REVISTA ESPAÑOLA DE FISIOLOGIA, 34, 389-394. 1978

Alternance of States Within the Sleep Wakefulness Cycle. An Approach to Its Study *

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(Received on September 27, 1977)

J. GOMEZ-MONTOYA, E. GUTIERREZ-RIVAS, I. DE ANDRES and F. REINOSO-SUAREZ. *Alternance of States Within the Sleep Wakefulness Cycle. An Approach to Its Study.* Rev. esp. Fisiol., 34, 389-394. 1978.

Intrinsic and dynamic aspects of the sleep-wakefulness cycle (SWC) are studied. From a dynamic point of view, results indicate a tendency to maintain vigilance (alerta wakefulness-W-and drowsiness-D) or sleep (slow sleep-SS-and paradoxical sleep-PS). Transitions from vigilance to sleep are more probable than the reverse. Drowsiness plays an important role as a distributor stage in the SWC of the normal cat since the same probabilities of passing from it to W than to SS exist. Furthermore transitions from eleep (SS and PS) were more frequently observed to D than to W.

The evaluations in experimental studies on sleep research have mainly been focussed on certain parameters of the sleep wakefulness cycle (SWC). Quantitative analysis has principally been concerned with the time spent in each state of the cycle and the number and duration of its episodes. More dynamic aspects of the SWC have frequently been omitted. In the cat, in spite of being the species most widely used in sleep experiments, only a few studies have dealt with the hourly distribution of sleep and wakefulness states (1, 3, 5, 11, 13) and, with the exception of a study outlined by URSIN (14), no attention has been paid to the patterns in the alternance of the distinct states throughout the SWC. This parameter is clearly related to the intrinsic and dynamic aspects of the SWC and these aspects should be systematically considered in sleep studies. The purpose of this paper was, therefore, to define the characteristics in the alternance of the different phases of the SWC in the normal laboratory cat living in the habitual conditions provided by a cat colony and with

* Supported by CAICT Grant n.° 1776.

the absence of other experimental situations.

Materials and Methods

Eleven adult cats weighing 2.5-3.5 kg served as experimental subjects. By a surgical procedure 8 electrodes were implanted for the recording of EEG, EMG of neck muscles and EOG (ocular movements).

After recovery from surgery, 3 polygraphic recordings were taken from each cat, at weekly intervals. Each recording lasted 23 h.

During the recording, each animal remained in its own cage but with other cats in the same room. They received standard food twice a day (at 9 and 16 h). Artificial light was maintained from 8 to 20 h and was switched off from 20 to 8 h. Room temperature was maintained at 15-20° C. Throughout the recording sessions the habitual background noises of

Table I. *Mathematical model to obtain, from the matrix of data the three others matrices that represent the probabilities of changes between the four stages of SWC.*

	W	D	SS	PS	
W		n(W→D) a_2	n(W→SS) a_3	n(W→PS) a_4	$a_2+a_3+a_4$ A
D	n(D→W) b_1		n(D→SS) b_3	n(D→PS) b_4	$b_1+b_3+b_4$ B
SS	n(SS→W) c_1	n(SS→D) c_2		n(SS→PS) c_4	$c_1+c_2+c_4$ C
PS	n(PS→W) d_1	n(PS→D) d_2	n(PS→SS) d_3		$d_1+d_2+d_3$ D
	$b_1+c_1+d_1$ I	$a_2+c_2+d_2$ II	$a_3+b_3+d_3$ III	$a_4+b_4+c_4$ IV	A+B+C+D = I+II+III+IV S

MATRIX OF DATA

	W	D	SS	PS
W		$\frac{a_2}{A}$	$\frac{a_3}{A}$	$\frac{a_4}{A}$
D	$\frac{b_1}{B}$		$\frac{b_3}{B}$	$\frac{b_4}{B}$
SS	$\frac{c_1}{C}$	$\frac{c_2}{C}$		$\frac{c_4}{C}$
PS	$\frac{d_1}{D}$	$\frac{d_2}{D}$	$\frac{d_3}{D}$	

