Chapter 9

Metabolic Catalysts in the Efficiency Complex:
Diurnal Rhythms

Science started with the organization of ordinary experience. A. N. Whitehead

9.1: Introduction. We became interested in the problem of diurnal rhythm when we obtained some unexpected results in a study of the heat increment of feeding (SDA, Ch. 4) of the rat. The anomalous result could be explained only by assuming the presence of a diurnal metabolic rhythm in which the difference between crest and trough exceeded the SDA effect of the feed (Fig. 9.1). This led to the performance of a series of experiments, and the discovery of a profound (25–30 per cent difference) diurnal metabolic rhythm in the rat which is not extinguished by a month of continuous light alone, by a month of continuous feeding alone (\(\frac{1}{2}\) of the day's maintenance ration at 3-hour intervals), nor by a combination of continuous light and fast. It is extinguished, however, by a week of continuous light and continuous feeding. The object of this chapter is to summarize some of these results and integrate them with the literature on diurnal rhythms in general as a logical sequence to the preceding chapter on seasonal rhythms in general, with special reference to the efficiency complex.

There is an evident analogy between diurnal and seasonal rhythms, both being ultimately activated by the sun rhythm; and metabolic effects—however different in nature—are exerted not only on photosynthetic plants but also on animals endowed with visual or related exteroceptive apparatus. The timing of the rhythmic activity in animals, whether they are diurnal or nocturnal, depends on the nature of their visual apparatus, whether they see best in bright light (day) or in dim light (night). The diurnal light rhythm, through the intermediacy of the amplifying visual apparatus, exerts a profound effect on all life processes. Sleep is a conspicuous illustration; so are there rhythms in body temperature and nervous irritability which are interrelated with muscular activity, with energy metabolism, with food intake, and so on. It seems instructive to review the literature in some detail so as to get a view of the situation as a whole.

9.2: The literature. When travelling, the body temperature rhythm follows the light rhythm. In man, the average minimum daily temperature, 36.5° C, is in the early morning (2 to 5 a.m.) and the maximum, 37.5° C, in the afternoon (2 to 5 p.m.). In the pigeon the midnight temperature, 41.5° C, is below the noon temperature, 42.2° C.

The most dramatic feature of the diurnal rhythm is sleep. Kleitman gave a good description of its natural history in man (1929).

"Darkness makes for poor vision and discourages movements. This leads to inactivity and relaxation, and sleep follows. Repeating the performance a great many times results in the establishment of a conditioned reflex of a temporal character, relaxation at a certain time. This is the theoretical history of diurnal sleep.

Practically we are born into a social organization where diurnal sleep is the uni-

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Fig. 9.1. Apparent difference in heat increment of feeding in rats following morning and afternoon feeding.

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versally accepted mode of sleeping. The first habit that a mother tries to develop in a baby is that of an unbroken night’s sleep. As he gets older other functions develop a periodicity that coincides with the enforced sleep periodicity. For instance, a temperature curve develops with a minimum at night, and produces a disinclination to night activity. Even the modest tear apparatus stops its function at bedtime procuring dry eyes, favoring their closure.”

Nervous irritability follows a similar rhythm. The reaction of normal man to light and sounds is lowest in the morning, when body temperature is lowest, and increases with increasing body temperature in the afternoon, then returns to the morning minimum. When the body temperature is at a minimum, irritability is likewise at a minimum, and it is then most difficult to keep awake. Skills of coordination are at a minimum during these early hours.

The influence of nervous irritability on metabolism and body temperature may be inferred from the facts that about half of the peripheral nerves supply the skeletal muscles and about half of the body mass is muscle. The increase of the contractions of skeletal muscle is proportional to the increase in nervous irritability.

The literature on the development of activity rhythms is somewhat conflicting. Thus Richter reported that the rhythms gradually develop (first appear in rats about 12 days after birth), presumably because of social conditioning. Barott, on the other hand, reported that the metabolic rhythms “decrease rapidly with age” in young chicks. “At the average age of 1 week... an average maximum difference of about 24 per cent was observed between the oxygen consumption at 8 a.m. and 8 p.m. values.” (The peak occurred at 8 a.m. and the trough at 8 p.m.) Richter reported that the diurnal rhythmic activity of the fasting rat persisted even in the absence of light cycles. On fasting, during the early period of fast, the total activity was greater than during five previous feeding days. We found the same to be true.

