ON VARYING WORK-SLEEP SCHEDULES: THE BIOLOGICAL RHYTHM PERSPECTIVE

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The rhythmic alternation between activity and sleep is based on endogenous mechanisms, but is subject to exogenous influences. The endogenous basis of the alternation is shown by the persistence of circadian rhythms in a constant environment free of time cues. Under these conditions, the freerunning rhythms that can be observed in different variables may either remain in synchrony but out of phase with each other, or become desynchronized, each showing a different frequency. Exogenous factors, when present continuously, may determine the parameters of a freerunning rhythm of this sort; when occurring periodically, they may synchronize it. Exogenous stimuli that affect the endogeneously generated rhythm can be of a physical nature (e.g.,light, temperature), or they can consist of signals with social connotations. The latter are the most effective zeitgebers for the human circadian system.

In assessing characteristics of the activity-sleep cycle, it is helpful to examine endogenous and exogenous influences separately. When exogenous factors are kept constant, the periods of freerunning rhythmic functions, as well as particular aspects of them such as the duration of sleep-time, are exclusively determined by endogenous processes, i.e., they are not due to social conventions, or to time-related changes in motivation. However, in view of the fact that different physiological variables interact with each other and, in addition, may affect the activity-sleep cycle, two states of the circadian system that occur in this situation will be differentiated: (1) a state of internal synchrony in which each rhythm has a consistent frequency and a constant temporal order is maintained, and (2) a state of internal desynchrony in which, due to differences in frequency between different rhythms, temporal disorder results. The effects of exogenous factors will be assessed by considering experiments in which the influence of such factors was studied by exposing subjects to a variety of zeitgebers. The discussion will be mainly restricted to two variables: the rhythm of wakefulness and sleep, and the rhythm of deep body temperature, the latter being representative of physiological rhythmicity in general. The present review is not aimed directly at the practical problems of shiftwork and the like, but rather provides the background for the solution of such problems.

Freerunning, Interally Synchronized Rhythms

When isolated from environmental time cues, human circadian rhythms persist with periods that deviate slightly from 24 hours. In the majority of cases,the rhythms of all variables measured remain synchronized, with a common period close to 25 hours. In the experiment shown in Figure 1, the rhythms of activity and rectal temperature had equal and consistent period values of 25.3 hours throughout 5 weeks of isolation. Apart from the deviation of the period from 24 hours, this figure illustrates another peculiarity of freerunning rhythm. In the steady state, the maxima and minima of rectal temperature occur at much earlier phases of the activity rhythm than they do in the normal 24-hour day. As a consequence, the subject sleeps predominantly during a period of increasing deep body temperature, in contrast to what happens in a normal

