued that strong segmental reflexes might be counterproductive in the head-movement system, where mobility of the head must be governed to a large extent by the requirements of the eyes and ears. Changes in EMG activity produced by segmental reflexes might destabilize the head as a sensory platform. Further, it is difficult to understand the advantage that might be gained from some of the reflex connections that seem so well developed in the hindlimb. For example, the paired extensor muscles on the nuchal midline (e.g., BC) would gain little from having crossed (contralateral) inhibitory reflexes, although a rationale for such reflexes in limb muscles can be readily proposed. These studies underline the fact that models of neural circuitry developed in one motor system – the cat hindlimb – must not be generalized to the neck (and perhaps other motor systems) without experimental validation that the same functional and organizational principles exist.

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