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Crossed flexor reflex responses and their reversal in freely walking cats

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A 'phase-dependent reflex reversal' occurs when antagonistic muscle groups are activated depending on the time of stimulus application within the step cycle[6]. Such reflex reversals may occur not only in the stimulated hindlimb[2,3,5–7], but also between fore- and hindlimbs[11,13]. Contralateral phase-dependent reflex reversal has not yet been described. However, in the resting acute spinal cat, injected with clonidine, crossed extensor reflexes can be reversed to crossed flexor reflexes by changing the position of the contralateral hindlimb from flexion to extension.

The present study was undertaken to explore crossed reflexes and their reversal in intact walking cats. Two cats were implanted bilaterally with bipolar EMG electrodes[10] in tibialis anterior (TA) and gastrocnemius medialis (MG). In addition, the left hindlimb contained electrodes in flexor digitorum longus (FDL) and in two skin areas (i.e. lateral surface of the ankle and plantar surface of the foot). While the cat walked on a treadmill, a single pulse of 1 msec duration was applied every 4 sec through a pair of skin or muscle electrodes. The movements of the animals were recorded using two video cameras (60 frames/sec), one on each side of the treadmill.

Inspection of the averaged EMG responses to a series of stimuli to one of the skin electrode pairs revealed that both the crossed flexor (coTA) and the crossed extensor (coMG) responses appeared at a latency of 20–25 msec (Fig. 1). By using stimuli of graded intensity it was found that crossed flexor responses had a lower threshold than crossed extensor responses (Fig. 1). This finding is in agreement with earlier reports stating that crossed flexor responses are obtained by stimulation of the largest, fast conducting, cutaneous afferents from the foot of immobile spinal cats, while crossed extensor responses require stronger stimuli, recruiting smaller afferents as well[9,12].

The involvement of cutaneous afferents in the presently described reflex effects was evidenced by the fact that denervation of a given skin area (i.e. sural nerve) abolished the crossed responses obtained from the corresponding area (i.e. lateral

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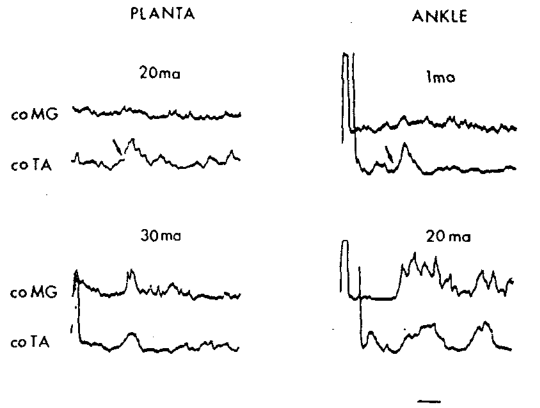

Fig. 1. Crossed flexor responses were seen at a lower threshold than crossed extensor responses following single stimuli applied to the plantar surface of the foot or to the lateral surface of the ankle. During walking 16 consecutive EMG responses in the contralateral TA and MG were rectified, processed by a digital integrator and computer averaged. The vertical and horizontal scale (calibration = 10 msec) was identical for the top (planta 20 mA, ankle 1 mA) and bottom (planta 30 mA, ankle 20 mA) experiments which were done on the same day in the same cat. Arrows, onset of crossed flexor response; time calibration, 10 msec. Note large stimulus artefacts in the first 10 msec following stimulation. A second late response at 60 msec is seen with 20 mA stimulation of the lateral surface in the ankle.

surface of the ankle). Nevertheless, crossed flexor and extensor responses could be obtained following stimulation of certain muscles such as FDL, but it is not known to what extent this was due to activation of muscle afferents or to current spread to neighboring skin afferents.

When, during walking, a stimulus was used which was strong enough to evoke either a crossed flexor or a crossed extensor response, it was found that crossed MG responses without concomitant coTA responses were seen for most stimuli used during the step cycle. However, crossed flexor responses replaced crossed extensor responses for stimuli given during a small period around the end of the contralateral stance phase. The switch from crossed extensor to crossed flexor responses is illustrated in Fig. 2 for 8 stimuli given during the first 100 msec following ipsilateral footfall. Initially (A–E) the stimuli evoked a crossed extensor but no crossed flexor response (Fig. 2, top two traces). Behaviorally, the cat responded to these stimuli by briefly lifting the stimulated hindlimb ('ipsi' in Fig. 2A–E) and prolonging the contralateral stance phase (see also refs. 4 and 7). However, when the stimulus was given slightly later, i.e. some 70–100 msec after ipsilateral foot placing (Fig. 2G, H), the stimulated foot remained on the belt and a large crossed flexor response appeared in coTA, while the coMG response was small or absent (Fig. 2, bottom). A transitory response is seen in Fig. 2F.

