

Continuous Light Inside a Cave Abolishes the Social Synchronization of the Circadian Rhythm in a Bat

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Summary. The bat *Hipposideros speoris* regulates its flight activity rhythm in the absence of time cues in a totally dark natural cave. The flight activity rhythm even of captive bats in total darkness entrained to the social cues available from free flying conspecifics. The social synchronization of the circadian rhythm was abolished in continuous illumination (LL) of 10–20 lx. All the captive bats ‘freerun’ in LL with τ longer than 24 h. The social entrainment was re-established following a few cycles of transients when total darkness was restored.

Introduction

Circadian rhythms ‘freerun’ during the continuous darkness (DD) of the arctic winter or the continuous light (LL) of the arctic summer, albeit with small fluctuations in light levels and temperature (Swade and Pittendrigh 1967; Müller 1968; Erkinaro 1969). Circadian rhythms also freerun under DD and LL conditions in the laboratory undergoing appropriate changes in period and frequency predicted by the Aschoff and Circadian Rules (Aschoff 1960; Hoffmann 1965; Pittendrigh 1960; Subbaraj 1979; Sundararajan 1980). Apart from the dominant role of the light/darkness cycles, biotic factors such as social stimuli are also capable of entraining biological rhythms (Rusak 1981; Chandrashekar 1982). We have investigated how the members of a colony of microchiropteran bats inhabiting a true cave under DD and constant temperature and constant humidity conditions still time their activity. Such conditions normally release circadian rhythms into freeruns. Experiments with trapped bats and flight activity monitoring inside a few such caves indicate that there is clear-cut evidence for social synchronization of the circadian rhythm in the bat *Hipposideros speoris* (Marimuthu et al. 1978, 1981). Bats held captive some 40 m inside a cave in DD still began their nightly

activity to coincide with the onset of the foraging activity of the colony. We undertook a new series of experiments producing LL conditions inside the natural cave, which interestingly abolished the social synchronization.

Materials and Methods

Four *H. speoris* were trapped and held in flight activity cages and their flight was recorded on mechanical thermohygrograph drums under DD and LL conditions. The details about the study site and the recording techniques have been given elsewhere (Marimuthu et al. 1981). LL conditions were created by using incandescent bulbs and an automobile lead-acid battery. The incident light at the cage level varied between 10 and 20 lx. The battery was changed after 36–60 h at random intervals for recharging, by replacing a second freshly charged battery. The captive bats were hand-fed at irregular hours of day and night with minced cockroaches. In addition each bat was provided with 2–3 drops of ‘vitamin B₁₂ B complex liquid’ and water was available ad libitum. The caged bats could obviously hear orientation and/or communicative sounds from their unrestrained conspecifics. The darkness inside the cave when the light was turned off is absolute (as measured on the log scale of a UDT optometer) and the temperature and relative humidity remain constant at 27 ± 0.2 °C and $95 \pm 1\%$ respectively.

Results

Figure 1 sets forth data for one bat. During the initial period of DD its daily activity rhythm coincided precisely with that of the free flying conspecifics thus undergoing social entrainment. However, the same bat (and 3 other bats whose activity data are presented in Fig. 2a, b and c) freerun in LL of 10–20 lx *in spite of the social cues still available to them*. The period (time between onset of activity from one day to the next) is longer than 24 h in LL. LL seems to have abolished the social synchronization of the circadian rhythm in this bat. Bats 2a and 2b (Fig. 2) exhibited, *in addition to freerunning rhythms*, activity bouts for 28 days and 13 days, respectively, corresponding to onset of activity of the conspecifics. The bats flew inside activity cages for about 11–100 min just as the con-

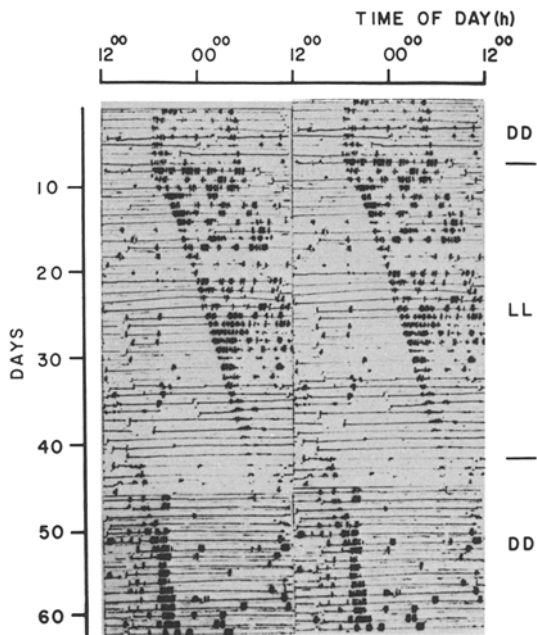


Fig. 1. The flight activity patterns of a captive bat for 62 days recorded 40 m inside a narrow cave with just one opening. Days 1–7: DD (continuous darkness); days 8–41: LL (continuous light) of 10–20 lx; days 42–62: DD. Activity bouts are indicated by vertical patches and the horizontal lines indicate rest. The activity/rest data containing the original felt pen tracings are double-plotted so that activity data for successive days are staggered to facilitate visual evaluation. In this scheme of presentation the activity data for day 1 would lead horizontally to data for day 2, data for day 2 to data for day 3 and so forth

specifics flew out of the cave to forage. Such flights of these bats coinciding with the onset of the colony activity account for a clear-cut *exogenous* component which expresses itself regardless of the phase of the freerunning rhythms. These exogenous components merge into the activity bouts when the rhythm crosses them during the freerun. The onset of the freerunning oscillatory component for bat 2a crosses the exogenous component around days 37 and 38 without any sign of even a temporary synchronization, i.e. there is no 'relative coordination' (von Holst 1939) during the whole run. The freerunning rhythm re-entrained to the social cues as seen in Fig. 1 when DD was restored. The light was turned off at phase which was 180° off course relative to colony activity. Re-entrainment set in after a few 'transient cycles'. The onset component of the re-entrained rhythm exactly coincided with the onset of colony activity accounting for phase angle close to 0°.

