CIRCADIAN ACTIVITY RHYTHMS IN CHAFFINCHES (FRINGILLA COELEBS) UNDER CONSTANT CONDITIONS

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The 24-hour rhythms of activity and other physiological as well as psychological functions are based on an endogenous biological oscillation. This has been proven by experiments in which animals kept in constant conditions continued to show a rhythm with a frequency of about that of the earth's rotation (ASCHOFF 1963a). In order to indicate that the period of such a free-running rhythm deviates more or less from 24 hours, it has been called circadian (from the latin circa=about and dies=day; HALBERG 1959). Under natural conditions, the circadian period is synchronized to exactly 24 hours by means of periodic factors in the environment, called Zeitgeber (ASCHOFF 1951, 1954). In constant conditions, the frequency of the rhythm depends on several factors among which the intensity of illumination is of first order. Observations of many species allow formulation of the following circadian rule (ASCHOFF 1960): With an increase in light intensity, the circadian period becomes shorter in light-active animals and longer in dark-active animals. Two other properties of the oscillation are also correlated to light intensity: a) the total amount of activity during each period and b) the ratio between the time span when the animal is active (activity-time) and the time span when the animal is at rest (rest-time). The sign for both correlations is positive in light-active and negative in dark-active animals. The data published in this report give further support to the validity of the circadian rule for all three measurements in a light-active species.

METHOD AND PROCEDURE

Eight male and eight female chaffinches (Fringilla coelebs L.) were kept individually in cages and enclosed in four sound-proof chambers with constant temperature and only artificial illumination. Activity of the birds was measured by means of microswitches below the perches. Each contact elicited by a bird hopping on the perch was recorded simultaneously on an event-recorder and on a print-out counter.

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Food and water was always available. In a first series of experiments, the birds were kept consecutively in the following conditions of constant illumination: 17 days in about 5 lux, 8 days in 0.2 lux, 19 days again in 5 lux and the final 7 days in 1.0 lux. Two out of the 16 birds showed now clear rhythm, mainly because of a more or less continuous activity. For the remaining 14 birds, the measurements from all four conditions were used for the results. Seven out of the 14 birds were tested two months later in a second series of experiments; the birds were exposed for 7 days to about 5 lux and for 8 days to about 1.0 lux. Depending on the position in the chamber, the light-intensity in all experiments varied from cage to cage; for the final analysis, the individually measured intensities were used.

**RESULTS**

The systems used for recording activity make it possible to graph the results in two ways. The event recorder shows when the bird is active and when it is at rest. The printout counter gives the number of perch-hoppings for the unit of time chosen. Based on the figures for hourly accumulated and printed contacts, Fig. 1 demonstrates the pattern of activity of a chaffinch for two different intensities of illumination. There is a clear circadian period (τ), conventionally measured from one sharp onset of activity to the following one.

![Fig. 1. Activity rhythm of a chaffinch in constant conditions. Intensity of illumination alternating from approximately 5.0 lux to 0.2 lux and back to 5.0 lux.](image)

Each period is divided into two sections: The activity-time (a), measured from onset to end of activity, and the rest-time (p). From the graph, it is evident, that in 5 lux the rhythm differs from that recorded in 0.2 lux. In brighter light, the bird is more active and the ratio between activity-time and rest-time is greater than in dimmer illumination.

A careful examination of the graph in Fig. 1 indicates that the circadian period τ is shorter than 24 hours both in 5 lux as well as in 0.2 lux. This becomes more conspicuous in Fig. 2, where original records of the event-recorder are reproduced. The daily strips for one bird have been pasted beneath each other on a chart; the whole chart then is duplicated. On the event-recorder, each perch-hopping results in a single mark; when the bird becomes more active, the marks fuse into a black horizontal bar. In constant
Fig. 2. Original records of the activity rhythm of a chaffinch in constant conditions. The daily strips of the eventrecorder are pasted beneath each other on a chart. The whole chart is then duplicated. Intensity of illumination for the four sections of the experiment are given on the right margin.

Illumination of 4.8 lux, there is some activity all the time. Nevertheless, a clear circadian rhythm is to be seen from the onsets of main activity (left end of the black bars). These onsets occur each day about two hours earlier than on the preceding day, indicating a circadian period of roughly 22 hours. At day 17, shortly after noon, the intensity of illumination is lowered to 0.16 lux. As a consequence, the circadian period immediately becomes a little longer than 24 hours. Contrary to this, the activity-time is shortened to only 11 hours and a rest-time of about 13 hours appears (white area in Fig. 2). When after 7 days the bird is again exposed to 4.8 lux, it reassumes a circadian period of about 22 hours with an activity-time as long as the whole period. Finally, in 1.3 lux, the circadian period and the activity-time reach values which are in between those measured in 4.8 and 0.16 lux.
Examples of circadian rhythms for four more finches are given in Fig. 3. The graphs are redrawn from the original records and combined in one picture with a five-times extended abscissa; the picture shows only the activity-times. In all cases, a change from brighter to dimmer illumination results in a longer circadian period and a shorter activity-time. The slope lines through onset and end of activity, drawn by eye, emphasize the mean period for each condition and its abrupt change with the change in light intensity. Although different from bird to bird the frequencies are remarkably stable for each individual. The changes in activity-time are also distinct, but sometimes less abrupt than the changes in frequency. With a turn to dimmer illumination, it may happen that activity-time shortens continuously through all 7 days; and after again presenting brighter illumination, it may last several days until a new steady-state of activity-time is reestablished (third bird from the left in Fig. 3). In those cases, from the lines drawn through onsets or the lines drawn through ends of activity, different values for the mean period can be computed. For this reason, the period always is measured by using the midpoints of activity-time. The merits of such a procedure and its theoretical base are explained elsewhere (ASCHOFF 1964a, 1965).

