SPINO-BULBO-SPINAL AND PROPRIOSPINAL REFLEXES IN CATS DURING NATURAL SLEEP AND WAKING

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Supraspinal influences associated with different states of sleep and waking have different (during the attention response) and sometimes even opposite (during "desynchronized" sleep) actions on propriospinal and spino-bulbo-spinal reflexes.

Stimulation of the dorsal roots or peripheral nerves of unanesthetized decerebrate cats causes a reflex discharge in the corresponding ventral roots, after the propriospinal mono- and polysynaptic reflexes, with a much longer latent period [16, 17]. This late discharge has been called the spino-bulbo-spinal (SBS) reflex; its center has been located at the level of the reticular formation in the medulla [16].

Recent work has shown that the propriospinal reflexes vary considerably depending on the state of sleep or waking of the animal or man [4, 8, 10, 11, 13, 14]. However, the behavior of SBS reflexes at this time has not yet been investigated and the present study was carried out for this purpose.

Changes in the SBS reflexes depending on the state of sleep or waking of the animal were compared with changes in the simultaneously recorded propriospinal mono- and polysynaptic reflexes.

EXPERIMENTAL METHOD

Experiments were carried out on seven unanesthetized and unimmobilized cats. Electrodes were implanted on the sciatic, common peroneal, and tibial nerves of one or both hind limbs 1-2 days before the experiments began. Electrodes for recording the EEG, the EMG of the neck muscles, and the electrooculogram were implanted at the same time. The method of implantation of all these electrodes has been described previously [13]. Propriospinal and SBS reflexes were evoked by stimulating the sciatic nerve with single or paired square pulses, 0.05-0.1 msec in duration, applied once every 5 or 10 sec. The reflexes were recorded by mono- or biphasic techniques in the common peroneal nerve and in the tibial nerve of the same or the contralateral hind limb.

EXPERIMENTAL RESULTS

In the waking cat in a resting state, and also in a state of superficial ("synchronized") sleep, single stimulation of a muscular nerve by a current strong enough to cause excitation of group II nerve fibers evoked propriospinal mono- and polysynaptic reflexes, with latent periods of 3.5-4 and 7.5-11 msec respectively, initially in this nerve immediately after the artefact, and these were followed by a much later discharge with a latent period of 21-27 msec (Fig. 1A; Fig. 2A, B). The relatively low threshold and long latent period of this late discharge, its appearance not only in the ipsilateral, but also in the contralateral nerves (Fig. 1B, C; Fig. 3A, B, D), and, finally, the extremely long recovery period when paired simuli were used (Fig. 1C) – all these features of the late discharge indicate that it is an SBS reflex, similar to that investigated by other workers [1, 3, 6, 7, 16, 17].

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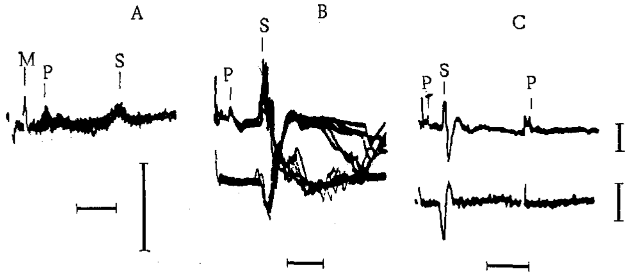

Fig. 1. Monosynaptic (M), polysynaptic (P), and spino-bulbo-spinal (S) reflex discharges in unanesthetized cats. A) Reflex discharges in tibial nerve evoked by single stimuli applied to ipsilateral sciatic nerve. Cat in a state of superficial ("synchronized") sleep; B, C) another cat, waking state (lying quietly). Reflex discharges in peroneal nerve of left (top beam) and right (bottom beam) limbs evoked by single (B) or paired (C) stimulation of left sciatic nerve. When the interval between stimuli was 100 msec (C) no SBS reflexes appeared in response to the second stimulus. All curves of this and later figures (except curves C in Fig. 1, where one sweep of the beam was recorded) are formed by superposition of five responses. Time calibration: A) 10 msec; B) 20 msec; C) 40 msec. Voltage calibration 100 μV.

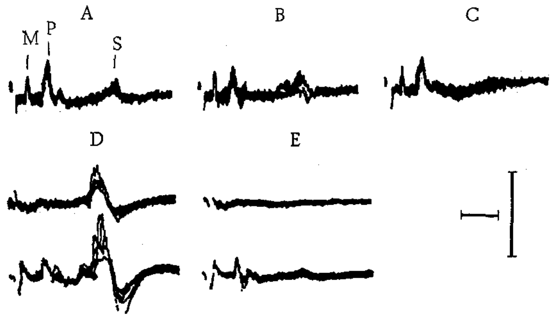

Fig. 2. Inhibition of SBS reflexes during attention response. A, B, C) Same cat as in Fig. 1A. Reflex discharges in tibial nerve evoked by single stimulation of ipsilateral sciatic nerve. Cat in waking state, lies quietly (A), in a state of "synchronized" sleep (B), and during attention response evoked by gentle tapping on the table (C). D, E) Another cat. Reflex discharges in common peroneal nerve (top beam) and in tibial nerve (bottom beam) evoked by single stimulation of ipsilateral sciatic nerve. Cat in waking state: D) lying quietly; E) walking about the room. Time calibration 10 msec. Voltage calibration: 100 μV for A, B, C; 150 μV for E. Remainder of legend as in Fig. 1.