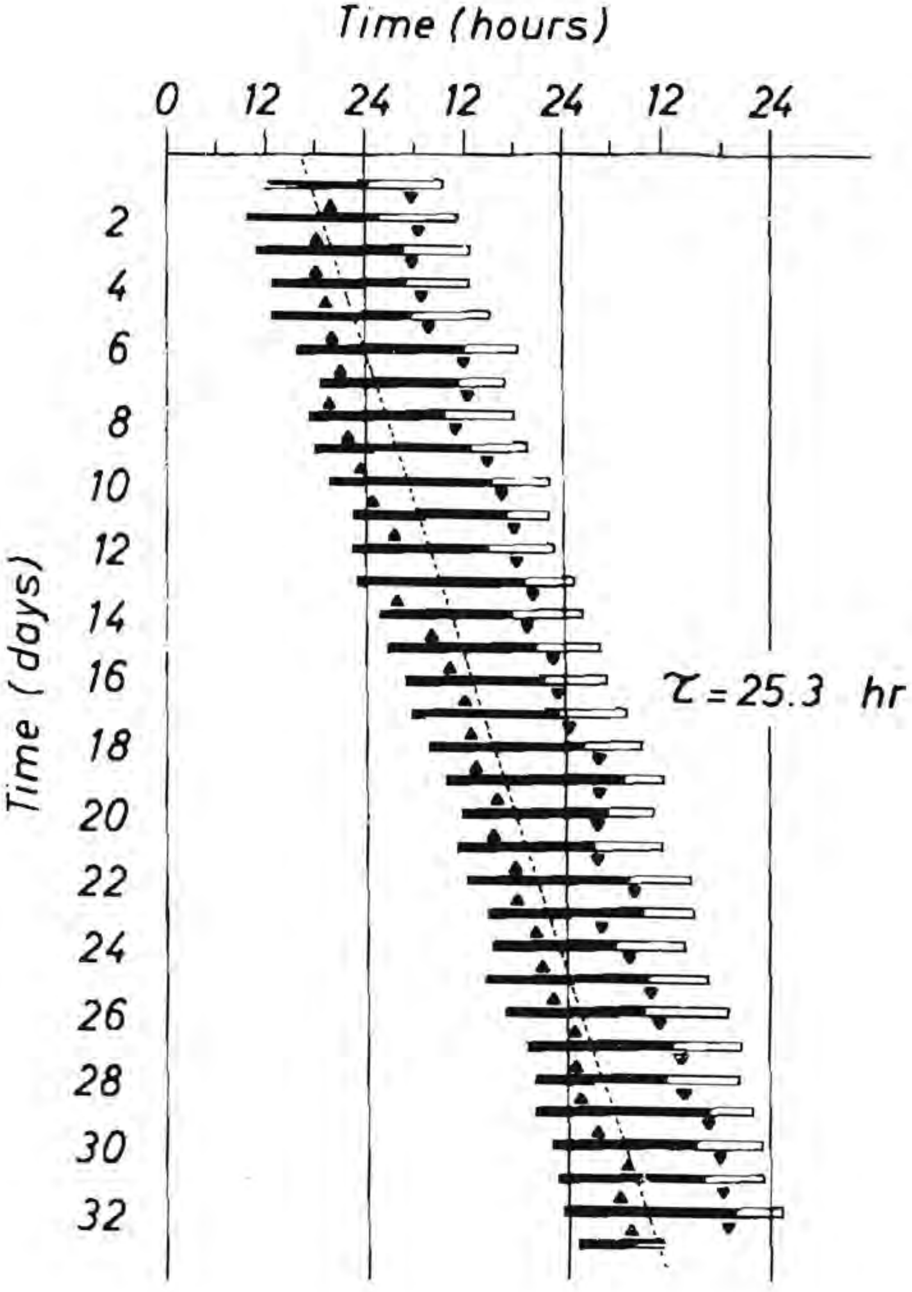

Figure 1. Autonomous rhythms of a subject (A.G., ♂ 26y) living under constant conditions without environmental time cues. The activity rhythm is represented by bars (black: activity; white: rest) and the rhythm of rectal temperature by triangles indicating the temporal positions of maximum (▲) and minimum (▼) values. Abscissa: local time; ordinate: sequence of the subjective days. From Wever (1971).

situation, where temperature decreases during most of a typical night's sleep. The results shown in Figure 1 are representative of more than 100 similar experiments with freerunning, internally synchronized rhythms (Wever, 1979a).

Freerunning, internally synchronized human circadian rhythms can be remarkably stable. This conclusion arises from the observation that the properties of these rhythms are more or less independent of the constraints that are unavoidable in preserving constant conditions in isolation. In this respect, the social deprivation of the subjects might be considered a special burden; in an experiment of the type exemplified in Figure 1, the isolated subject has no direct contacts with other humans for several weeks. To assess the possible influence of this kind of deprivation on the rhythm, groups of subjects have been isolated collectively. As an example, Figure 2 shows the results of an experiment in which two subjects lived together in an isolation unit in constant conditions without environmental time cues. Two conclusions can be drawn: (1) the continuous social contact between the subjects resulted in mutual synchronization of their rhythms, and (2) the joint rhythm had a period close to that of a singly isolated subject (cf. Figure 1). Many similar experiments are required to prove statistically that the periods of freerunning rhythms in collectively isolated groups are slightly but significantly longer than those of singly isolated subjects (Wever, 1975b).

Stimuli of various kinds seem to have little effect on human circadian rhythms. This applies not only to light, which is the most effective external stimulus in nearly all animal experiments, but also to physical workload (cf. Figure 3). The two parts of this figure are taken from two sections of a representative experiment in which a subject lived under constant conditions for a month, but refrained from physical activity as much as possible during the first two weeks and exercised frequently on a bicycle ergometer during the second two weeks. In contrast to the relatively smooth daily temperature curves seen during the first section, those in the second section are chatacterized by large increases in value associated with the ergometer sessions. However, despite these effects of workload, the rhythm parameters, as assessed from separate analyses of the two time series, are essentially identical in both sections. In particular, the period of the freerunning rhythm, and likewise the fraction of sleep within the sleep-wake cycle, are independent of the workload. Eight more experiments of this series, with alternating sections with and without workload, confirm the statistical significance of this result (Wever, 1979b).

