A Survey on Biological Rhythms

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The recurrence of any event within a biological system at more-or-less regular intervals can be considered a biological rhythm (Kalmus, 1935). The notion of a rhythm is sufficiently vague (i.e., not defined in physical terms) to be useful in listing a wide variety of phenomena that might reflect quite different underlying mechanisms. In the attempt to classify rhythms, restrictive descriptions become necessary that depend on the criteria chosen. Rhythms may be distinguished according to (1) a characteristic such as frequency; (2) the biological system (e.g., a population) in which the rhythm is observed; (3) the kind of process that generates the rhythm; or (4) the function that the rhythm fulfills. Some of these aspects are briefly touched upon in the following paragraphs.

A SPECTRUM OF RHYTHMS

Biological rhythms extend over many logarithmic units of frequency from one cycle per millisecond to one cycle per several years. They can be observed in single cells, in networks of tissues and organs, in the whole organism, or in populations only. The seven rhythms depicted in Figure 1 are selected to give an impression of the range of frequencies as well as to indicate the various levels of integration at which rhythms manifest themselves. The figure is also useful to introduce the basic question whether a rhythm reflects merely a response to a periodic input coming from outside the biological unit in which it is observed (exogenous rhythm) or whether the rhythm originates from within that unit (endogenous rhythm). In technical terms, exogenous rhythms are analogous to forced oscillations of passive systems, that is, systems that can oscillate only under the influence of external periodic perturbations or signals (driving force), and whose oscillations damp out if the input becomes constant. On the other hand, endogenous rhythms are often considered analogous
to self-sustaining oscillations of active systems, that is, systems whose oscillations continue undamped when the energy supply is kept constant. A less restrictive definition of endogenous includes free damped oscillations of passive systems, for which no special term is available in biology, but which may occur frequently in biological systems.

There can be no doubt that rhythms such as the firing rate of a cold receptor in response to a constant thermal stimulus of 33.2°C (Figure 1, a) or the autonomous periodic activity of a pacemaker cell (b) belong to the class of endogenous rhythms. However, rhythms with periods of 24 hr (d) or of one year (f) could be caused by periodic factors in

![Diagram with Figure 1: Biological rhythms. Sources: (a) Hensel and Zotterman, 1951 (background noise from the original record omitted); (b) Courtesy: H. D. Lux, Munich; (c) Daan and Slopsema, 1978; (d) Heusner et al., 1971; (e) Kinder, 1927; (f) Instituto Nacional de Estadistica, Madrid, 1959; (g) Elton and Nicholson, 1942.]
the environment; specially designed experiments are necessary to demonstrate that these rhythms can be also endogenous (see below). The three remaining examples in Figure 1 (c, e, g) pose problems for a variety of reasons. The ca. 10-year cycle in density of a lynx population (g) is not, as was once assumed, a response to the sunspot cycle but results from a prey–predator interaction (Nicholson, 1955); to classify it as an endogenous rhythm, the definition of the biological “unit” has to comprise both prey and predator (Aschoff, 1959). The 5-day estrous cycle of the rat (e) is most likely an endogenous rhythm like the ovarian cycles of many other species, including man; to justify this classification in its strict sense, it must be demonstrated that the 5-day cycle is not generated by but only coupled to the daily periodic input (cf. Fitzgerald and Zucker, 1976). Finally, for the alternation between activity and rest in intervals of about 2.0 hr (c), the question has to be asked whether it truly represents a “rhythm”; pictures that resemble those of more-or-less regularly recurring bursts in an activity record can be produced on the basis of specific classes of purely stochastic processes (Lehmann, 1976; see also Chapter 19 in this volume). Other rhythm-like phenomena, such as episodic hormone secretion, may fall into the category just mentioned but may as well represent damped oscillations or the outcome of a programmed central neuronal mechanism (Yen, Vandenbarg, Tsai, and Parker, 1974).

