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Acoustical Entrainment of Circadian Activity Rhythms in House Sparrows: Constant Light is not Necessary

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With 3 figures

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Abstract

Cycles of presence/absence of social factors can sometimes entrain the circadian activity rhythms of diurnal animals kept under constant light. This might represent a special case of photic entrainment; social factors might awaken the subjects and make them see the light at times when they are normally unaware of it because of sleep. The present study attempted to falsify this hypothesis by entraining the activity rhythms of house sparrows (*Passer domesticus*) kept in constant darkness. The zeitgebers used were daily 2-h playbacks of conspecific vocalizations, and daily 1.5-h acoustical (non-conspecific) disturbance. 7 birds were tested; four (all males) entrained to both stimuli, while the other three (all females) mostly showed relative coordination. Entrainment took place when the stimuli coincided with the late part of the birds' normal sleep time. No anticipatory activity preceded the daily stimulus presentations. In a second experiment, 8 more male sparrows in constant darkness began their free-running activity earlier (phase-advanced) on days that followed the presentation of a single 2-h bout of acoustical disturbance in the last half of their normal sleep time. Stimulus presentations at other times had no effect. Opening the eyes and seeing the light are not necessary for acoustical (and social) entrainment, but other physiological consequences or correlates of sleep interruption may be involved.

Introduction

When kept in constant light (LL) or constant darkness (DD), animals usually exhibit sleep/activity cycles with a period different than 24 h (for reviews, see BRADY 1981; RUSAK 1981). This "free-running period" reflects the endogenous rhythmicity of an internal clock responsible for the generation of circadian activity. This clock is sensitive to a number of exogenous factors. The most powerful of these factors is light. It is relatively easy to force an animal to adopt a period of, for example, 24 h by exposing it to pulses of light or dark presented at 24-h intervals in an otherwise constant light environment (e.g. ASCHOFF et al.

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1982). The animal's activity rhythm is then said to be "entrained" to 24 h by light, and light is called a "zeitgeber". The mechanism involved in this type of photic entrainment is thought to be one whereby light pulses "phase-shift" the rhythm daily relative to its normal free-running phase (see PITTENDRIGH 1981; MOORE-EDE et al. 1982).

Social factors constitute another class of zeitgebers. Social entrainment has been observed in studies where animals were exposed to cycles of presence/absence of conspecifics (MARIMUTHU et al. 1981; VISWANATHAN & CHANDRASHEKARAN 1985; MROSOVSKY 1988) or playbacks of conspecific vocalizations (GWINNER 1966; MENAKER & ESKIN 1966). Social entrainment has also been inferred from observations of synchronous free-run (MENAKER & ESKIN 1966; BOVET & OERTLI 1974; WEVER 1979; CROWLEY & BOVET 1980; KAVALIERS 1980; REGAL & CONNOLLY 1980; DAVIS & GORSKI 1985; see also TAKAHASHI et al. 1984). Despite this relative abundance of data, the mechanisms underlying social entrainment are unknown. One possibility is that social agents awaken animals during their normal sleep period, making them open their eyes and see the light at a time when they would normally be unaware of it because of sleep. Thus light, not the social agents per se, could be responsible proximally for social entrainment. This hypothesis is especially relevant in the case of diurnal animals, because their clocks are sensitive to light during their normal sleep time (e.g. ESKIN 1971), and because all social entrainment studies on diurnal animals have so far been conducted in LL (people being an exception, see ASCHOFF et al. 1971; WEVER 1979). The hypothesis is less relevant in the case of nocturnal species because their clocks are not normally sensitive to light during their normal sleep time (MOORE-EDE et al. 1982).