The feeding rhythms naturally follow the activity rhythms, being usually confined to times when vision functions best, which is night for rats and other nocturnal animals and day for fowl and other diurnal animals. There are corresponding nutrition-function rhythms. Thus glycogen storage in rabbits, rats, and mice is maximal and bile formation is minimal during the night. In nocturnal animals, the assimilatory phase when the glycogen


is deposited occurs during the night when the animals naturally feed\textsuperscript{10}. The glycogen deposition at this time tends to be counteracted, however, by physical activity; this occasionally results in a bimodal curve of glycogen storage.

In diurnal animals the blood-sugar and adrenaline peaks occur during the day (and the calcium peak at night), opposite to the liver glycogen peak\textsuperscript{11}. Incidentally, in diabetics the blood-sugar level falls during the evening, often below the fasting level\textsuperscript{12}. Lactating cattle tend to exhibit blood-sugar rhythms\textsuperscript{13}. The trend is likely to be confused because of the sensitiveness of the blood-sugar level to psychic disturbances involved in securing the blood. (In lactating cows the blood-sugar level reached a high of 70 mg sugar per 100 cc blood at noon and a low of 58 mg at 9:30 a.m. There was no such trend in non-lactating cows or sheep.)

Diurnal rhythmicity was also reported for blood volume\textsuperscript{14}, non-protein nitrogen\textsuperscript{15}, serum calcium\textsuperscript{16}, red corpuscles and hemoglobin\textsuperscript{17}, water and minerals\textsuperscript{18}.

There is an apparent diurnal rhythm in the composition of milk\textsuperscript{19} (Fig. 9.5). The diurnal difference in fat percentage is attributed to differences in time-interval between day and night milkings. Morning milk is richer in bacteria than evening milk, and evening milk is richer in chlorine and catalase than morning milk\textsuperscript{20}.

Domestic fowl lay eggs only during the day (7 a.m. to 5 p.m.)\textsuperscript{21}.

The "alkaline tide"\textsuperscript{22} (urinary-acidity rhythm) is obviously associated with the diurnal feeding rhythm. The sensitiveness of urinary reaction to diet is indicated by the fact that ingestion of 5 g sodium bicarbonate results in an immediate rise in alkalinity of the urine. The urinary-volume rhythm tends to parallel the body-temperature rhythm\textsuperscript{23}. The blood pH in humans rises from morning to late at night\textsuperscript{24}.

\textsuperscript{10} Higgins, G. M., Berkson, J., and Flock, E., \textit{Am. J. Physiol.}, 102, 673 (1932); 106, 177 (1935).
\textsuperscript{13} Allcroft, W. M., \textit{Biochem. J.}, 27, 1827 (1933).
\textsuperscript{15} Forsgren, E., \textit{Acta Med. Scand.}, 73, 213 (1930).
\textsuperscript{16} Ehrstrom, M. C., \textit{Acta Med. Scand. Suppl.}, 59, 97 (1934). Holmquist\textsuperscript{11}.
\textsuperscript{18} Norm, M., \textit{Scand. Arch. Physiol.}, 56, 184 (1929).
\textsuperscript{23} Simpson, G. E., \textit{J. Biol. Chem.}, 59, 107 (1924); 84, 393 (1929).
\textsuperscript{24} Cullen, G., and Earle, I. P., \textit{J. Biol. Chem.}, 83, 545 (1929).
The stomach-activity rhythms are presumably associated with feeding habits. There is an extensive literature on this problem.

Many miscellaneous diurnal rhythms have been observed, such as the mitotic rhythm in human tissue, spermatogenic rhythm in the sparrow, enamel deposit rhythm in the rat, retinal rhythm in catfish, cell-division rhythm in the thyroid, and so on.

According to Szymanski, in addition to diurnal rhythmicity, some species are polyphasic, exhibiting several periods of activity and rest during the day; others are monophasic, exhibiting one prolonged period of activity followed by one of rest during each day. Rabbits are polyphasic, having 16 to 21 periods of activity alternating with rest; albino rats have 10 periods of activity concentrated, as in other nocturnal animals, at night; canaries are monophasic, active during day and quiet during night; young dogs exhibit 8–13 periods of activity at night; cats exhibit 2/3 of their activity during the day, and 1/3 during the earlier part of night; human infants are polyphasic, human adults monophasic, with the aged resembling infants in being polyphasic. There are obvious difficulties in differentiating between such inherent phasic rhythms and merely spurious movements.