THE FOUR “CIRCARHYTHMS”

Within the entire spectrum, rhythms differ extremely with regard to their variability in frequency. This wide difference is indicated in Figure 2 by horizontal bars representing intraindividual (black bars) or interspecific variability (white bars). Most of the rhythms that can be observed in the central nervous system, in the circulatory system, or in respi-

![Fig. 2. Spectrum of biological rhythms. White bars (mammals) indicate interspecific variability; black bars (man), intraindividual variability. REM: rapid eye movement. Modified from Hildebrandt (1958) and Aschoff (1959).](image-url)
Other endogenous rhythms, such as the ovarian cycle, show little intraindividual but large interspecific variability. Finally, there are four rhythms (indicated in Figure 2 by vertical lines) that do not vary in frequency under natural conditions because they are synchronized with cycles in the environment. These geophysical cycles are the tides, day and night, the phases of the moon, and the seasons. All four are reflected in the tidal, daily, lunar, and seasonal rhythms of biological systems, and it has been shown in at least a few species that each of these rhythms can persist when isolated from the respective environmental cycle (Aschoff, 1967). Under those artificially constant conditions, the period of the rhythm usually deviates slightly from that of the cycle to which it is normally synchronized; that is, it freeruns with its own “natural” frequency. If such a freerunning rhythm can be shown to persist for many periods without attenuation, the rhythm can be said to belong to the class of systems that are capable of self-sustaining oscillations (endogenous rhythms, in the strict sense of the definition). As a representative example, taken from the domain of daily rhythms, Figure 3 shows records of oxygen consumption in two chaffinches, kept first in light–dark cycles (LD) and thereafter in constant dim illumination. The period \( \tau \) of the freerunning rhythm is slightly longer than 24 hr in the upper record, and shorter in the lower record (for variability of \( \tau \), see Chapter 6).

Since the period of the freerunning rhythm only approximates that of the environmental cycle that it reflects, the prefix \textit{circa} was introduced by Halberg (1959) to characterize daily as \textit{circadian} rhythms and then was later adopted for the three other endogenous rhythms that correspond to cycles in the environment: circatidal, circalunar, and circannual rhythms (Aschoff, 1967). All four circarhythms have common features that are characteristic of self-sustaining oscillations (see Chapter 5). It seems useful to apply the prefix \textit{circa} only to those rhythms that are usually synchronized to environmental cycles and that show their natural frequency (immanent in the system) only under special conditions. As opposed to such a restrictive use of the term, it has been suggested, for example, to call the episodic hormone secretion a \textit{circoral} rhythm (Dierschke, Bhattacharya, Atkinson, and Knobil, 1970); a consistent application of this usage would lead to designations such as \textit{circasecond} rhythm for heart rate.

![Fig. 3. Rhythms of oxygen uptake in two chaffinches *Fringilla coelebs*, kept for six days in light–dark cycles (LD), thereafter in constant dim illumination (LL). (Unpublished data from Pohl.)](image)
The predominant role of circadian rhythms has been the reason for a subdivision of the spectrum into ultradian rhythms (with periods shorter than circadian) and infradian rhythms (with periods longer than circadian) (Halberg, Engeli, Hamburger, and Hillman, 1965). Typical examples of ultradian rhythms in man are provided by the repetition of phase of rapid eye movements (REM) during sleep in about 90-min intervals (see Chapter 26 in this volume), and by cycles of similar duration that can be observed during wakefulness, for example, in oral activity (Friedman and Fisher, 1967; Oswald, Merrington, and Lewis, 1970) and gross motor activity (Globus, Phoebus, and Boyd, 1973), in performance (Globus, Phoebus, Humphries, and Boyd, 1972; Kripke, 1972; Orr, Hoffman, and Hegge, 1974), in renal excretory activity (Lavie and Kripke, 1977), or in the perception of apparent motions (Lavie, 1976). However, the great variability in frequency, and a progressive elongation of intervals observed in some of these rhythms (Lavie, 1977), render their interpretation difficult. In the rhesus monkey, behavioral ultradian rhythms have been reported with periods of about 45 min (Maxim, Bowden, and Sackett, 1976) and of 90-min duration (Lewis and Kripke, 1977).