The remarkable internal shift between the rhythms of activity and rectal temperature due to the slight lengthening of the period after elimination of the 24-hour zeitgeber (Aschoff, Gerecke, & Wever, 1967a) also has consequences with regard to the structure of sleep (Zulley, 1976; Czeisler, 1978). A section of a 29-day single-subject experiment performed under constant conditions is shown in Figure 4, which presents the polygraphic records of sleep behavior, together with the curves of rectal temperature, on several consecutive days. As can be seen, the minimum of body temperature always occurs immediately after sleep onset, which means that most of the subject's sleep occurs while his body temperature is increasing. The fractions of the different sleep stages are, on average, equal to those observed during normal sleep in a 24-hour day. However, the distribution of REM sleep differs: its latency is shorter, its first phase is always the longest rather than the shortest, and

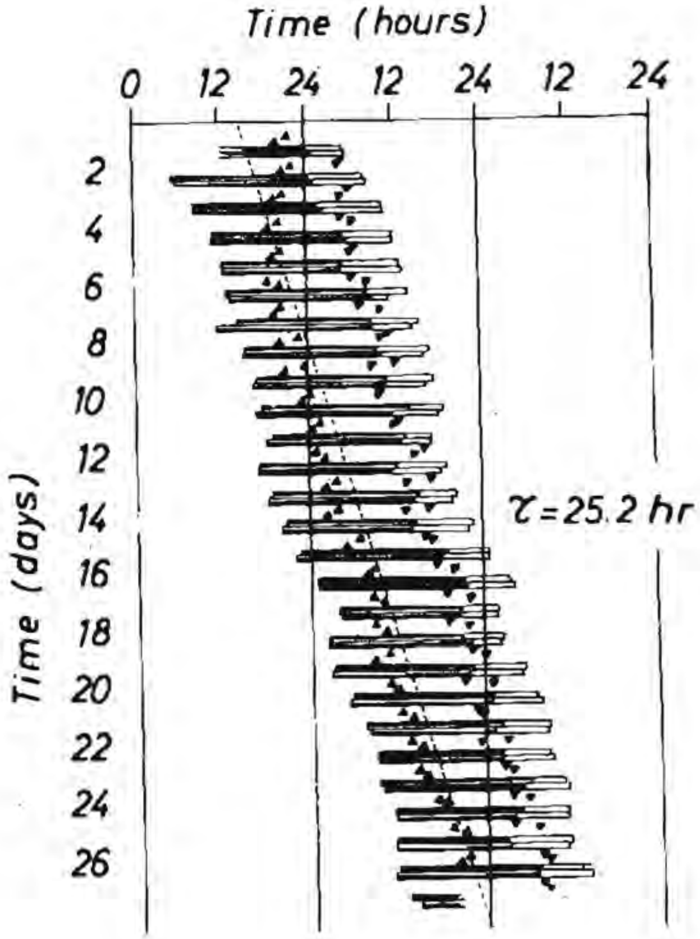

Figure 2. Autonomous rhythms of two subjects (W.S., ♂ 25y, & H.O. ♂ 25y) living together under constant conditions without environmental time cues. The rhythms of activity and rectal temperature are shown as in Figure 1, the records from two subjects being plotted one below the other. From Wever (1978).