We are mostly interested in the energy-metabolism rhythms, which reflect all the others.

Lusk quotes the following table from Johansson on the diurnal rhythm of CO₂ production in man:

<table>
<thead>
<tr>
<th>Night CO₂</th>
<th>Day CO₂</th>
<th>Author</th>
</tr>
</thead>
<tbody>
<tr>
<td>Complete muscular rest</td>
<td>100</td>
<td>105</td>
</tr>
<tr>
<td>Ordinary rest in bed</td>
<td>100</td>
<td>110</td>
</tr>
<tr>
<td>Ordinary life (no hard work)</td>
<td>100</td>
<td>142</td>
</tr>
<tr>
<td>&quot; &quot; &quot; &quot; &quot; &quot; &quot;</td>
<td>100</td>
<td>128</td>
</tr>
<tr>
<td>&quot; &quot; &quot; &quot; &quot; &quot;</td>
<td>100</td>
<td>147</td>
</tr>
</tbody>
</table>

Benedict and Riddle reported that muscular activity of pigeons in dark chambers is less during night than during day. After excluding the periods showing muscular activity, day metabolism was about 15 per cent above night metabolism.

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The pigeon was reported to have a 15 per cent diurnal basal metabolism and a 1°C rectal-temperature rhythm\textsuperscript{34}. The fowl was reported to have a 30 per cent basal metabolism and a 1°C rectal-temperature rhythm\textsuperscript{35}. The following (slightly rounded) data on rectal temperatures in fowl from Heywang\textsuperscript{36} are illustrative of the course of the rhythm.

<table>
<thead>
<tr>
<th>Time</th>
<th>Rectal temp. (°F)</th>
<th>Environmental temp. (°F)</th>
</tr>
</thead>
<tbody>
<tr>
<td>8 a.m.</td>
<td>106.8</td>
<td>53</td>
</tr>
<tr>
<td>10 a.m.</td>
<td>106.5</td>
<td>68</td>
</tr>
<tr>
<td>12 noon</td>
<td>106.4</td>
<td>74</td>
</tr>
<tr>
<td>2 p.m.</td>
<td>106.8</td>
<td>79</td>
</tr>
<tr>
<td>4 p.m.</td>
<td>106.8</td>
<td>76</td>
</tr>
<tr>
<td>6 p.m.</td>
<td>105.9</td>
<td>64</td>
</tr>
<tr>
<td>8 p.m.</td>
<td>105.5</td>
<td>56</td>
</tr>
<tr>
<td>10 p.m.</td>
<td>105.4</td>
<td>50</td>
</tr>
<tr>
<td>12 night</td>
<td>105.6</td>
<td>48</td>
</tr>
<tr>
<td>2 a.m.</td>
<td>105.9</td>
<td>46</td>
</tr>
<tr>
<td>4 a.m.</td>
<td>106.3</td>
<td>44</td>
</tr>
<tr>
<td>6 a.m.</td>
<td>106.5</td>
<td>42</td>
</tr>
<tr>
<td>8 a.m.</td>
<td></td>
<td>54</td>
</tr>
</tbody>
</table>

Note that the environmental temperature happened to be changing at the same time, and Heywang suggested that there might have been a causal or dependent relation between rectal and environmental temperature. Of course, all aspects are interrelated, but it appears from other data that, in the main, the rectal-temperature rhythm would not have decreased appreciably if the environmental temperature had been kept constant at the mean value of about 60°F.

Kayser\textsuperscript{34} demonstrated that the diurnal metabolic rhythm in the pigeon is due to the diurnal variation in tonicity of posture, especially of the pectoral muscles, which in turn is caused reflexly by the excitation produced by the diurnal light rhythm upon the nerves controlling muscle-tone.

Several reports are available on the inversion of body temperature obtained in animals by changing the light rhythm. This was accomplished on monkeys\textsuperscript{37} and birds\textsuperscript{38} in about 15 days. The results in inversion of body temperature and metabolism on man, however, are conflicting\textsuperscript{39}, because it is difficult to isolate him psychically and intellectually from the social rhythm of the environment even though he is isolated from the light rhythm.