To falsify the hypothesis that light is necessary for social entrainment in diurnal animals, one should try to entrain the activity rhythms of individuals kept in DD. I conducted such an experiment with the house sparrow (*Passer domesticus*), one of the few diurnal species that is known to remain healthy and rhythmic in constant darkness (see ESKIN 1969, 1971). MENAKER & ESKIN (1966) have previously obtained cases of social entrainment in sparrows kept in dim LL and exposed to daily playbacks of conspecific vocalizations. I used a similar acoustical stimulus in the present DD experiment. To determine whether the conspecific nature of the stimulus was essential for entrainment, I also tried to entrain sparrows in DD to a nonconspecific acoustical stimulus. Finally, to determine whether acoustical entrainment could result from daily phase-shifts of an otherwise free-running rhythm (as in photic entrainment), I obtained a preliminary phase response curve (PRC, see DECOURSEY 1960) for the nonconspecific acoustical stimulus.

Material and Methods

Subjects and General Procedures

All sparrows were mist-netted in Toronto. Adult birds were brought in the laboratory and put into individual 24 × 35 × 43 cm cages with free access to water and ground-up chicken starter mash (Purina Start and Grow). Each cage was placed in an individual, partially soundproof, chamber (internal dimensions 62 × 60 × 55 cm or 72 × 70 × 60 cm). Each chamber was equipped with a remote fan (for continuous ventilation and low background noise), a fluorescent tube (General Electric F15T12 Cool White) connected to a remote timer, and an 8-ohm speaker (diameter 10 cm) connected to a remote auto-reverse tape player (Realistic SCP-25). The 10 chambers were in the same temperature-controlled soundproof room. Temperature within the room and chambers was 13 ± 2 °C in DD. Food and water were replaced once a week, always during the birds' normal period of activity. No obvious phase-shifts of activity were observed on the records (see below) following cage maintenance.

Each cage had two hopping perches, each equipped with a microswitch. The two microswitches were connected in parallel to a remote Esterline-Angus recorder. Successive 24-h records of hopping activity were pasted below each other to obtain actograms. Times of daily onset of activity were measured directly on the actograms. Activity onsets were defined as the first hop that was followed by at least one more hop within the next 50 min. To prevent using obvious outliers, a daily time of onset also had to be within 2 h of the previous daily time of onset. Free-running periods (taus) were measured by calculating the slope of lines that were either eye-fitted (entrainment experiment) or fitted by least-square regression (PRC experiment) through the activity onsets of selected portions of the rhythms.

Entrainment Experiment

For this experiment, 10 sparrows were captured in Nov.—Dec. 1986. They were maintained under LD 10 : 14 for 8—36 days, and then put in DD for the remainder of the experiment. Three of the sparrows were not tested for entrainment: one showed insufficient activity, and two had taus too close to 24 h, the chosen period of entrainment. The remaining 7 birds (four males and three females, all free-running with tau > 24 h) were subjected to two consecutive entrainment schedules.

After an initial 13—47 days in DD, they first received daily 2-h playbacks of conspecific vocalizations, starting at the same time each day. The tape was a 60-min recording obtained at a sparrow roost on the morning of 15 June 1986. It contained persistent "chirrup" calls from 1—4 individuals, and occasional "alarm" calls from 1 individual. A 2-h playback consisted of the tape being played twice, at 90 db (measured at the speaker). This zeitgeber presentation lasted 18—37 days. Following this, the sparrows were allowed to free-run again for 22—49 days. Then, for 23—34 days, starting at the same time each day, the birds were disturbed at 12—15 min intervals for 1.5 h.

As a means of disturbance, I opened the soundproof chambers and ran a fingernail along the side of the cages five times, thus producing a rattling sound that always alarmed the birds (opening the chambers allowed me to observe the sparrows' behavior with a FJW infra-red visionscope; use of the scope was usually limited to the first, middle, and last disturbance of each 1.5-h series). Disturbance was the nonconspecific stimulus used to determine whether a stimulus had to be conspecific for entrainment to occur. After this treatment, the sparrows were allowed to free-run again for more than 14 days.

Entrainment was considered to have taken place if the following three criteria were met: (1) the phase of the post-entrainment rhythm could not be predicted by extrapolation of the pre-entrainment rhythm, (2) the rhythm period during zeitgeber presentation was within 0.05 h of the zeitgeber period, and (3) both pre- and post-entrainment taus differed from the zeitgeber period by more than 0.05 h.

