Reticular and Cortical Influences on the Kinetic and Tonic Components of Evoked Electromyogram

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The electromyogram taken with surface electrodes is a vector summation of the kinetic and tonic activities. These two are separated by the difference of the thresholds to the dorsal root stimulation as well as by the conduction velocity of the motor fibers concerned. Test stimuli were given to the dorsal root filaments and the conditioning stimuli were applied to the reticular formation and the sensorimotor cortex of the cat. Stimulation of the bulbar reticular formation resulted in an inhibition of the tonic activity both in the gastrocnemius and in the tibialis anterior muscles. On the other hand, the midbrain reticular formation has a facilitatory effect on the kinetic components. Cortical stimulation induced a facilitation of both the kinetic and tonic components.

The evoked electromyogram taken with bipolar surface electrodes does not always show pure tetraphasic deflections, which are typical of a recording from the volume conductor, but reveals rather complex wave forms. The reason of this is that both kinetic and tonic activities are involved in the response and the summation of these two results in a variety of wave forms, because the conduction velocity of the kinetic motor fiber is faster than that of the tonic one, and the forms of the muscle action potential of these two are not necessarily the same. The kinetic component of the evoked electromyogram has a lower threshold to the ventral root stimulation but has a higher threshold to the dorsal root stimulation.

Cortical and reticular influences on the spinal motoneurones have been subjected to various investigations. The magnitude of the mechanical response of the whole muscle, spike height of the monosynaptic response or the membrane potential of the motoneurones have been the index of excitability changes. On the other hand, the functional differentiation of the spinal motoneurones into kinetic and tonic types has been established by a series of works made by Eccles et al. and Granit et al. Thus, the effects of cortical and reticular stimulation must be reinvestigated from the standpoint of kinetic and tonic activities. In this regard, the surface electromyogram has been proved to be a useful method. In the present studies, observations of the electromyograms recorded from the surface of the gastrocnemius and tibialis anterior muscles were made.

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during the stimulation of the brain stem reticular formation and the sensorimotor cortex in cats.

**METHODS**

Under introductory ether anesthesia, cats were tracheotomized and decerebrated at the intercollicular level for the experiments of bulbar stimulation. For the cortical and the midbrain stimulation, animals were anesthetized with pentobarbital sodium (30 mg/kg) or with urethane (1.2 g/kg). The head, spinal vertebrae, femur and ankle were fixed to an animal board and the respiration was aided by artificial ventilation. Laminectomy was made between $S_1$ and $L_2$ and the cavity thus made was filled with warm liquid paraffin. The dorsal root filaments were stimulated with a rectangular pulse of 0.5 to 1 msec in duration. The stimulus intensity was so adjusted that both kinetic and tonic responses could be elicited in the calf muscles. Muscle action potentials were recorded with a pair of 2×2 mm silver plate electrodes which were placed on the belly of the gastrocnemius and tibialis anterior muscles through small holes of the skin.

The sensorimotor cortex and the brainstem reticular formation were stimulated by square pulses, 1 msec in duration and 0.5 to 10 V in intensity for various length of time at a frequency of 60 to 100 cps. A concentric needle electrode with an outer diameter of 0.5 mm and exposed tips 1.5 mm apart was used for the reticular stimulation and a pair of small silver balls for the cortical stimulation.

**RESULTS**

*Effect of the reticular stimulation.* The tonic component has a lower threshold to the stimulation of the dorsal root filaments, possibly because the tonic motoneurones receive more dense projection of the Group Ia afferent than the kinetic motoneurones. In Fig. 1, which shows the action potentials of the tibialis anterior muscle, the stimulus intensity of the $S_1$ dorsal root filaments was raised, as indicated therein. At the stimuli of more than 5 V, the kinetic components are involved in the responses which are manifested by shortening of latency. Dotted line in the figure shows the onset of the tonic action potential.

In Fig. 2, the action potentials of the tibialis (upper trace) and gastrocnemius muscles (lower trace) were recorded simultaneously every two seconds and the bulbar reticular formation was stimulated as indicated with a vertical bar. The stimulus intensity of dorsal root filaments in this case was so reduced that only tonic component was excited. The reticular formation was stimulated at the level 2 mm lateral to the midline and 4 mm rostral to the obex. As is seen, the response was completely abolished both in the ankle flexor and extensor muscles. The inhibitory area, though not systematically explored, was not sharply localized but rather distributed widely in the medial portion of the medulla.