The persistence of the diurnal rhythm in spite of prolonged rest and fast stimulated speculations on cosmic influences other than the sun, including cosmic rays and ionized air\textsuperscript{40}. Deighton\textsuperscript{41} observed a diurnal rhythm in

\textsuperscript{34} Kayser, C., et al.\textsuperscript{3}
\textsuperscript{36} Terroine, E. F., "De l'existence d'un rythme nycthoréméral de metabolisme chez les oiseaux," Id., 5, 842 (1929).
\textsuperscript{38} Heywang, B. W., Poultry Sci., 17, 320 (1938).
\textsuperscript{40} Galbraith and Simpson, Id., 30, XIX (1903).
\textsuperscript{42} Benedict, F. G., Am. J. Physiol., 11, 145 (1904).
\textsuperscript{43} Toulouse, E. F., and Pieron, H., J. Physiol. path. gen., 9, 245 (1907).
\textsuperscript{44} Gessler, H., Pfüger's Arch. ges. Physiol., 207, 390 (1928).
\textsuperscript{45} Völker, H., Pfüger's Arch. ges. Physiol., 215, 43 (1926).
\textsuperscript{46} Deighton, T., Physiol. Rev., 13, 427 (1933).
metabolism of swine screened from changes in electrical conductivity. As previously noted, the thyroid, the prime metabolic regulator, has a diurnal growth (cell-division) rhythm.

9.3: Diurnal metabolic rhythm in the rat, its control and effect on the apparent SDA. The heat production per hour is the sum of: (1) the basal energy metabolism; (2) the energy expense of muscular activity and muscle tonus; and (3) the SDA (Ch. 4). As the rat is nocturnal, his muscular activity, nervous irritability, muscle tonus, feeding, and body temperature tend to be high during the night when his vision is best and low during the day when his vision is poorest. We may then expect high metabolic rates during the night and low metabolic rates during the day, just as Kayser found the opposite conditions in the pigeon. Our problems were: (1) to evaluate under our laboratory conditions the magnitude of the "normal" diurnal rhythm; (2) to investigate the conditions which may abolish the rhythm and thus obtain an insight into the mechanisms involved.

The magnitude of the diurnal metabolic rhythm under "normal" conditions is shown in Figs. 9.1 to 9.3; there is 25 to 30 per cent difference between the peak and crest in the curve.

The investigation on abolishing the rhythm brought to light several facts: (1) The muscular activity and metabolic rhythms are parallel. (2) Continuous lighting alone for a month did not abolish the diurnal rhythm. (3) Continuous feeding alone (feeding \( \frac{1}{3} \) of the day's maintenance ration every 3
Fig. 9.3. Diurnal metabolic rhythms of white rats under continuous light of constant intensity when fasting (upper curve), and when consuming \( \frac{1}{3} \) of the maintenance ration at 3-hour intervals throughout day and night for over a week (lower curves). The rhythm is maintained in the fasting rat, but is extinguished in the continuous-feeding rats, so that only residual "autogenous" rhythms remain.
hours) for a month did not abolish the rhythm. (4) A week of fast under continuous lighting did not abolish the rhythm. (5) But a combination of continuous lighting and continuous feeding ($\frac{1}{3}$ of the daily ration every 3 hours) extinguished both the activity and the metabolic rhythms.

The metabolic result of fast under continuous lighting is shown in the top curve of Fig. 9.3. The first midnight peak is above the other peaks because it includes the heat increment of feeding (SDA) of the prefasting meal (6.4 g feed eaten at 3 p.m.); it includes, in other words, (1) the normal 25 per cent diurnal metabolic difference and (2) a 25 per cent feed intake effect. This is shown by the following data:

<table>
<thead>
<tr>
<th>24-hour period of fast</th>
<th>Maximum Cal/day</th>
<th>Maximum time</th>
<th>Minimum Cal/day</th>
<th>Minimum time</th>
<th>Difference (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>37.4</td>
<td>midnight</td>
<td>24.4</td>
<td>3 p.m.</td>
<td>53.3</td>
</tr>
<tr>
<td>2</td>
<td>30.7</td>
<td>9 p.m.</td>
<td>23.2</td>
<td>3 p.m.</td>
<td>52.3</td>
</tr>
<tr>
<td>3</td>
<td>30.2</td>
<td>midnight</td>
<td>24.1</td>
<td>3 p.m.</td>
<td>25.3</td>
</tr>
<tr>
<td>4</td>
<td>30.2</td>
<td>3 a.m.</td>
<td>24.0</td>
<td>noon</td>
<td>25.8</td>
</tr>
</tbody>
</table>