Phase Response Curve Experiment

For this experiment, 10 adult sparrows (all males) were captured in May 1987. They were placed in LD 12 : 12 for 8—15 days, and then in DD for the remainder of the experiment. Two of the sparrows could not be used because of diffuse activity in DD. The other 8 birds received single pulses of disturbance (as above, except that the pulses were 2-h long) at various circadian times. All birds but one received a total of four such pulses (the other bird received three pulses) at 17—19 days intervals. The first pulse was given no earlier than 20 days after transfer into DD.

Phase-shifts were measured by calculating two separate least-square regression lines on the actograms, one going through the first 8 definable activity onsets immediately preceding the pulse, and one through the 8 subsequent onsets (excluding the first onset immediately following the pulse).

The two regression lines were extrapolated to the day of the first onset immediately following the pulse; the time interval between the two lines was taken as the amount of phase-shift. Circadian time (CT) for the onset of the 2-h pulse was calculated relative to the onset of activity following it (CT = 0) as determined by the extrapolation of the pre-pulse regression line.

In order to assess the inherent variability of unmanipulated rhythms, "baseline phase-shifts" were also measured by the method described above on segments of rhythms between pulses. This was done three times per bird, using the three 17-d segments of rhythm between first and second, second and third, and third and fourth pulses respectively, and using the day in the middle of each segment.

Results

Entrainment Experiment

All four males entrained to both the daily playbacks and the daily disturbances. Entrainment took place when the stimuli coincided with the late part of the birds' sleep time (Fig. 1 A, B). No anticipatory activity preceded the daily stimuli. After entrainment, the birds' activity rhythms resumed free-running from a time 0—2.5 h after the last daily stimulus. Taus before, between, and after entrainment schedules varied between 24.11 and 25.00 h for these males (Table 1).

One female (Fig. 1 C) entrained to the daily disturbance regime in a manner similar to that of the males. She did not completely entrain to the daily playbacks but nevertheless showed "relative coordination" (the phase of the rhythm after zeitgeber presentation could not be predicted by extrapolation of the rhythm before zeitgeber presentation, and tau during the entrainment schedule got closer

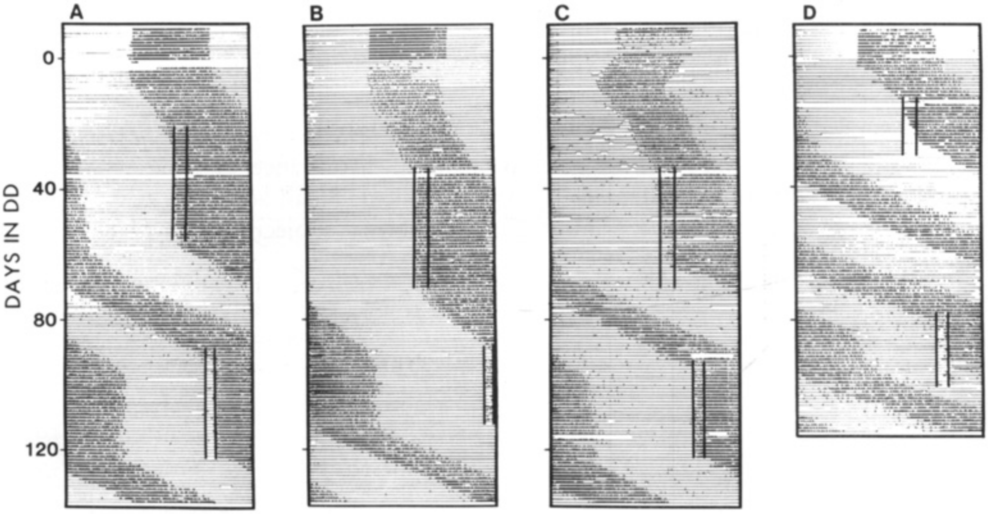

Fig. 1: Actograms (perch-hopping) of four house sparrows kept in DD and exposed to daily 2-h playbacks of conspecific vocalizations (top set of parallel vertical lines) and to daily 1.5-h acoustical disturbances (bottom set of parallel vertical lines). Each horizontal line represents 24 h, and successive days are below each other. (A) and (B) Males no. 2 and 4 (see Table 1) respectively, showing entrainment to both stimuli. (C) Female no. 5, showing relative coordination to the daily playbacks and entrainment to the daily disturbances. (D) Female no. 6, showing relative coordination to both stimuli