As indicated in Fig. 3, it is easy to compute average values for period $\tau$ as well as for activity-time $\alpha$ for each individual and for each of the four sections of the experiment. These average values are presented in Fig. 4 on the ordinate against a logarithmic scale of light intensity on the abscissa. The results for the first and third section, both with an illumination of about 5 lux, have been averaged. The graph also includes the values for total amount of activity per 24 hours; for 10 out of the 14 birds, these data are
available only for two light-intensities. In all cases, the period is negatively correlated and the activity-time positively correlated to light intensity. The amount of activity also increases in all but one bird with an increase in intensity of illumination.

**Table 1.**

<table>
<thead>
<tr>
<th>lux</th>
<th>τ (hours)</th>
<th>α (hours)</th>
<th>α : ρ</th>
<th>Amount of activity</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Amount of activity</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(contacts/24 hours)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>February</td>
<td>4.58</td>
<td>22.45±0.39</td>
<td>17.77±1.76</td>
<td>3.8</td>
</tr>
<tr>
<td>0.98</td>
<td>23.40±0.24</td>
<td>13.71±0.80</td>
<td>1.4</td>
<td>4060±970</td>
</tr>
<tr>
<td>April</td>
<td>4.68</td>
<td>22.11±0.53</td>
<td>16.97±1.20</td>
<td>3.3</td>
</tr>
<tr>
<td>0.98</td>
<td>23.42±0.38</td>
<td>12.60±0.77</td>
<td>1.2</td>
<td>2450±710</td>
</tr>
</tbody>
</table>
There is a fair amount of interindividual variability in the data. The results, however, for one individual are quite reproducible, at least with regard to period. The data for seven birds which have been tested a second time after a two month interval in two light intensities, are listed in Table 1. The values for $\tau$ are nearly identical in both sets of experiments. Activity-time is shortened by roughly one hour in the second test, and the amount of activity is reduced to about half that what has been measured first. Apart from these changes, the dependency of the parameters on intensity of illumination is the same in both series.

**DISCUSSION**

Circadian rhythms can be treated as self-sustained oscillations in a technical sense (PITTENDRIGH and BRUCE 1957, PITTENDRIGH 1958, ASCHOFF 1960, 1964b). The graphs in Fig. 3 indicate a relatively high degree of precision of these oscillations which change machine-like from one frequency to another one in response to a change in environmental conditions. Furthermore, the graph in Fig. 1 demonstrates, that the oscillation continues undamped and keeps an average, although variable, range which again is determined by light intensity. (For the use of 'range' instead of 'amplitude' c.f. ASCHOFF, KLOTTER, WEVER 1965).

Of special interest are the changes of the ratio between activity-time and rest-time in combination with the changes of total activity (c.f. Table 1). The always positive correlations between these two parameters has given rise to a special circadian model. (ASCHOFF and WEVER 1962a, 1962b, ASCHOFF 1963b). In view of this concept, the discontinuous rhythm of activity and rest is based on an underlying continuous oscillation and on a threshold. Activity starts when the basic oscillation passes upwards through the threshold, and it ends when—after about half a period—the oscillation crosses the threshold downwards. The mean value of all instantaneous values of the basic oscillation has been called the level. Obviously, the relative position of the level to the threshold determines the ratio between activity-time $\alpha$ and rest-time $\rho$. An increase in the $\alpha : \rho$-ratio means an upward movement of the level relative to the position of the threshold. This will be accompanied by an enlargement of that integral area of the oscillation which is above the threshold. If this area is related to activity, the total amount of activity has to be increased more than only proportional to the lengthening of activity-time. The date in Table 1 support this conclusion: With an increase in the $\alpha : \rho$-ratio from 1.4 to 3.8 (February experiment) or from 1.2 to 3.3 (April experiment) there is an increase of the activity not only for 24 hours but also for one hour of activity-time (last column of Table 1). In line with this reasoning is the fact that the general decrease in activity from February to April is accom-
panied by a shortening of $\alpha$ and a small decrease in the $\alpha:\rho$-ratio. However, activity as measured by perch-hopping is influenced by many factors, including mechanical disturbances of the microswitches. It is therefore plausible that the amount of activity is highly variable, and subjected to long term trends depending on the physiological state of the bird as well as on functioning of the recording system. The two other parameters, period and $\alpha:\rho$-ratio, are less influenced by those side-effects. They primarily reflect properties of the oscillation. For a given environmental condition, their values are reproducible even after longer time intervals (c.f. TABLE 1), indicating that the oscillator is fairly stable.

SUMMARY

Under constant conditions of temperature and light, with food and water always available and without perturbation by periodic noises, individually caged chaffinches (Fringilla coelebs L.) show a clear circadian rhythm of locomotor activity. The period $\tau$ is divided in activity-time $\alpha$ and rest-time $\rho$. Period and activity-time as well as the average amount of activity per 24 hours depend on intensity of illumination. With an increase in light intensity from about 0.2 lux to about 5.0 lux, the period becomes shorter and the activity-time longer. The amount of activity increases more than proportionally to the lengthening of activity-time. These results are in agreement with the circadian rule for light-active animals. They are interpreted in view of a special model. This model describes the discontinuous rhythm of activity and rest by a continuous basic oscillation which passes twice during each period through a threshold. The bird is active as long as the oscillation is above the threshold. Changes in the $\alpha:\rho$-ratio, in combination with the changes in amount of activity, are explained as changes in the position of the level of the oscillation relative to the position of the threshold. Level and frequency of the circadian oscillation are positively correlated to each other and to the intensity of illumination.

REFERENCES