INITIAL MATRIX
PROSPECTIVE PROBABILITIES

	W	D	SS	PS
W		$\frac{a_2}{II}$	$\frac{a_3}{III}$	$\frac{a_4}{IV}$
D	$\frac{b_1}{I}$		$\frac{b_3}{III}$	$\frac{b_4}{IV}$
SS	$\frac{c_1}{I}$	$\frac{c_2}{II}$		$\frac{c_4}{IV}$
PS	$\frac{d_1}{I}$	$\frac{d_2}{II}$	$\frac{d_3}{III}$	

FINAL MATRIX
RETROSPECTIVE PROBABILITIES

	W	D	SS	PS
W		$\frac{a_2}{S}$	$\frac{a_3}{S}$	$\frac{a_4}{S}$
D	$\frac{b_1}{S}$		$\frac{b_3}{S}$	$\frac{b_4}{S}$
SS	$\frac{c_1}{S}$	$\frac{c_2}{S}$		$\frac{c_4}{S}$
PS	$\frac{d_1}{S}$	$\frac{d_2}{S}$	$\frac{d_3}{S}$	

GENERAL MATRIX
GLOBAL PROBABILITIES

an animal community were present together with those of the people looking after the animals.

All recordings were analysed by the same researcher in accordance with the polygraphic patterns of wakefulness (W), drowsiness (D), slow sleep (SS) and paradoxical sleep (PS) (6). The minimum duration of the episodes considered was 30 seconds.

For the study, each recording was summarized in a matrix of data (table I), which consisted of 4 rows and 4 columns corresponding to the distinct stages of the SWC. Each square contained the number of transitions from one stage (row) to another (column). The time spent in each stage of the SWC per hour of recording was measured and expressed in percentages of the total time. The hourly distribution of sleep stages has been reported in another paper (3).

From the matrix of data, three other matrices were made: 1) The «initial matrix» aimed at calculating the prospective probabilities, i.e. the frequency of transition from one particular stage to each of the other three. The different prospective probabilities were calculated as the ratio of a numerator (the number of times the animal passed from a given stage to each of the others) and a denominator (the total number of transitions from this initial stage to all other stages). The initial matrix therefore comprises the ratios of the number in each square of the matrix of data and the total sum of its row (the total number of periods of the considered stage) (table I).

2) The «final matrix» aimed to calculate the retrospective probabilities, i.e. the frequency of transition to a particular stage from the other three. The retrospective probabilities were the ratios between the number of times the animal passed to a final stage from each of the other stages and the total number of transitions to this final stage. The «final matrix» was, thus, calculated as the ratio between the number in each square of the matrix of data and the total sum of its column (this also being the total number of periods of the stage under consideration) (table I).

3) The «general matrix» aimed to calculate the global probabilities, i.e. the relative frequency of transition between any two stages. The global probabilities were the ratios between the number of times the animal passed from one stage to another and the total number of transitions scored. The general matrix contained, therefore, the ratio between the number of each square of matrix of data and the total sum of rows or columns (i.e. the total number of episodes of W, D, SS and PS) (table I).

Results

Table II shows the mean of the total number of episodes of each state of the

Table II. *Mean of the total number of episodes of each stage of the SWC and the number of transitions from each one into another.*

	W	D	SS	PS	SUM ROWS
W		51.9	0.1	0	52.0
D	42.1		38.6	0.1	80.8
SS	6.5	20.1		53.9	80.5
PS	3.4	8.8	41.8		54.0
SUM COLUMNS	52.0	80.8	80.5	54.0	267.3

Stage	N.º periods
W	51.84 ± 5.42 *
D	81.51 ± 10.03
SS	80.29 ± 4.38
PS	54.03 ± 7.37

* Mean of the 11 cats analyzed on the present study.