The timing of the reversal point from crossed MG to crossed TA responses, some 70 msec following ipsilateral footfall, is readily understood since this is the time when major extensor muscles, such as semimembranosus (iSM in Fig. 3), start their main activity during stance so that the ipsilateral hindlimb presumably is ready to support the animal while the contralateral hindlimb flexes. In the preceding period the

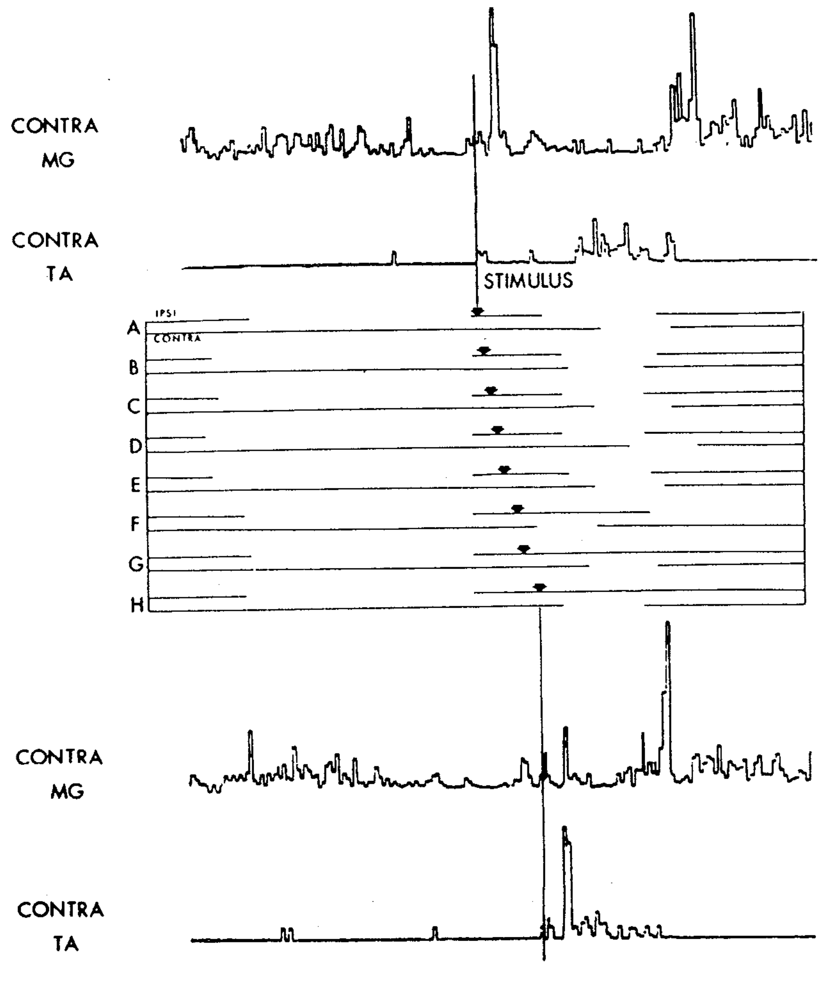

Fig. 2. Reversal from crossed extensor to crossed flexor responses following 20 mA stimuli of 1 msec applied to flexor digitorum longus (FDL) during the first 100 msec after footfall of the stimulated hindlimb. Foot contact times, as evaluated from video stills, is indicated by horizontal lines for 8 examples (A–H) with progressively later stimulus application. The corresponding EMGs in TA and MG of the hindlimb contralateral to the stimulation is given for examples A (top) and H (bottom). The EMG was integrated using a pulsed sample-and-hold integrator. The stimulus is indicated by arrows in A–H and by a vertical line in the EMG records. The coMG response amplitudes, expressed as a percentage of the maximum, were: 100, 78, 61, 199, 61, 11, 83 and 17% for A–H, and the corresponding coTA response amplitudes were 0, 0, 4, 0, 0, 96, 0 and 100%. Note the asymmetrical gait which was due to limping seen in the first days postoperatively. Time calibration, 100 msec.

animal was supported by the contralateral hindlimb so that crossed flexor responses would be rather inappropriate.

The appearance of large crossed flexor responses during the step cycle only partly overlapped with the coTA EMG burst and was typically limited to a 150 msec period centered around the onset of the coTA EMG burst (or iSM burst) (Fig. 3).