In one trial, one group of rats was fed a 10-gram meal at 4 a.m. which was followed not by a rise but a decline in metabolism until noon (8 hours); another group of rats was fed a 10-gram meal at 4 p.m. which was followed by a steady increase in metabolism, reaching a 40 per cent peak increment in 5 to 7 hours; it then declined to a minimum in 16 hours. It is thus evident that there is an algebraic summation of the effects of feed-intake and diurnal rhythm. If the animal feeds during the ascending slope (after 3 p.m.) of the diurnal rhythm, there is a reinforcement of effect with a resulting abnormally high metabolic peak; if it feeds during the descending slope of the rhythm (after 3 to 5 a.m.), the SDA is apparently below normal.
The metabolic results on continuous feeding (feeding 1.5 g food every 3 hours day and night) are shown in the middle and bottom curves in Fig. 9.3. Many metabolic, muscular-activity, and respiratory-quotient curves of individual animals and of their averages confirm those in Figs. 9.3 and 9.4.

"Welsh" argued that most diurnal rhythms are 'inherent', since prolonged periods of either continuous darkness or light do not always abolish the rhythms. The diurnal activity rhythm in the rat, among others, was cited as an illustration of 'inherent' rhythm. However, we have clearly demonstrated that the diurnal activity and metabolism rhythm in the rat can be quickly abolished under continuous light, provided that this is combined with continuous feeding; and that the rhythm in the young is developed by "social conditioning". The interesting observation is cited that certain phases in the estrous cycle occur at certain definite times in the diurnal rhythm (maximum estrus in the rat occurs at midnight).

Fig. 9.5. Apparent diurnal rhythm in fat percentage in morning (a.m.) and evening (p.m.) milk during the lactation period.

9.4: Summary. There is an impressive analogy between diurnal rhythms discussed in this chapter and seasonal rhythms discussed in the preceding chapter, both being ultimately actuated by the sun-earth rhythm; metabolic effects, however different in nature, are exerted not only on plants endowed with chlorophyll but also on animals endowed with eyes. The timing of the rhythmic activity in animals depends on the nature of their visual apparatus, whether they are adopted for relatively dim night light or bright daylight.

The diurnal difference between the metabolic peak and trough is shown

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42 Detailed curves of the rhythms of muscular activity, respiratory quotients, metabolism, and also descriptions of apparatus are given in the original report, Univ. Missouri Agr. Exp. Sta. Res. Bull. 274.


to be about 25 per cent of the average. The metabolic rhythm reflects activity, feeding, nervous irritability, and related rhythms, although the metabolism was measured during rest.

These rhythms in adults have their ultimate developmental roots in the sun rhythm, transmitted and amplified in the organism by the nature of the visual apparatus, and secondarily in a superimposed social conditioning. The nocturnal rat, for example, develops ingrained habits—conditioned reflexes—of sleeping during the day and feeding, etc., during the night. These reflexes gradually come to include muscle tone, urination, defecation, and intermediate metabolism, including blood composition and perhaps body composition. These rhythms are so persistent that in the rat they cannot be extinguished by a month of continuous light alone, nor by a month of continuous feeding (at 3-hour intervals of the day's maintenance ration) alone, nor by a week of continuous lighting and fasting. But a combination of continuous lighting and continuous feeding (of daily ration every 3 hours) extinguished the metabolic rhythm in about a week.

In addition to their scientific and philosophic interest (from the organismic viewpoint) these rhythms are practically important in studies on the influence of desired conditions on metabolism and related phenomena. Unless the rhythm is taken into consideration, or is extinguished as described in the text, the metabolic (or related activity) difference due to the conditioned diurnal and related rhythms may exceed the metabolic differences caused by the factors under investigation and thus confuse the problem.

In addition to the diurnal rhythms, there are shorter rhythms in the rat, such as Richter's two to four-hour 'spontaneous' rhythms, 3-hour feeding and 'washing-up' rhythms, and numerous digestive, circulatory, respiratory, secretory and excretory rhythms, blood and tissue (especially liver and adrenal) composition, and brain-potential rhythms, all of which influence the metabolic level. There are also longer rhythms. Activities of rats in revolving cages indicate the presence of 4-day rhythms, and even longer sex- and seasonal-cycle rhythms. There are also several longer body-temperature rhythms in humans. Thus Zucker, Cary, and many others, reported monthly body-temperature rhythms in women, the lowest temperature coinciding with ovulation and increased cervical secretion (Ch. 7).