In Fig. 3, the reticular formation was stimulated at the level 1 mm lateral and caudal to the obex and the stimulus intensity was 7 V and 15 V in A and B,
Fig. 1. Surface electromyograms of the cat's tibial anterior muscle to stimulation of the dorsal filaments. Stimulus intensity was raised as indicated. Dotted line shows the onset of the tonic action potential.

Fig. 2. Electromyograms of the tibial anterior (T.A.) and gastrocnemius (G.) muscles during the stimulation of the bulbar reticular formation (10 V, 100 cps and 1 msec). Stimuli given to the dorsal rootlets every two seconds were so weak that only the tonic components were presented in the control record.

respectively. In A, stimulus intensity of the dorsal root filament was 3 V, and the action potentials obtained showed only tonic response, while kinetic components made their appearance in B of the dorsal root filament stimulation at 8 V. A shows the overall reduction of tonic response during stimulation. The kinetic component, as is apparent in B, was not influenced by the bulbar stimulation, but only the slow component was inhibited.

Stimulation of the brainstem facilitatory area resulted in a facilitation of the kinetic component both in the ankle flexor and extensor muscles. Fig. 4 shows the effect of stimulation given to the points Fr. 4, L3 and H–1 of the Jasper's stereotaxic atlas. The early components of the muscle action potentials were augmented during stimulation and the effect was more clearly demonstrated with the gastrocnemius muscle. The facilitatory effect was not long-lasting and was often followed by inhibition, but the augmented response was still obtained in these inhibited states (see Fig. 5). Facilitation of the kinetic component was
Fig. 3. Effects of the bulbar reticular stimulation upon the tonic and kinetic activities in the tibialis anterior and gastrocnemius muscles. Reticular formation was stimulated at intensities of 7 V and 15 V, 100 cps in A and B, respectively. A: The stimulus intensity of the dorsal filaments was 3 V and only the tonic responses were observed. B: Stimulus applied to the dorsal filaments was increased to 8 V and the latencies of the responses were shortened, showing the kinetic component newly evoked.

Fig. 4. Effects of the mesencephalic stimulation upon the EMG of the tibialis anterior and gastrocnemius muscles.

ascertained also by the fact that the midbrain stimulation caused the shortening of the latency when test stimuli were just enough to give tonic responses.

Effect of the cortical stimulation. Stimulation of the sensorimotor cortex caused facilitation of both the kinetic and tonic components. As is seen in A of Fig. 6, the latency was shortened by 1.5 msec in the gastrocnemius muscle indicating that the kinetic component made its appearance during cortical stimulation. At the stimulus intensities used, the cortical stimulation alone did not elicit any bodily movement. A tendency was observed toward continuation of the facilitatory effect for 3 to 10 sec after stimulation and the effect was more obvious in the gastrocnemius muscle. When both kinetic and tonic components were involved in the control record, the early component increased its amplitude, as seen in B of Fig. 6. Similar results were obtained from the tibialis anterior muscle. However,
Fig. 5. Effects of the mesencephalic stimulation upon the tibialis anterior and gastrocnemius muscles. In A, the early component was augmented during stimulation followed by an overall reduction of the amplitudes of EMGs. B shows that even in this inhibited state the augmentation of the early component can be brought about by mesencephalic stimulation.

it is not clear in Fig. 6 whether the tonic component was also augmented or inhibited by the cortical stimulation. Stimulation of the sensorimotor cortex sometimes gave rise to a purely tonic facilitatory effect, as shown in Fig. 7. In this case, only the tonic action potential was presented in the control record when weak stimuli were applied to the dorsal filaments. Increased amplitude of action potentials in both the ankle flexor and extensor muscles without changes in the wave forms indicates that the tonic activity was augmented by cortical stimulation. The effect of tonic facilitation was more prominent in the tibialis anterior muscle. No appreciable inhibitory effects were exerted by cortical stimulation and the systematic exploration of the sensorimotor cortex failed to separate the points yielding tonic facilitation from those yielding kinetic facilitation.