Since the average amplitude of the coMG responses during this 150 msec period was only 14% of the average value obtained outside this period, and since coTA and coMG responses occurred at the same 20–25 msec latency, it is justified to call this change from extensor to flexor responses a 'phase-dependent reflex reversal'. In previous reports[2,5–7] on ipsilateral phase-dependent reflex reversals it was noted that the appearance of a particular reflex response did not simply depend on whether the corresponding motoneuron pool was activated due to the locomotory process ('passive gating'). Therefore an active gating process had to be invoked and some direct

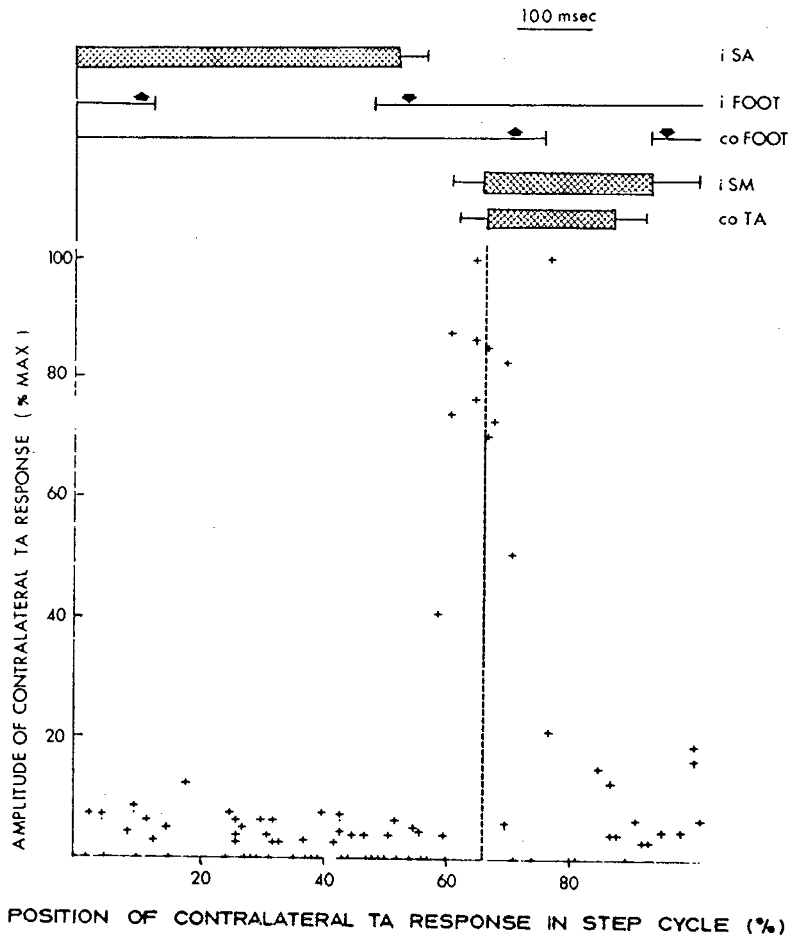

Fig. 3. Gating of coTA responses during the step cycle. Same experiment as Fig. 2. The amplitudes of the responses are expressed as percentages of the maximum response while the position of the coTA responses is given as a percentage of the preceding step cycle (between onsets of consecutive EMG bursts in the ipsilateral sartorius, iSA). Top: ipsilateral (i) and contralateral (co) foot contact time (horizontal bars), foot lift or placing (upward and downward arrows), and EMG bursts in ipsilateral semimembranosus (iSM), sartorius (iSA) and contralateral TA (coTA) as calculated (mean and S.D.) from 10 control step cycles and scaled to fit the abscissa of the plot. Note that the largest coTA responses were found around the time of onset of the EMG burst in iSM and coTA (vertical striped bar).

evidence for it was recently obtained in a study on fictive locomotion[1]. The present finding that coTA responses occur only during the first half of the rhythmic coTA EMG burst further supports the notion of active gating. Moreover, the latter finding agrees well with some ipsilateral reversal data in the walking premammillary cat, showing that TA excitatory responses are only obtained when stimuli are applied during the early part of the TA EMG burst[2]. It then seems likely that this early part of the TA burst is controlled by a central mechanism which opens the 'gate' for TA excitatory reflex pathways, whether from ipsi- or contralateral origin, while at the same time suppressing extensor excitatory actions. In principle, reflex reversal may be due either to the same afferent activity being routed in different reflex pathways, or else to the facilitation or inhibition of either one of two separate parallel pathways. The present finding that crossed flexor reflexes have a lower threshold than crossed extensor reflexes favors the second explanation for crossed reflex reversal.

Their very low threshold suggests that crossed flexor reflexes do not belong to the category of protective reflexes, as do the flexor and crossed extensor reflexes. Rather, crossed flexor reflexes, elicited by activation of low threshold cutaneous receptors from the foot during early stance, seem likely to play a role in facilitating the initiation of the contralateral swing phase during normal walking of the intact cat.

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