Table III. *Probabilities of the different changes of stage (data relative to 11 cats), grouped on three different matrices.*
Each of them contains, respectively, the prospective, retrospective and global probabilities.

	prospective probabilities Initial matrix:					*Final matrix: retrospective probabilities*					*General matrix: global probabilities*			
	W	D	SS	PS		W	D	SS	PS		W	D	SS	PS
W	—	99.8	0.2	0.0	W	—	66.4	0.2	0.0	W	—	19.14	0.04	0.0
D	52.2	—	47.6	0.2	D	78.9	—	49.7	0.1	D	15.50	—	14.33	0.02
SS	8.5	25.7	—	65.8	SS	13.1	21.4	—	99.9	SS	2.42	7.23	—	20.65
PS	6.4	21.4	72.2	—	PS	8.0	12.2	50.1	—	PS	1.27	3.45	16.10	—

SWC and number of transitions from one state into another. These were the total figures resulting from the three 23 h recording sessions on the eleven animals. The greatest number of episodes registered were those of SS and D in almost equal proportions. Episodes of W and PS were present in minor quantity and were also similar in proportion.

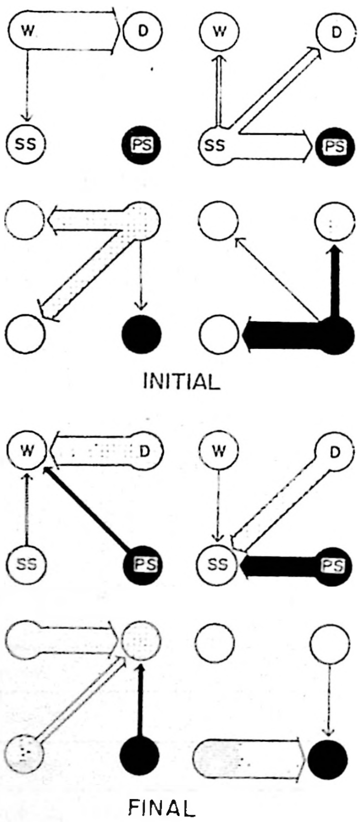

Fig. 1. *Scheme of the different changes from one stage to the others (initial matrix) and the transitions to one stage from the other three (final matrix).*

1) Prospective probabilities (see initial matrix, table III). Commencing with W, the most frequently following stage was D (99.8 %). Only in 0.2 % was there a direct transition from W to SS. Transition from W to PS was not found.

Commencing with D, there existed similar probabilities of transitions to W and SS. Transition from D to PS was unusual. From SS the most probable stage that followed was PS (65.8 %), the second most probable was D (25.7 %) and finally W (8.5 %). From PS the transition to SS most frequently occurred (72.2 %). The probabilities of transition to D and W were 21.4 and 6.4 % respectively (fig. 1).

2) Retrospective probabilities (see final matrix, table III). W was preceded by D in 78.9 % of cases. Transitions recorded from SS and PS to W were 13.1 % and 8 % respectively. W most frequently preceded D (66.4 %). SS preceded D in 21.4 % of the cases and PS in 12.2 %.

D and PS preceded SS with similar probabilities (49.7 % and 50.1 % respectively). Transition from W to SS was rare (0.2 %).

In 99.9 % of the cases PS was preceded by SS. Only in 0.1 % were transitions from D to PS recorded (fig. 1).

3) Global probabilities (see general

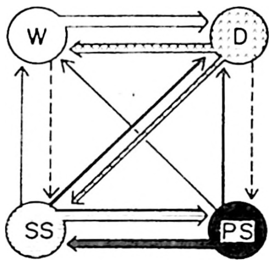

Fig. 2. *Scheme of the relative frequences of transitions between any two stages of SWC.*

matrix, table III). The most frequently occurring transitions from any two stages were from SS to PS and from W to D, with almost equal probabilities (20.65 % and 19.14 % respectively). In order of decreasing probability these were followed by transitions from PS to SS (16.10 %) and from D to W (15.50 %) (fig. 2).

Discussion

Although sequential analysis of items of behaviour has frequently been used in behavioural studies on the cat (7, 8, 12), this approach has been almost completely omitted in studies of such an important part of behaviour as the SWC. The present paper specifies in detail the relationships between the transition of the different stages of the SWC of the normal cat, conditioned to living in a cat colony and ready to serve as subject for further sleep experiments.

