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RAPID EYE MOVEMENTS DURING THE PARADOXICAL SLEEP OF RABBITS

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It is generally accepted that rapid eye movements (REM) are the most characteristic phenomenon of paradoxical sleep among birds and mammals. This is the reason why Dement and Kleitman (1957) who first described this kind of sleep, called it REM-sleep. The occurrence of REM during paradoxical sleep is fairly well described in humans (Mouret and Jeannerod 1964, Gabersek and Scherrer 1969), monkeys (Fuchs and Ron 1968), and cats (Jeannerod et al. 1965). In view of the work of Pompeiano and Morrison (1965) and Fuchs and Ron (1968) REMs are qualitatively different phenomena from eye movements connected with the vision reflexes during wakefulness. Therefore its high specifity for the paradoxical sleep would be out of question. The knowledge of REMs in rabbits is scanty. It is only generally accepted that REMs appear in paradoxical sleep of this species, therefore the aim of work presented here is the quantitative study of REM during paradoxical sleep in rabbits.

MATERIAL AND METHOD

Experiments were performed on seven rabbits of both sexes, four male and three female, weighing between 2.9 and 3.6 kg. Each animal had chronically implanted electrodes (Narębski et al. 1966). Positions of EEG and EMG electrode implantation and the experimental procedure during the 24 hr duration of the experiments were described in the previous paper (Narębski et al. 1969). Electrooculographic (EOG) electrodes were implanted horizontally on both sides of the right eye. EOG was recorded with the ink writer of the electroencephalograph Kaizer 55, with a time constant 0.3 sec. One EMG and three EEG leads were used.

RESULTS

The experimental data comprise twenty five polygraphic, 24 hr records. Out of seven rabbits, three were recorded twice for 24 hr, two–three times, and for the remaining two rabbits one was recorded five times and the other eight times. In all animals investigated 973 paradoxical sleep episodes were recorded. The average number of paradoxical sleep episodes during 24 hr was 39±18, and the mean value of duration of one such episode was 81±27 sec. Both values mentioned are very close to the ones presented in our previous paper (Narębski et al. 1969). The total number of individual REMs registered was 10 984; its mean value for 24 hr was 439±179 with dispersion from 256 to 883.

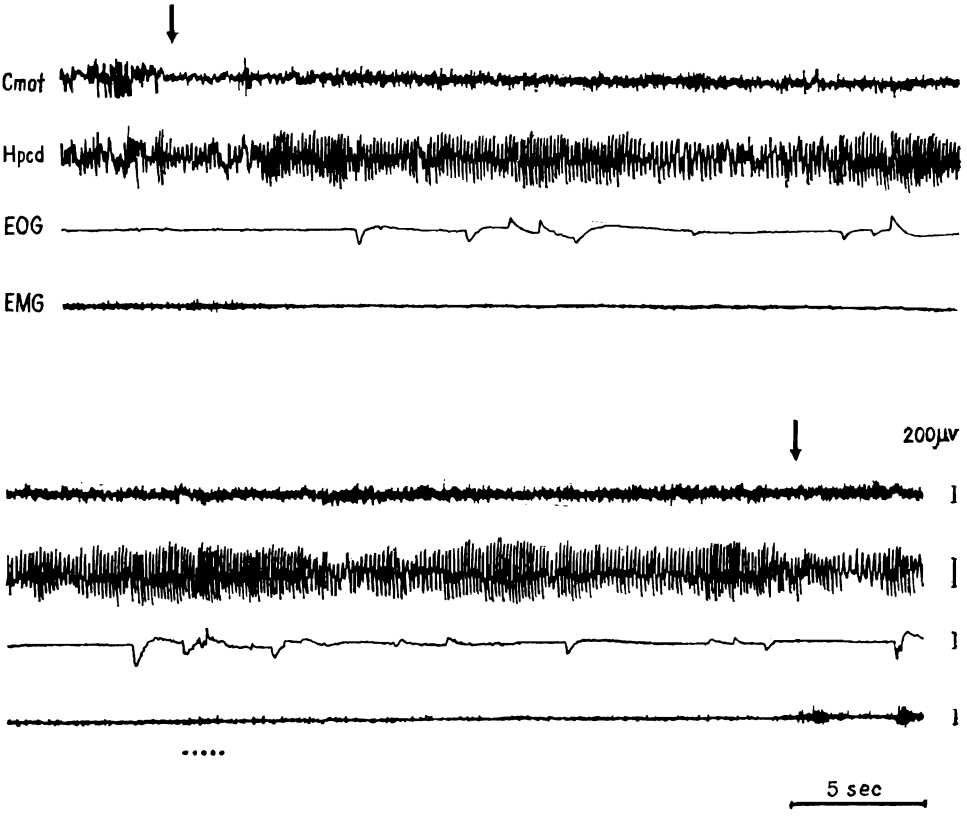

FIG. 1. The paradoxical sleep episode of 58 sec duration. Leads: Cmot, cortex motoricus; Hpcd, hippocampus dorsalis; EOG, electrooculogram of the right eye ball; EMG, electromyogram of the neck muscles. Arrows, the beginning and the end of the paradoxical sleep episode. Points, head movement.