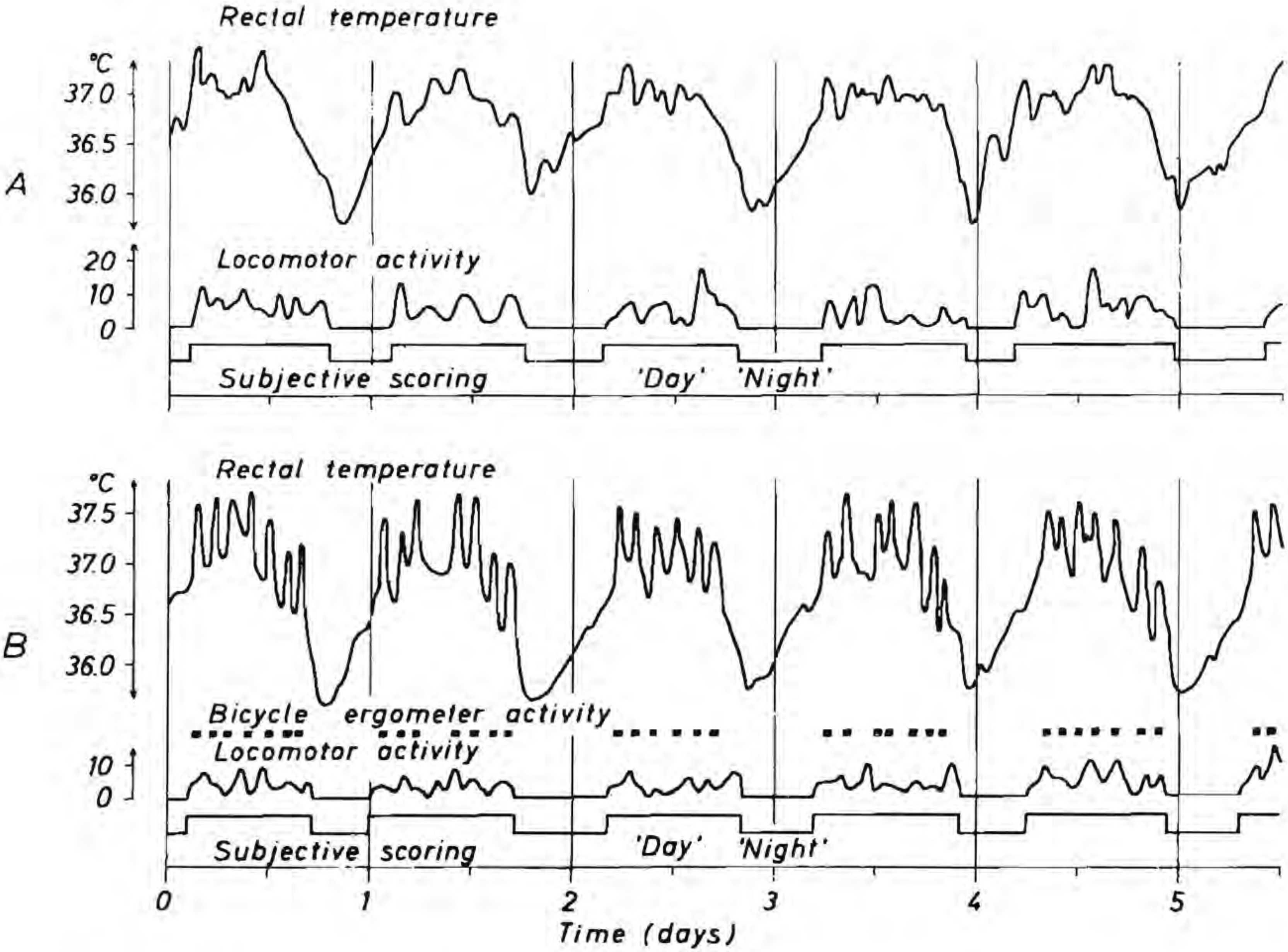

Figure 3. Autonomous rhythms of a subject (T.S., ♂ 25y) living under constant conditions without environmental time cues, and during the second section (B) with a heavy ergometer workload (100 W for about 20 min, 7 times per activity cycle). The records of rectal temperature (measured continuously), locomotor activity (measured from invisible contact plates under the floor), and subjectively scored alternation between 'day' and 'night' are shown, together with the times of the ergometer sessions. For clarity, only short periods (Days 5 to 9 and 19 to 23) of the two week sections are illustrated. From Wever (1979b).