In acute experiments, SBS reflexes can usually be recorded only in nerves innervating the flexors [3, 17]. In the present experiments, however, SBS reflexes were found sufficiently clearly not only in nerves supplying the flexors (Fig. 1B, C; Fig. 2D; Fig. 3A, B, D) but also in nerves to the extensors (Fig. 1A; Fig. 2A, B, D). This difference between the results is evidently due to the fact that in acute experiments SBS reflexes are usually recorded in animals with an exposed spinal cord. Laminectomy, as has recently been shown [7], almost completely inhibits SBS reflexes in extensors, so that they persist only in flexors.

SBS reflexes, like propriospinal mono- and polysynaptic reflexes, were most marked in cats lying quietly, either in a waking state (Fig. 1B, C; Fig. 2A, D) or in a state of superficial ("synchronized") sleep (Fig. 1A; Fig. 2B; Fig. 3A). Against this background any stimulus attracting the animal's attention, such as gentle tapping on the table, approaching the cat by the experimenter, tactile or, in particular, nociceptive stimulation of any part of the body surface led to strong inhibition of the SBS reflexes (Fig. 2C). SBS reflexes were also inhibited "spontaneously," when the animal began, for example, to wash itself or to walk about the room (Fig. 2E). The propriospinal mono- and polysynaptic reflexes, on the other hand, were not appreciably changed during the attention response (Fig. 2C, E).

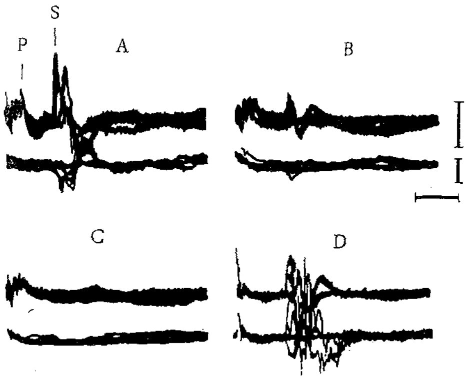

Fig. 3. Changes in propriospinal and SBS reflexes during "desynchronized" sleep. Reflex discharges in peroneal nerve of left (top beam) and right (bottom beam) limb evoked by single stimulation of left sciatic nerve. Cat in a state of "synchronized" (A) and "desynchronized" (B, C, D) sleep. Remainder of legend as in Fig. 1.

If the animal remained quite, the phase of "synchronized" sleep was frequently followed by a phase of deeper sleep, characterized by desynchronization of the EEG, lowering of the tone of the skeletal muscles, and rapid movements of the eyes [5, 12]. During this period the propriospinal reflexes were always strongly inhibited, notably the polysynaptic discharges, which frequently disappeared completely (Fig. 3B, C, D), in agreement with observations made by other workers [4, 8, 10, 13, 14]. The SBS reflexes also were strongly inhibited as a rule (Fig. 3B) and sometimes they actually disappeared completely (Fig. 3C). However, in some cases during the desynchronized phase of sleep, very strong inhibition of the propriospinal reflexes was not accompanied by a perceptible inhibition of the SBS reflexes (Fig. 3D). The difference in the degree of inhibition of the SBS reflexes was not connected with the presence or absence of rapid eye movements at this time.

Hence, neither in the present experiments nor in those of other workers [4] did the attention response have any marked effect on the propriospinal mono- and polysynaptic reflexes. The SBS reflexes, on the other hand, are inhibited extremely strongly. Since SBS reflexes share the same primary afferent fibers and motoneurons as the propriospinal polysynaptic reflexes [1, 6], it is unlikely that inhibition of the SBS reflexes was due to a decrease in the effectiveness of the synaptic action of these afferent fibers or with a decrease in the excitability of the motoneurons. The possibility is not ruled out that the SBS reflexes are depressed as the result of inhibition of synaptic transmission at the spinal relays of the ascending or descending pathway of this reflex. However, a more likely explanation is that it is due to depression of conduction through the bulbar center of the SPS reflex. One of the causes of this inhibition could be that the attention response inhibits the corticofugal reflex which facilitates SBS reflexes at the bulbar or spinal level [2].

The strong tonic inhibition of both propriospinal and SBS reflexes during deep ("desynchronized") sleep can be attributed to the fact that during this phase of sleep the motoneurons [9, 15] and, evidently, the interneurons [14] of the spinal cord are exposed to tonic postsynaptic inhibition. On the other hand, cases in which inhibition of the propriospinal reflexes was not accompanied by marked inhibition of the SBS reflexes evidently indicate that, simultaneously with inhibition of the motoneurons and interneurons of the spinal cord, facilitation of conduction through the other relays of the SBS reflex takes place. Exactly where this facilitation takes place to compensate for the effect of the inhibition is not yet certain.

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