REMs during the paradoxical sleep of rabbits appeared mostly single, or in short series of two or three. The average interval between two successive individual REMs was 6.24 sec, but in the short series mentioned was about 1 sec. The existence of REM bursts containing ten or more eye movements which are typical for cats (Jeannerod et al. 1965) was never found in rabbits. The number of REMs for 1 min of paradoxical sleep in rabbits was 9.7 ± 1.9 with dispersion from 6 to 13 for a sigle 24 hr record. REMs pass mostly in the horizontal plane. Fifty seven per cent of the single movements had the reverse direction to the preceding movement. Each single REM starts with the rapid phase of about 70 msec duration and terminates with the slow phase of 1–2 sec duration (Fig. 1 and 2).

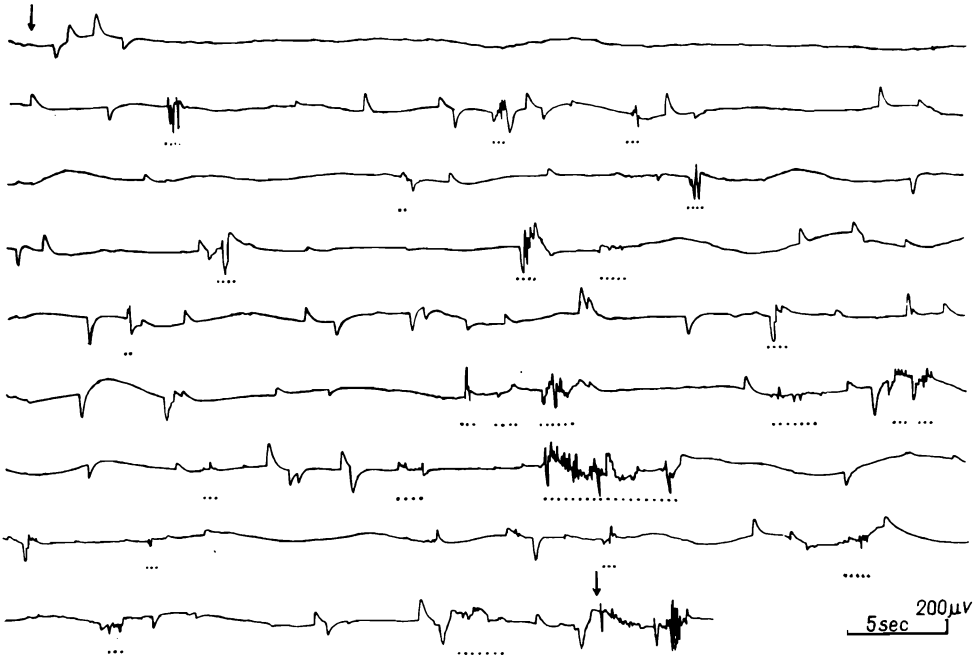

FIG. 2. The EOG of one paradoxical sleep episode of 7 min 20 sec duration. For explanations *see* Fig. 1.

REMs are recognized as phasic events within the paradoxical sleep episode. A group of electrophysiological symptoms, as for example the recruiting response threshold (Giaquinto 1968), has than an extreme value. In our experiments the frequency and regularity of hippocampal theta rhythm increased simultaneously with, or immediately after REMs (Fig. 1). On the other hand, the hippocampal theta waves mostly disap-

peared for a moment during movements of the rabbits head, which sometimes took place during paradoxical sleep. Figure 1 shows one of such artifacts and Fig. 2 as much as twenty one. Not all paradoxical sleep episodes contained REMs. Out of 973 paradoxical sleep episodes registered there were 116 without REMs (11.9%). Paradoxical sleep without REMs took place in all rabbits investigated, however this occurred almost exclusively with short episodes. Out of 116 paradoxical sleep episodes without REMs there were 68 (58%) lasting up to 18 sec, and only six (5.2%) longer than 37 sec (Fig. 3).