Discussion

The circadian rhythm in the flight activity of captive members of the microchiropteran bat *Hipposideros speoris* socially entrains to the rhythm of free flying conspecifics (Marimuthu et al. 1978, 1981). However, circadian rhythms of the captive bats freerun in LL of 10–20 lx *in spite of the social cues available* to them. LL thus apparently abolished the social synchronization of the circadian rhythm

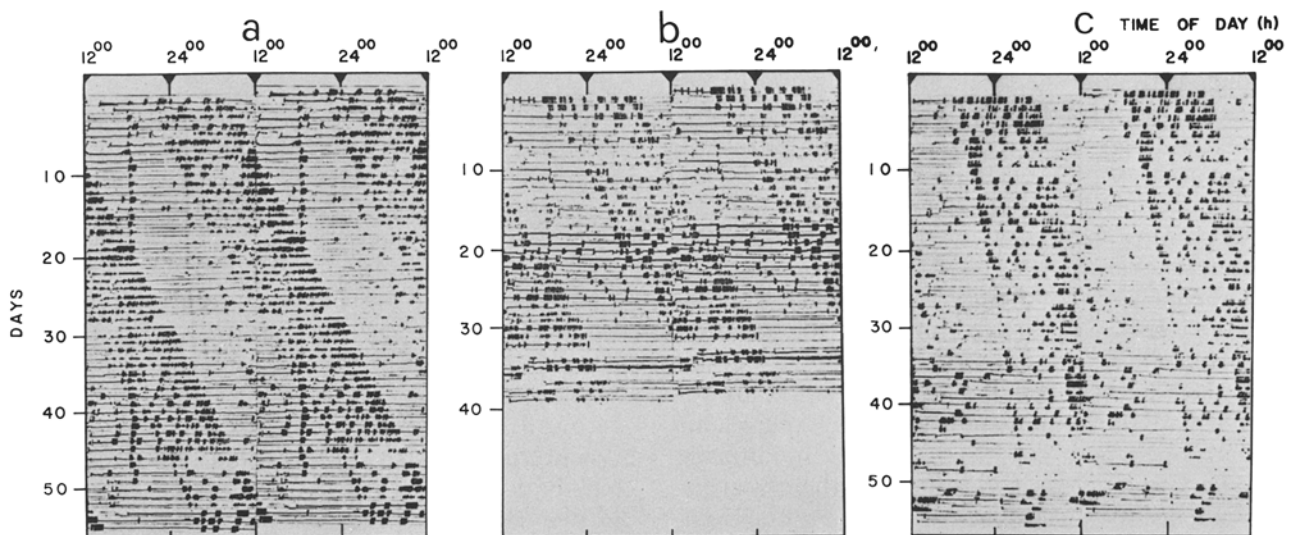


Fig. 2. The flight activity patterns of three captive bats for 39 days (b) and 55 days (a and c) in LL of 10–20 lx. Other details are as in Fig. 1

in this bat species. The exogenous components exhibited by two individuals (Fig. 2a and b) represent a stimulus-response situation and may not merit oscillator status. This may be the phenomenon of response that was termed 'positive masking' (Aschoff 1965, 1981; Daan and Aschoff 1975). Similar kind of exogenous components were exhibited by female crickets when the calling songs of male crickets were played back in a background illumination of 50 lx, in addition to their original freerunning period of 25.3 h (Loher 1979). Even though the freerunning oscillatory component of one of our captive bats crosses the exogenous component there is no evidence for any 'relative coordination' (von Holst 1939; Aschoff 1965; Lohmann and Enright 1967). We did observe that the artificial light that shone inside the cave scared away a few bats that roosted otherwise in and around the area inside the cave where the recording was carried out. To that extent the 'social cues' might indeed have attenuated in the immediate vicinity. However, within a week or so the bats returned to their original roosting sites, closer to the captive bats. The exogenous component seen so clearly in bats 2a and 2b is further evidence that the onset of the activity of the bat colony had made itself felt, *even though it could not synchronize the rhythm*. The freeruns indicate that whatever social cues that prevail are not 'reaching the clock'. In LL the circadian rhythm apparently uncouples from social 'zeitgebers'. This of course is a situation that does not obtain in nature much less in a cave. Aschoff (1960) stated that in birds, unspecific zeitgeber(s) if ever effective (at 0.4 lx) become ineffective if the continuous illumination is increased to higher intensities'. In our experiments even the specific zeitgeber(s), proven to be generated by conspecifics, became ineffective at relatively higher intensities of LL. The phenomenon might indeed arise from complex events. In addition to exerting an un-coupling influence of the circadian rhythm LL may also contribute to a conflicting zeitgeber-situation. The re-entrainment of the rhythm by the social cues after the light was turned off (Fig. 1) further confirmed that it is LL that uncoupled the circadian rhythm from the social cues.

Sulzman et al. (1977) reported that the locomotor activity of squirrel monkeys in noise/silence cycles of 24 h periods did not entrain or synchronize the rhythm in LL of 600 lx, but the food cycles did synchronize it. It would be of great interest in the context of our findings to know whether squirrel monkeys would have entrained to the noise cycles in DD.

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