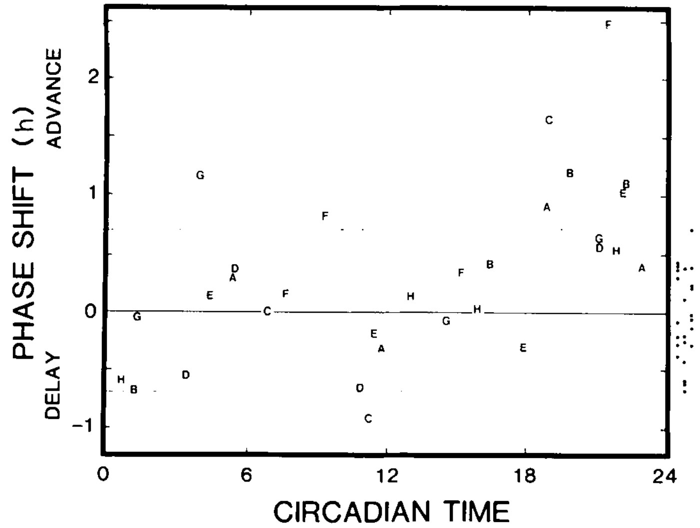

Fig. 2: Phase response curve for 2-h pulses of acoustical disturbance given to house sparrows kept in DD. Letters stand in place of data points, with each letter referring to an individual bird. The dots on the right show baseline phase-shift values, measured on segments of unmanipulated rhythms; the dotted lines indicate the range of these baseline shifts

to, but did not equal, 24.00 ± 0.05 h). A second female (Fig. 1 D) displayed relative coordination during both the playback and the disturbance regimes. The third female showed relative coordination during the disturbance regime, but was not affected by the playback schedule. For these females, taus before, between, and after entrainment schedules varied between 24.27 and 25.67 h (Table 1).

Phase Response Curve Experiment

Fig. 2 shows the PRC for the 2-h pulses of disturbance, and Fig. 3 shows some of the actograms obtained in this experiment. Small advances and delays were observed between CT 0 and CT 12 (the birds' subjective day, or normal

Table 1: Period lengths (in h) of activity rhythms of house sparrows kept in constant darkness. Columns show data before, during, and after consecutive presentations of two zeitgebers (first daily 2-h playbacks of conspecific vocalizations, then daily 1.5-h acoustical disturbance)

Bird # (sex)		Playback			Disturbance	
	before	during	after	before	during	after
1 (male)	24.31	24.00	24.50	24.50	24.00	25.00
2 (male)	24.33	24.00	24.75	24.83	24.00	24.80
3 (male)	24.35	24.00	24.11	24.25	24.00	24.50
4 (male)	24.25	24.00	24.60	24.60	24.00	25.00
5 (female)	24.27	24.00—25.00[a]	24.86	24.86	24.00	24.83
6 (female)	24.43	24.14—24.75[a]	24.80	25.17	24.17—24.75[a]	25.50
7 (female)	24.36	24.89	25.50	25.67	24.22—25.75[a]	25.67

[a] Period was unstable during relative coordination.