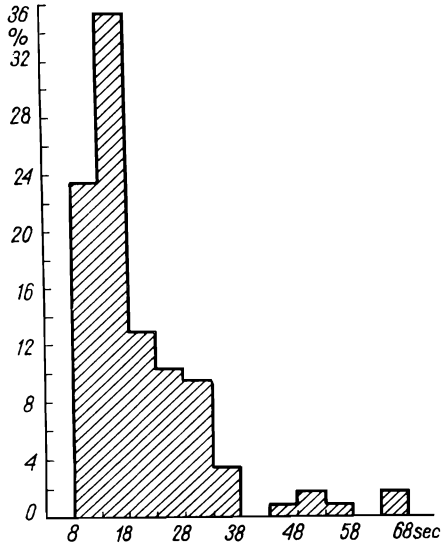

FIG. 3. Histogram of the frequency of paradoxical sleep without REM in relation to duration of such single paradoxical sleep episodes. Abscissa, duration of the particular paradoxical sleep grouped in intervals of 5 sec, above 8 sec. Ordinate, the frequency of the individual paradoxical sleep expressed as a percentage of the total number of episodes without REM (n-116).

DISCUSSION

The technique used here allowed us to record every REM which occurred. The value of dipoles of the eye ball movements ranged between 0.3–0.03 mv. The exact spheric geometry of eye movement could not be registered with the technique used; this would require much more complicated instrumentation (Fuchs and Ron 1968). The small REM in the perpendicular direction could be omitted, however in our opinion they could occur in the rabbit rather exceptionally. The time constant of 0.3 sec seems to be more appropriate than 0.1 sec used by Jeannerod et al. (1965). A time constant longer than 0.3 sec could be even better; however, because of artifacts it makes the record indistinct.

It was not possible to determine the angular speed of REM with the technique used. The deflexion of the eye ball of the single REM was not measured. We were able to calculate only, on the basis of the EOG record,

in approximation, the rapid REM phase duration which is about 70 msec. On the other hand, the slow REM phase may be deformed with the time constant used, i.e. shortened if it was longer than one sec.

In comparison with the data in cats, described by Jeannerod et al. (1965) we found striking differences in rabbits. They are as follows: (a) The number of REMs per 1 min of paradoxical sleep is in rabbit about eight times smaller. But the number of REMs per 24 hr continuous record is in rabbits about 40 times smaller, because in rabbits the circadian quantity of paradoxical sleep (Narębski et al. 1969) is about five times smaller than in cats (Delorme et al. 1964). (b) REMs during paradoxical sleep of rabbits never reached more than three closely consecutive eye ball movements, and therefore cannot be called bursts of REM. On the other hand, in cats half of the total number of REMs has a form of bursts composed of more than five single REMs, up to 50 (Jeannerod et al. 1965).

As it was shown, also in rabbits, REM is a highly specific paradoxical sleep symptom. For one average paradoxical sleep episode of 81 sec duration there were 13 single REMs. The average interval between two consecutive REMs is therefore 6.2 sec. This interval is only rarely shorter than 1 sec in such cases when REMs occurred in small series. REMs in rabbits are "rapid" only in their initial phase and they could not be recognized as rapidly occurring in succession. In every eighth paradoxical sleep episode in general, and in every fourth episode of those shorter than 20 sec, there is a lack of REM. Therefore, in view of the EOG records during paradoxical sleep of rabbits, the name REM-sleep seems to be less justified than in respect to human, monkeys and even cats. Consequently, for the comparative physiology the name REM-sleep is rather less justified than paradoxical sleep.

Up to now there are no quantitative investigations concerning REMs of species closely related to rabbits, e,g. rats, guinea pigs and mice, in which the paradoxical sleep is proved (Pellet and Béraud 1967).

Distinct differences between the REMs during paradoxical sleep of rabbits and cats were found. They may be explained generally by the existence of distinct differences in the neuronal organization of the visual analyser of these two species, and therefore in their physiology of vision.

SUMMARY

Twenty five, 24 hr experiments were performed on seven rabbits to investigate quantitatively the occurrence of the rapid eye movements (REMs), which constitute in this species a characteristic phasic pheno-

menon of paradoxical sleep (PS). Experimental data comprise 973 episodes of PS containing 10894 REMs. During 24 hr an average of 439±179 REMs occurred in rabbits, about 40 times less than in cats. For 1 min of PS there were 9.7±1.9 single REMs, that is about eight times less than in PS of cats. REMs occurred in rabbits mostly single, and never — as in cats — in bursts. 11.9% of PS registered was devoid of REM, but this involved almost exclusively the shortest PS episodes. The great quantitative difference between REMs during PS of rabbits and cats suggest the existence of essential differences in the neuronal organization of the vision analyser in these species.

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