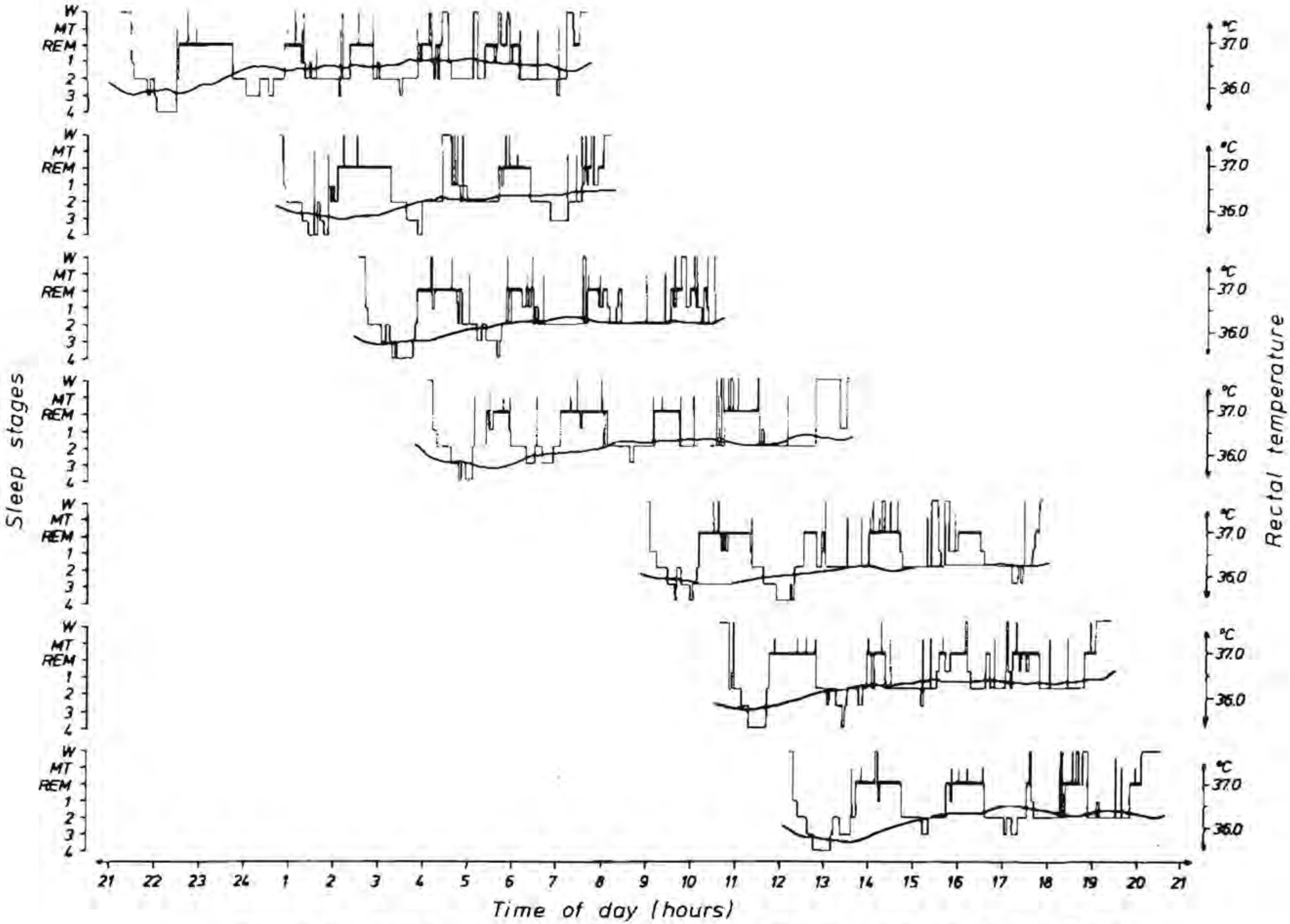

Figure 4. Parts of the autonomous rhythms of a subject (M.C., ♂ 25y) living under constant conditions without environmental time cues. Sleep stages (from polygraphic sleep recordings) and rectal temperature during successive sleeps are shown, as related to local time. For clarity, only days 10 to 16 of the 29-day experiment are illustrated. From Wever (1979c).

its propensity decreases over the sleep rather than increasing as normal (Zulley, 1979).

It can also be seen from Figure 4 that the relationship between the curve of temperature and sleep, and the pattern of sleep itself, are both very consistent, being quite independent of the objective time of day. This, of course, confirms the reliability of the experimental design, which was intended to eliminate any exogenous time reference.

From Figure 4, and from similar results obtained in other experiments, it can be concluded that sleep, when under only endogenous control, takes place at a phase of the temperature rhythm, and with a temporal structure, that both differ from what is observed when the additional influences of exogenous 24-hour signals are present (Wever, 1979c). However, it is not yet clear whether the two changes condition each other, or whether they are independent. Although human circadian rhythms have been shown to be remarkably persistent, they undergo slight cycle-to-cycle variations; in the present context, changes in the sleep/activity ratio, or in the sleep fraction, are relevant. As can be seen in Figure 1, both the duration of activity (activity-time) and of sleep (rest-time) vary slightly from day to day. One way of determining whether the values of these two alternating states are related is by computing serial correlations between them. This can be done by correlating each activity-time either with the preceding or with the following rest-time. Figure 5 shows both these correlations, computed from the data of the experiment shown in Figure 1 (Figure 5, top diagrams), and from two more typical experiments. In all three cases, the serial correlations between activity-time and following rest-time are negative, and statistically significant ($p < .001$). The same holds true for a sample of 38 experiments ($r = -.519 \pm .227$; $p < .001$; Wever, 1979a). On the other hand, the serial correlation between activity-time and preceding rest-time is inconsistent: in the top diagram, this correlation is positive ($p < .05$); in the middle diagram, there is no correlation at all; and in the bottom diagram, there is a negative correlation as strong as that between activity-time and following rest-time ($p < .001$). Again, the typicality of these findings is confirmed by the overall results found in the larger sample of 38 experiments. Although the mean of the correlations in the sample is effectively zero ($r = -.020 \pm .306$; Wever, 1979a), the actual distribution is, in fact, bimodal, with clear clusterings of positive and negative correlations.

The general effect of the serial correlations is to produce a stabilization of the total activity-rest cycle. An activity-time that is longer than average is typically followed by a rest-time that is shorter (and vice versa), and is preceded by a rest-time that, in some subjects, is likewise shorter than average, but, in others, longer; in only a few subjects are the durations of activity-time and preceding rest-time independent of each other.