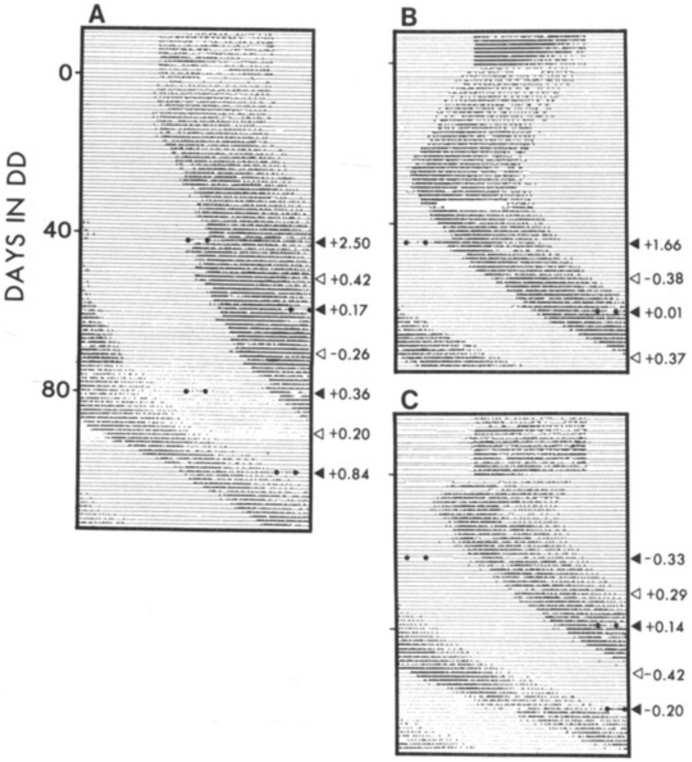

Fig. 3: Actograms of three male house sparrows kept in DD and exposed to single 2-h pulses of acoustical disturbance (between dots). Closed triangles on the right indicate pulse days. Open triangles indicate days when baseline phase-shifts were calculated on unmanipulated rhythms. Numbers give the calculated phase-shifts in h. (A) Complete record of bird F (see Fig. 2). (B) and (C) Partial records of birds C and E respectively

activity time) and between CT 12 and CT 18 (the first half of the birds' subjective night, or normal sleep time); only 14 % (3/21) of these advances and delays were outside the range of baseline values measured on unmanipulated rhythms (Fig. 2). Between CT 18 and CT 24 (the second half of the birds' subjective night), only advances were obtained, and 60 % (6/10) of these advances were greater than the largest baseline value (Fig. 2). Thus the free-running sparrows in constant darkness began activity earlier than expected on days that followed presentation of a 2-h disturbing stimulus given in the second half of their normal sleep period. In this experiment, pre-pulse taus were always greater than 24 h (range, 24.09—25.55 h; mean, 24.69 h; N = 30) except in one case (23.89 h).

Discussion

The results show that it is possible to entrain and phase-shift the activity rhythms of house sparrows by using acoustical stimuli in DD. All cases of entrainment involved activity rhythms free-running with tau > 24 h, and a zeitgeber period (T) equal to 24 h. During entrainment, both zeitgebers coincided with the late part of the birds' normal sleep time. This is consistent with the large advances observed in the PRC experiment between CT 18 and CT 24, the last half of a diurnal animal's sleep time. This shows that entrainment probably occurred via daily phase-advances caused by the stimuli falling on the appropriate part of the PRC. In this respect, entrainment by sound is similar to entrainment by light (see PITTENDRIGH 1981).

Not all animals entrained. Whereas all four males entrained, the three females showed mostly relative coordination. In this study, females exhibited the longest taus, especially when entrainment failed to take place (Table 1). Thus larger (too large?) daily phase-advances may have been required for entrainment to occur in those females. Longer taus may constitute a sex-specific character, but this seems unlikely in light of previous reports of no sex differences in tau in house sparrows (MENAKER & ESKIN 1966; ESKIN 1969). It also remains to be seen whether the females' lack of entrainment to T = 24 h was causally related to longer taus, or to some other, unknown, sex-specific character. Alternatively, given the small sample size, the relationship between sex, tau, and entrainability to T = 24 h may have been coincidental. Whatever the explanation, the fact that some subjects did not completely entrain indicates that the zeitgebers were weak.