Infradian rhythms, apart from those indicated in Figure 2 at the right end of the spectrum, are less well documented. Weekly rhythms observed in animals in the laboratory—for example, in locomotor activity of a centipede (Mead, 1970), in larviposition of a mosquito (Nash and Trewern, 1972), or in enzyme activity of the rat pineal (Vollrath, Kantarjian, and Howe, 1975)—are likely to be due to periodic disturbances and hence belong to the few examples of exogenous rhythms. In the case of man, they may be the result of habits, for example, in food intake of children (Debry, Bleyer, and Reinberg, 1975) or of treatment schedules for patients (Undt, 1976; Brüning, 1978). An explanation becomes more difficult if such a rhythm seems to freerun with a period only approximating 7 days as described for oviposition of the springtail Folsomia candida (Chiba, Cutkomp, and Halberg, 1973), but caution in interpreting those data is always warranted (cf. the critical analysis from Richter, 1976). In man, freerunning rhythms with periods of that order have been claimed to be present in the urinary excretion of 17-ketosteroids (Halberg et al., 1965) and of estrone (Exley and Corker, 1966). There are also data that suggest, in the human male, rhythm of about 21 days in testosterone excretion (Kihlström, 1966; Doehring, Kraemer, Keith, and Brodie, 1975) and in body temperature (Empson, 1977). Finally, the many cyclic phenomena should be mentioned that can be observed in medicine and that have given rise to a number of hypotheses, especially in psychiatry (Reiman, 1963; Richter, 1965).

**INTERACTION AMONG RHYTHMS AND THEIR TELEONOMY**

Rhythms of different frequencies can be interrelated in various ways (Figure 4). Well known is the modulation of heart rate by respiration. Similarly, many of the ultradian rhythms in the hourly range (e.g., activity bursts, hormone episodes) are modulated in their frequency on a circadian time scale, and the circadian rhythm, in turn, may depend for some of its parameters on a circannual rhythm (see Chapters 6 and 21). Of more interest
are those observations that suggest a hierarchical order among rhythms, with one rhythm being essential for the proper action of another rhythm. Typical examples are the interaction between the circadian system and the estrous cycle in hamsters (see Chapter 27) and the involvement of circadian rhythms in photoperiodic time measurement (see Chapters 22 and 23 in this volume). In what way ultradian and circadian rhythms may be related to each other still remains to be seen. On the basis of seemingly synchronized hormone episodes in a group of monkeys, a kind of coupling between the two systems has been suggested (Holaday, Martinez, and Natelson, 1977), but the data analysis and conclusions are open to criticism (Kronauer, Moore-Ede, and Menser, 1978). In this context, the question becomes of interest whether the 90-min rhythm (REM) continues from sleep into wakefulness, that is, whether there is a basic rest-activity cycle as suggested by Kleitman (1963).

To illustrate the diversity of functions that can be served by biological rhythms, a few examples should suffice. Within the nervous system, some receptors transfer information by controlled variations of spike frequency (cf. Figure 1, top curve); pulsations, kept in motion by pacemakers, are the basis for the pump functions of heart and lungs; high-frequency rhythms may be useful in stabilizing rhythms of lower frequency. (For a detailed discussion of these problems, cf. Aschoff and Wever, 1962). While these rhythms fulfill important tasks within the organism, the four circarhythms mainly serve in the interplay between the organism and its environment. They have evolved as an adaptation to "niches in time" (Aschoff, 1964) generated by the temporal structure of the environment. By incorporating into its own organization approximate copies of the external temporal programs, an organism acquires time-telling devices, that is, biological clocks (see Chapter 5).

REFERENCES


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