There are other serial correlations between the day-to-day variations of the total activity-rest cycle. As Figure 6 (left) demonstrates for the data from the experiment shown in Figure 1, there is a significant ($p < .05$) negative serial correlation between the duration of successive activity-rest cycles. This means that an activity-rest cycle that is longer than the average of all the cycles in this experiment is typically followed by a cycle that is shorter, and vice versa. Here, the cycle is defined from the midpoint of one rest-time to the midpoint of the next; however, almost identical correlations are ob-

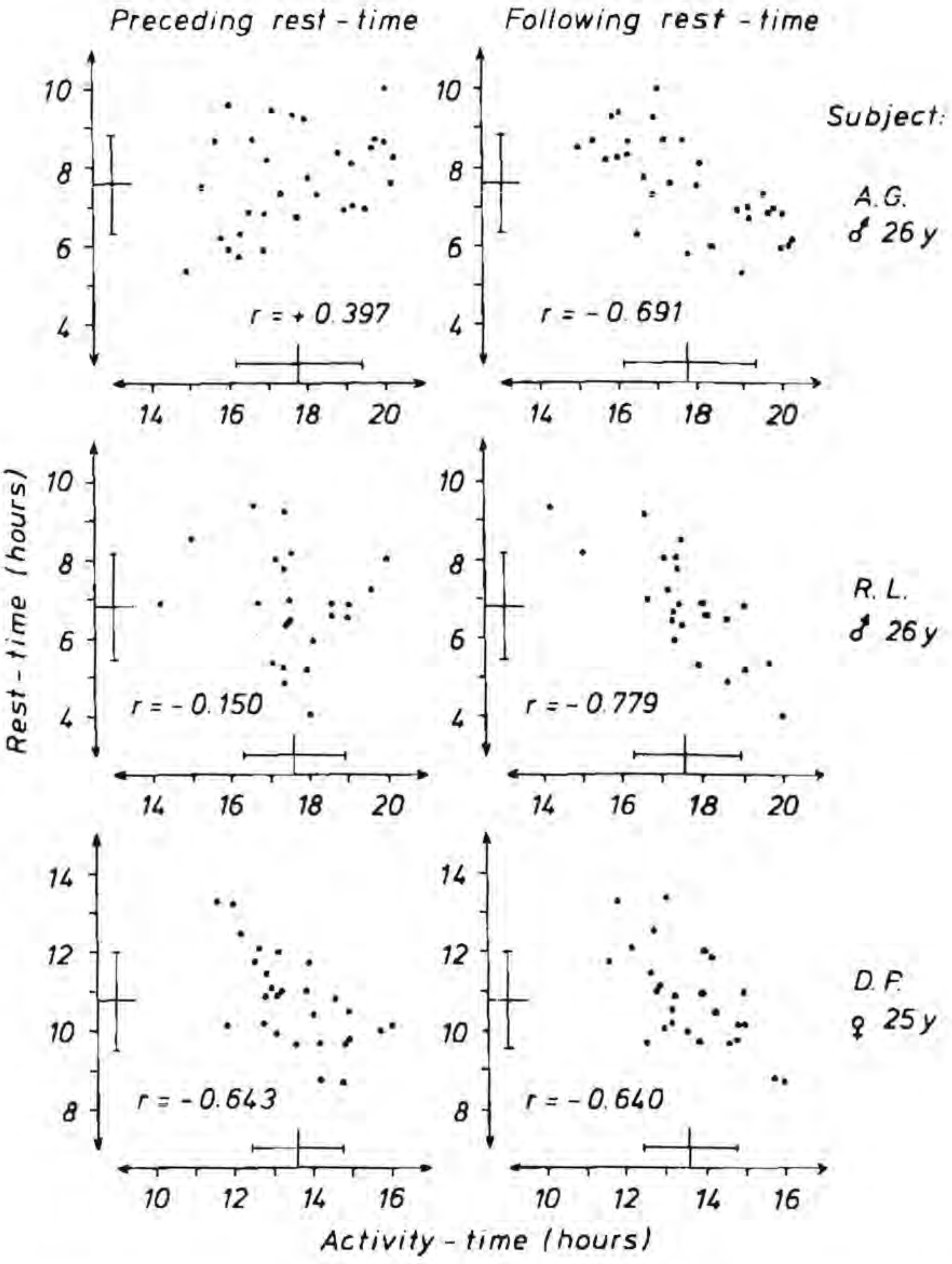

Figure 5. Serial correlations between activity-times and rest-times, computed from 3 experiments performed under constant conditions without environmental time cues. The lines indicate means and standard deviations.