DISCUSSION

Alpha motoneurones of the spinal cord are functionally not uniform, but are differentiated into phasic and tonic types.⁹–¹¹ Accordingly, the effects of stimuli
Fig. 6. Effects of cortical stimulation on the EMGs of the gastrocnemius. The control record of A shows only the tonic response, while in B both kinetic and tonic responses are involved. Stimuli given to the sensorimotor cortex were 1 msec, 17 V and 50 cps in A, and 1 msec, 14 V and 100 cps in B.

descending from the brainstem reticular formation and the motor cortex must be re-examined on this basis. The methods used so far, however, do not fulfill the requirement in the study of the ventral root reflex. This method, originally used by Lloyd\textsuperscript{13} to see the motoneurone population response, consists in the measurement of the amplitude of the action potential of the ventral root in response to the dorsal root stimulation. As was mentioned by Granit et al.,\textsuperscript{10} the action potential of kinetic motor fibers has a spike larger than that of tonic fibers. There is therefore the possibility that increased activity of the tonic components accompanied by decreased activity of the kinetic components may result in a decreased amplitude of the ventral root reflex. Furthermore, the intensity of the test stimulus to the afferent fibers is a matter of issue, because the tonic motoneurones have more dense projections of Group 1a afferents.\textsuperscript{12} Mechanical responses of the whole muscle cannot be the index of the response either. The tonic component generates slow but probably large tension, while the kinetic component causes rapid but small tension.\textsuperscript{9,14} Facilitation of the extensor muscles may be due to an increased activity of the tonic components, but the kinetic components may be reduced in their activity reciprocally.\textsuperscript{1} The method used in the present paper is to
Fig. 7. Effects of cortical stimulation on the EMGs of the gastrocnemius and tibialis anterior muscles. Only the tonic responses were presented in the control record. Stimuli given to the cortex were 1 msec, 17 V and 50 cps in A and 1 msec, 36 V and 50 cps in B.

record the compound muscle action potentials instead of the ventral root discharges. Because of the difference of the conduction velocities of the fibers concerned, the kinetic and the tonic action potentials made their appearance after different latencies. Thus, it is possible to see the effect of conditioning stimuli on the two components separately.

The argument whether the reticular influence is reciprocal or unreciprocal on the motoneurones of the extensor and flexor muscles seems to be unsettled. The current view is that the medial inhibitory and lateral facilitatory areas of Magoun and Rhines are the ‘bulbar reticular extensor inhibitory area’ and the ‘lateral reticular extensor facilitatory area’, respectively. The results presented in this paper show clearly that the tonic activity was inhibited by stimulation of the lower part of the reticular formation in both the ankle extensor and flexor muscles. Stimulation of the mesencephalic reticular formation caused facilitation of the kinetic activity. Our conclusion is that it would be appropriate to refer to the bulbar reticular formation as the ‘tonic inhibitory area’ and to the mesencephalic reticular formation as the ‘kinetic facilitatory area’. In this connection, the findings of Sharpless and Jasper would be of particular interest, since they suggest-
ed in regard to the ascending influences of the reticular formation that functionally
the upper portion of the activation system is phasic and the lower portion is
tonic. Sasaki et al.6,7 showed that the single stimulation of the bulbar reticular
formation produced usually two groups of facilitations upon the extensor
motoneurone population, the early and the late group facilitations. The former
is characterized by a brief latency of about 10 msec and is observed frequently in
phasic motoneurones but scarcely in tonic ones, while the latter has a longer latency
of 30 to 100 msec and a long lasting duration of 200 msec or more and is found
prominently in tonic motoneurones but scarcely in phasic ones. They suggested
that the pathways for the early group influence may be 'specific descending system'
with fast conduction velocity, while those of the late group influence may be
'unspecific descending system' which descends probably via short paths from the
bulbar reticular structure to the spinal motoneurones, polysynaptically and
tonically.

Repetitive stimulation of the pericruciate regions induced facilitation of both
the kinetic and tonic components. The descending pathways conveying these
influences are not known and the exact mechanism involved in these response
remains obscure. Uemura and Preston18 reported in their study with the
'pyramidal cat' that single shock stimulation of the motor cortex produced the
facilitation of hindlimb flexor motoneurone populations and the inhibition of
hindlimb extensor motoneurone populations. They could not explain their
results on the basis of phasic versus tonic neurone-muscle system, since they
observed the effects by the ventral root reflex discharges evoked by peripheral nerve
stimulation.

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