The analysis of the total number of episodes of the stages of the SWC showed that, in this parameter, the normal and stabled cat shows a certain equilibrium throughout the 23 h recording session. This equilibrium exists between the stages of the cycle that sustain the behavioural state of wakefulness (alert wakefulness and drowsiness episodes) and those that sustain the sleep state (slow and paradoxical sleep episodes). However, considering the individual values of each stage, the episodes of slow sleep and of drowsiness were in major proportion than those of alert wakefulness and paradoxical sleep.

Examining the dynamic relationships between the distinct stages, the results of the prospective probabilities (initial matrix) indicate that the highest incidence occurred in the transition from W to D. This is, however, to be expected when considering the normal trend in the sequence of the cycle but, due to the number of W episodes, these transitions represented only 19.14 % of the total number of changes in the cycle (global probabilities, general matrix).

The transitions from PS to SS and from SS to PS followed in proportion the changes from W to D. Since both SS and SP can also be the stages prior to those of W and SS, the high incidence in the transitions from SS to PS and from PS to SS brings out one noticeable feature in the SWC of the normal and stabled cat, i.e. its tendency to remain asleep if previously in SS or PS.

The retrospective probabilities (final matrix) between the two stages of sleep showed that, in 50.1 % of the cases SS was preceded by PS and that PS was almost always (99.9 %) preceded by SS. This latter fact, that PS normally follows a period of SS, was recognised in the early stages of sleep studies (2). The transistions from SS to PS were 20.65 % of the total number of changes (global probabilities, general matrix).

In many sleep studies (1, 4, 13, 14) drowsiness is not considered as an independent stage of the SWC. However, in addition to the fact that its periods were almost as numerous as those of SS, results in the initial matrix showed that, from D there are practically the same probabilities of passing to W or to SS. This indicates that drowsiness plays an important role as a distributor stage in the SWC of the normal cat. This role was also confirmed in the results of the retrospective probabilities (final matrix): D was mainly preceded by W (because rarely do transitions take place from W to SS) but the transitions from sleep (particularly from SS) were more frequent to D than to W. REINOSO-SUÁREZ and DE-ANDRÉS (9) established the criteria that allows the distinction of D as an individual stage of the SWC.

URSIN (14) in his analysis on the alternation of sleep stages in the cat, reports values that differ considerably from those of the present study. However, he does not include drowsiness as an independent stage of the SWC but he makes a further subdivision of SS into light and deep slow sleep. For these reasons, it is difficult to establish an accurate comparison between the two studies. On the other hand, the living conditions of his animals prior to the recordings are not reported and the sleep recordings were carried out, in that particular experiment, with the cats isolated in a soundproof chamber. It has been demonstrated that everyday living conditions of the animals and those found during recordings may be important factors for the dynamic aspects of the SWC (3, 10).

Finally, it can be concluded that a greater understanding of the SWC can be reached if, together with the quantitative evaluation of each phase of the cycle, further analysis of the changes from one stage to another is carried out. In other words, an evaluation of the alternance that exists between the stages, a factor that can vary under certain experimental conditions.

Acknowledgements

The authors gratefully acknowledge the assistance provided by Dr. R. E. Peinado of the Puerto Rico University who proposed the mathematical approach used in this study.

Resumen

Se han estudiado 11 gatos a los que se les han tomado 3 registros poligráficos de 23 h de duración.

Los estadios diferenciados dentro del ciclo vigilia-sueño (CVS) fueron: Vigilia (V), somnolencia (S), sueño lento (SL) y sueño paradójico (SP). Los datos tenidos en cuenta fueron los cambios habidos de un estado a otro, en cuanto a sus probabilidades prospectivas, retrospectivas y globales (matrices inicial, final y general).

Del análisis dinámico de estos datos se observa que existe en el CVS «normal» del gato una marcada tendencia a mantenerse despierto (V y S) o dormido (SL y SP) y solamente de forma ocasional pasa de una situación a la otra, siendo más frecuentes las transiciones de despierto a dormido que las contrarias.

El comportamiento dinámico del CVS apoya la tesis mantenida en anteriores ocasiones, en cuanto a la diferencia de la S como un estado más del ciclo, distinto de la V, SL y SP.

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