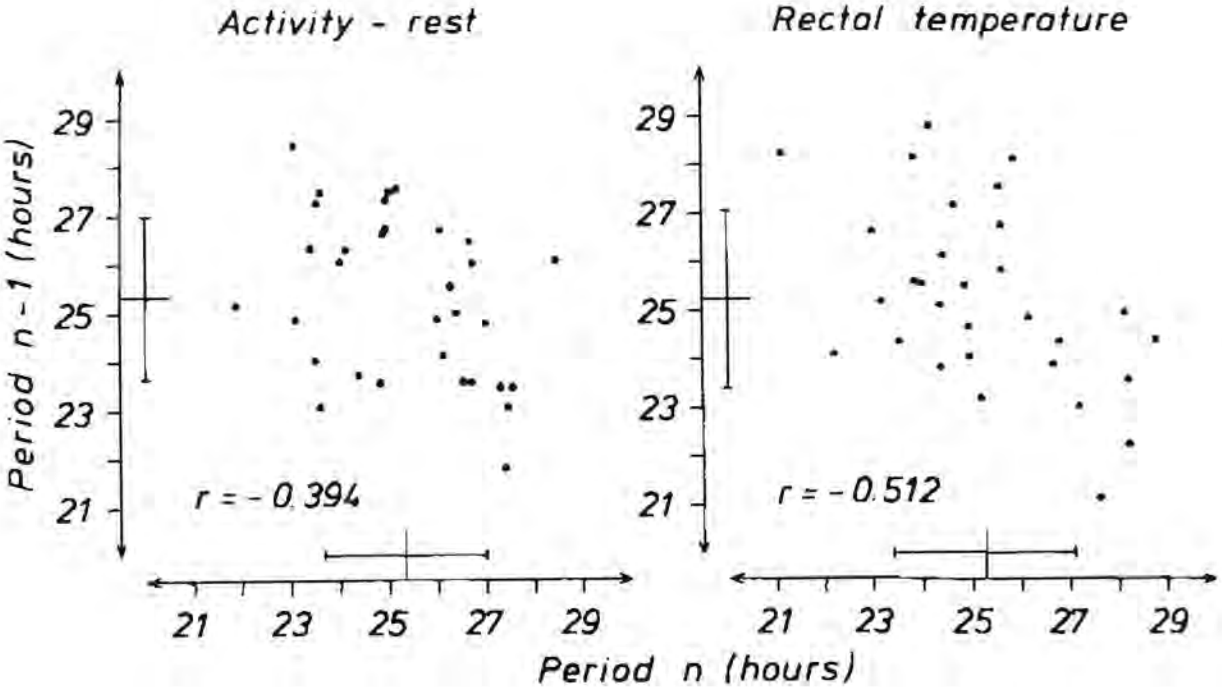

Figure 6. Serial correlation between successive cycles of activity-rest (measured from one midpoint of rest-time to the next) and of rectal temperature (from one minimum to the next), computed from the experiment shown in Figure 1. The lines indicate means and standard deviations.

tained if the cycle is defined in other ways, e.g., from one activity onset to the next. Moreover, there are higher order serial correlations: that between the duration of one cycle and the next but one is also significantly negative, indicating that the deviation of any cycle from the overall average is corrected by an opposite deviation, not only of the immediately following cycle but, also, of the next but one cycle. Again, this latter finding is confirmed by the overall results from the sample of 38 experiments with freerunning, internally synchronized rhythms ($r = -.401 \pm .166$; $p < .001$; Wever, 1979a); because of the obvious consistency in these results, the demonstration of one single example here would appear to be sufficient. Another illustration of the serial correlations within the activity-rest cycles is provided by the observation that the variability of activity onsets around a computed regression function is generally smaller than that of sleep onsets (this is in noteworthy contrast to the subjective feelings of the subjects).

The duration of the cycles of rhythms other than that of activity-rest are also serially correlated. The right-hand diagram of Figure 6 shows the correlation between sucessive period lengths of the temperature rhythm (meaured between minima), calculated from data obtained in the same experiment as were the activity-rest cycles shown in the left-hand diagram (cf. Figure 1). As can be seen, the negative serial correlation within the rectal temperature rhythm is even stronger than that within the activity rhythm. Again, this result is confirmed in the results from the sample of 38 experiments($r = -.461 \pm .118$; $p < .001$; Wever, 1979a). The concurrence of the serial correlations in the two different rhythms is the more remarkable since they are not directly dependent on each other. When, in the data of Figure 6, the activity-rest cycles are correlated with their accompanying temperature rhythm periods, the coefficient does not differ significantly from zero ($r = .353$); the same is true for the mean correlation in the larger sample of 38 experiments. This result means that the different overt rhythms are stabilized independently of each other.

So far, we have discussed spontaneous short-term variations of rhythm parameters; these variations could be considered as 'biological noise'. In addition, however, long-term changes induced by alterations in experimental conditions can occur. The period of a freerunning rhythm is lengthened in subjects in an isolotion unit who are permitted to select their own light-dark cycles (Wever, 1969a), or cycles in ambient temperature (Wever, 1974); or who are in a "self-control" mode because of special conditions, e.g., when they have social contacts within a group (Wever, 1979a). On the other hand, up to the present time, only one physical stimulus is known which affects subjects equally during both activity and sleep, and which modifies human freerunning rhythms in a regular and reproducible manner, and that is a weak electric AC-field (frequency 10 Hz; Wever, 1967, 1969b). When present continuously, this completely imperceptible stimulus shortens the period and, in addition, reduces the sleep fraction and the variabilities of activity and sleep onsets around their computed regressions. Within the rhythm of rectal temperature, it raises the mean value and increases the amplitude; all these effects are statistically significant (Wever, 1971).

