Circadian Rhythms of Locomotor Activity in the Squirrel Monkey, *Saimiri sciureus*, under Conditions of Self-controlled Light-Dark Cycles

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**Abstract** Locomotor activity was recorded from three squirrel monkeys, *Saimiri sciureus*, housed singly in cages inside a sound-proof chamber. Each animal was exposed twice to each of three conditions: continuous dim illumination (dim LL), continuous bright illumination (bright LL), and conditions in which the animal could turn on bright light by itself (self-controlled light-dark cycle: LDs). The mean circadian period, \( \tau \), the activity time, \( \alpha \), and the amount of activity, \( A \), were computed for each single condition. It was found that, in LL, \( \tau \), \( \alpha \) and \( A \) were positively correlated with the intensity of illumination. In LDs, \( \tau \) was longer and \( A \) larger than in either dim or bright LL. The lengthening of \( \tau \) in squirrel monkeys by a self-controlled light-dark cycle is compared with similar findings in birds and man, and is discussed in view of the observation that the \( \tau \)-characteristics of diurnal mammals deviate from those known from other diurnal species of vertebrates.

When kept in constant conditions, most animals exhibit a circadian rhythm that 'freeruns' with a mean period slightly deviating from 24 hr. The direction and amount of this deviation depend on the species, the individual and its physiological state and on environmental conditions. Among the environmental factors which can influence \( \tau \), light has especially attracted the attention of many investigators. In many nocturnal species, \( \tau \) gets longer when the intensity of illumination is increased while the opposite holds true for diurnal species, at least among reptiles, fishes and birds. Mammals do not seem to obey this rule as \( \tau \) is positively correlated with the intensity of illumination in nocturnal, as well as in many diurnal species (Aschoff, 1979). Such dependencies of \( \tau \) on light intensity are usually studied under conditions in which the illumination is kept constant at various levels of intensity for many days. However, freerunning rhythms can also be
observed in the presence of a light-dark cycle if the cycle is produced by the experimental animal itself and hence does not provide an entraining zeitgeber for the rhythm. It has been shown in birds that under the influence of such a self-controlled light-dark cycle, the period of the rhythm is longer than in either continuous light or continuous darkness (ASCHOFF et al., 1968). In this paper, evidence is presented that similar effects can be observed in the squirrel monkey, Saimiri sciureus.

METHODS

Three adult male squirrel monkeys were kept in individual cages, separated from each other by fiberboard partitions and black curtains within a sound-proof chamber. The activity of each monkey was recorded by means of contact switches mounted to a movable perch which was suspended in the middle of the cage. Impulses elicited by movements of the animal on the perch were fed into an event recorder and a magnetic tape. Food and water were available continuously and replenished every second or third day. In each cage, there was a continuous dim background illumination (dim LL), as well as a secondary light source for bright illumination that could be turned on continuously (bright LL) or controlled by the animal with a ring suspended in the cage near the perch. The self-controlled bright light turned off automatically 30 min after being turned on by the animal. When given access to the ring, the animal usually handled it repeatedly for several hours, and then rested for another couple of hours in dim illumination, thereby producing a self-controlled light-dark cycle (LDS). Each animal was exposed to the three conditions (dim LL; bright LL; LDS) twice for an average of 19 (10 to 33) days per condition.

The period of the freerunning rhythm was computed by means of a combined Fourier and periodogram analysis (WEVER, 1978). Duration of activity time, as opposed to rest time (or sleep) was determined on the original records of the event recorder by five persons (animal 1 and 2) or according to a prefixed arbitrary rule (animal 3). To estimate the amount of activity, all the 10-min intervals in which activity had been recorded, were summed over each circadian period. In view of the large interindividual differences in the level of activity, the mean values, computed separately for each of the three conditions, were expressed as percentage deviations from the overall mean amount of activity for each animal.

RESULTS

Under all three conditions, the animals had freerunning rhythms with a period \( \tau \) longer than 24 hr. A typical record is reproduced in Fig. 1. The mean \( \tau \)-values, derived from the slopes of the lines drawn through onsets of activity, are: 26.18 hr in LL 150 lux, 26.52 hr in LDS, and 26.01 hr in LL 3 lux. (The \( \tau \)-values...

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that are obtained by computer analysis and used for the final analysis differ slightly from the values based on onsets only.) Activity-time, $\alpha$, is relatively long in LL 150 lux, shortest in LL 0.3 lux, and of intermediate duration in LD$_5$. The mean values of $\tau$, $\alpha$ and amount of activity, $A$, computed separately for each animal and each condition, are given in Fig. 2. Solid lines connect the data obtained in the two conditions with constant illumination, and dashed lines connect these data with those obtained in LD$_5$-conditions (crosses). The results can be summarized in a few sentences:

1. Without exception, $\tau$ and $\alpha$ are longer in bright LL than in dim LL. There is also, on average, a positive correlation between $A$ and intensity of illumination in LL.