I used two stimuli as zeitgebers, one conspecific and the other not. Both proved effective. Moreover, results from both entrainment schedules present similarities. First, in both cases, not all animals entrained. Second, entrainment took place when the stimuli coincided, at least in part, with the late portion of the birds' normal sleep time. Third, no anticipatory activity preceded the daily presentations of stimuli. These three features can also be found in the results of other studies where various conspecific or nonconspecific stimuli were used for entrainment (to T < tau), in diurnal as well as nocturnal species. These stimuli included playbacks of conspecific sounds in house sparrows (MENAKER & ESKIN 1966), social interaction in bats (*Hipposideros speoris*) (MARIMUTHU et al. 1981) and in hamsters (*Mesocricetus auratus*) (MROSOVSKY 1988), cage shaking in a house finch (*Carpodacus mexicanus*) (ENRIGHT 1975), and cage changing in hamsters (MROSOVSKY 1988). The similarities also extend to other studies where the animals were entrained to T > tau, except that the stimuli then coincided with the early part of the sleep period instead of the late part, and no activity followed them [playbacks of conspecific vocalizations in a serin (*Serinus serinus*) and pine siskins (*Carduelis spinus*), GWINNER 1966; mechanical noise in greenfinches (*Carduelis chloris*) and chaffinches (*Fringilla coelebs*), LOHMANN & ENRIGHT 1967; removal of mother in mice (*Mus booduga*), VISWANATHAN & CHANDRASHEKARAN 1985].

These similarities suggest that conspecific and nonconspecific zeitgebers share a common feature in their mode of action. That entrainment occurs when the stimuli coincide with part of the normal sleep time, in both diurnal and nocturnal animals, suggests that (1) the stimuli awaken the animals, and (2) a correlate or a consequence of prolonged sleep interruption is involved.

Regarding the first of these two points, conditions in which animals are kept for entrainment studies are usually as uniform and constant as possible, and therefore new stimuli, even when nonconspecific and repeated day after day, may easily be arousing enough to maintain the subjects awake during part of their normal sleep time. If not, then the animals may not entrain; this may be the reason for the observed lack of entrainment in some individuals. Direct behavioural observations or constant EEG recordings during zeitgeber presentation are necessary to further investigate this question.

As to the possible role of various correlates or consequences of sleep interruption, my results show that, at least for one diurnal species, one possible consequence, opening the eyes and seeing the light, does not play a major role because typical entrainment can still be obtained in DD (see also MARIMUTHU et al. 1981, for an example of social entrainment in DD with a nocturnal species, the bat *H. speoris*).

Among other possible correlates of sleep interruption are changes in brainwave activity (AMLANER et al. 1985; DEWASMES et al. 1985; VAN LUIJTELAAR et al. 1987), and possible stress caused by the sleep-interrupting stimuli, along with an associated release of adrenal corticoids in the bloodstream (see MEIER et al. 1973). The question of whether these neural and humoral phenomena can reach and affect the internal clock has not yet been addressed.

Theory holds that the timing of activity and sleep states is under the control of the internal clock. This does not preclude the possibility of exogenously-provoked arousal or sleep having input to the clock. This possibility has been raised in previous studies. After working on the rhythms of canaries (*Serinus canaria*), WAHLSTRÖM (1971) proposed that light itself might affect the internal clock by arousing the birds at specific times. Certainly light seems to be arousing for birds, and house sparrows often are active whenever lights are on (BINKLEY 1977; BINKLEY & MOSHER 1985).

In another study (GWINNER & BENZINGER 1978), pinealectomized starlings (*Sturnus vulgaris*) were entrained to daily injections of melatonin; the authors pointed out that melatonin often has sedative or sleep-inducing effects, and that entrainment might have resulted from a direct effect of the drug on the pattern of sleep and wakefulness.

Another environmental factor that may affect the clock via arousal and sleep is ambient temperature. ESKIN (1971) obtained evidence that activity rhythms of house sparrows in DD can be entrained by high-amplitude cycles of temperature. It appears that sleep onset often followed the daily temperature drops in that study, and birds are known to become inactive and sleepy under very cold temperatures (REEBS 1986 a, b, and references therein).

The influence of such exogenously-provoked arousal or sleep on the internal clock could compete with that of light. In the case of acoustical stimuli, my results suggest that, in house sparrows under LD, activity onset could be phase-advanced relative to light onset by the introduction of acoustical disturbances in the second half of the dark period.

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