2. In self-controlled light-dark cycles, $\tau$ is longer than in either dim or bright LL. According to the t-test for matched pairs (two-tailed) this difference is signif-
Fig. 2. Mean values of circadian period, activity time and amount of activity, computed from the records of three squirrel monkeys, Saimiri sciureus, kept alternately in constant conditions with different intensities of illumination (closed and open circles) or in conditions of self-controlled light-dark cycles (crosses). Arrow indicates the sequence of conditions.

icant at $p=0.028$, or using the $U$-test of Mann-Whitney at $p=0.027$. Similarly, there is significantly more activity in LD$_s$ than in dim or bright LL. Contrary to these results, $\alpha$ in LD$_s$ has, on average, values in between those observed in dim or bright LL.

DISCUSSION

The results, first, convincingly demonstrate that, in the squirrel monkey, both the period, $\tau$, and the activity time, $\alpha$, are positively correlated with the intensity
of illumination. This contradicts a rule proposed by ASCHOFF (1959) according to which diurnal species should shorten τ with an increase in intensity of illumination, and it further contradicts the so-called circadian rule that predicts a negative correlation between τ and α (ASCHOFF, 1960). Critical examinations of these rules have been published by HOFFMANN (1965, 1967) and LOHMANN (1967). Much more data is available. These data indicate that all diurnal species of primates tested so far lengthen τ when the intensity of illumination is increased (TOKURA and ASCHOFF, 1978), and that similar correlations apply to the majority of other diurnal mammalian species (ASCHOFF, 1979). There is also increasing evidence that, in mammals as well as in other groups of animals, no consistent correlation exists between τ and α, and that both these parameters are separately controlled by light (GWINNER and TUREK, 1971; POHL, 1972; cf. also PITTENDRIGH and DAAN, 1976a,b). Under conditions of self-controlled light-dark cycles, the squirrel monkey has τ-values longer than those found in either dim or bright LL, and has α-values that are intermediate between those found in dim and bright LL. These findings agree well with those obtained from chaffinches, Fringilla coelebs and greenfinches, Carduelis chloris (ASCHOFF et al., 1968). In these two avian species, a mean τ of 24.9 hr was found in LD₈ as compared with 23.9 hr in dim LL (about 0.3 lux) and 22.6 hr in bright LL (about 80 lux); the α-values were 14.2 hr in LD₈, 11.0 hr in dim LL, and 17.1 hr in bright LL. With regard to τ, similar effects have been observed in man. Isolated subjects, living in an environment without time cues, had a mean τ of 24.89 hr in conditions of constant illumination as opposed to 25.34 hr in conditions of self-controlled light-dark cycles (p < 0.001; WEVER, 1973). The lengthening of τ under the influence of a self-controlled light-dark cycle represents the effect of a feed-back mechanism between the circadian system and the light stimuli. The effects can be understood on the basis of principles that are implicit in the processes underlying the entrainment of circadian rhythms (WEVER, 1967), and that are related to the general shape of phase-response curves (ASCHOFF, 1965). It should be noted that these considerations do not apply to light-dark cycles resulting from movements of an animal in space, e.g. between a lighted cage and a dark shelter (cf. ASCHOFF et al., 1968).

Normally, animals do not turn on and off lights by themselves as was the case in these experiments. However, it has been argued that mammals, even if kept in conditions of constant illumination, do in fact produce a light-dark cycle due to closing their eyes during sleep (WEVER, 1969). It is here that mammals differ fundamentally from other vertebrates. Reptiles, fishes and birds can perceive light by means of extraretinal photoreceptors within the brain (ERIKSSON, 1972; UNDERWOOD, 1973; MENAKER and UNDERWOOD, 1976) while, for mammals, the only known photoreceptors are the eyes. It seems possible that, in mammals, the alternation between closed eyes (during sleep) and open eyes (during activity time) has effects similar to those of a self-controlled light-dark cycle; under this assumption the relatively long periods shown by most mammals in LL could, at least partly,
be explained. It remains to be seen whether the difference in receptor mechanisms contributes to the fact that diurnal mammalian species, contrary to other diurnal vertebrates, mainly show a positive correlation between $\tau$ and intensity of illumination. This hypothesis could be tested indirectly in non-mammalian vertebrates by shielding photoreceptors in the brain against light (cf. MCMILLAN et al., 1975) and testing the influence of intensity of illumination of $\tau$ via the eyes only.

REFERENCES


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