Of the various rhythm parameters, the range of the temperature rhythm is most strongly correlated with the fraction of sleep, intra- as well as inter-individually. In Figure 7, pairs of these two parameters are plotted from 12

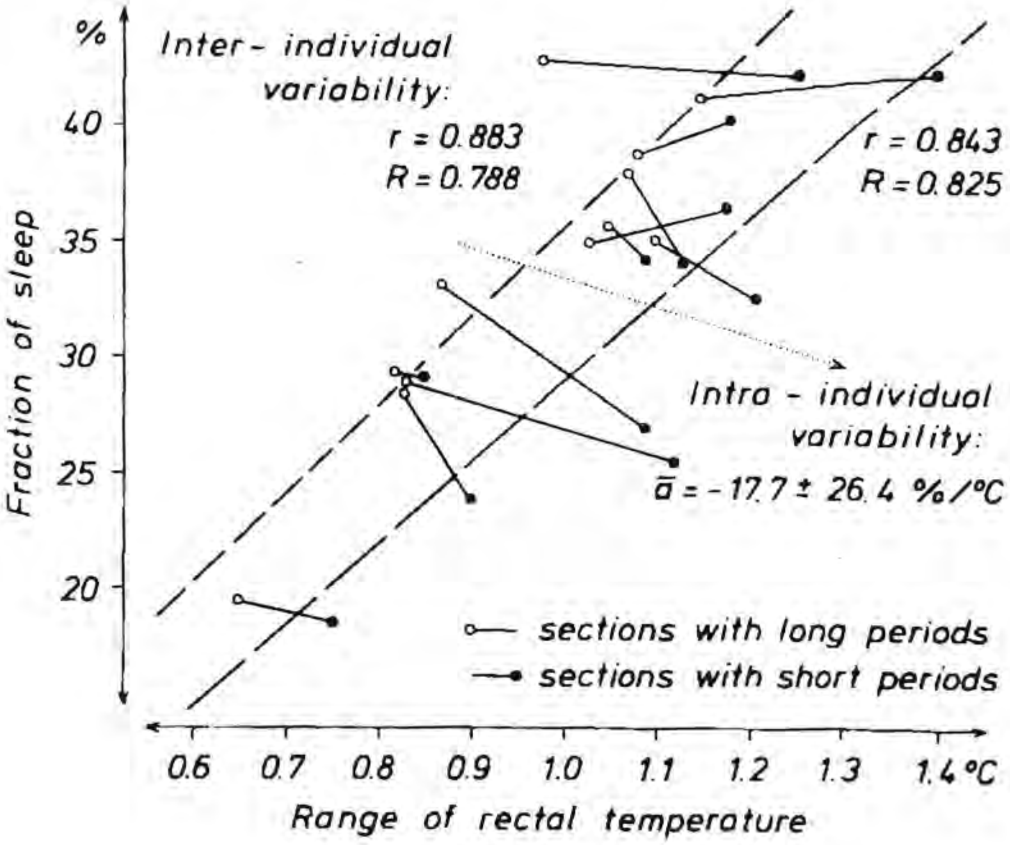

Figure 7. Correlations between range of rectal temperature and fraction of sleep, measured in 12 experiments performed under constant conditions without environmental time cues. In one section of the experiments, the subjects were exposed to a weak electric AC field (10 Hz) which shortened the period. Values from the two sections of each experiment are joined by lines; the mean and standard deviation of the individual regressions constituted by these lines are shown, as are also the inter-individual coefficients of correlation (parametric correlation r, and rank-order correlation R) computed separately for the values obtained in the two different sections of the experiments.

subjects whose freerunning periods were shortened, during one section of an experiment, by exposure to 10-Hz field. For each subject, the plotted points from the sections with and without the field, i.e., with short and long periods, respectively, are joined by lines. As can be seen, the fraction of sleep decreases in most subjects when the temperature range increases. Inter-individually, however, the two parameters are correlated positively: the larger the range of the deep body temperature rhythm, the greater is the fraction of sleep. This is true for both experimental conditions. As mentioned earlier, nearly all rhythm parameters are mutually correlated intra-individually with changing conditions; however, in this experiment, there are no other significant inter-individual correlations between any parameters (for instance, the correlation between fraction of sleep and period is $r = .110$ in the sections with the short periods and $r = .258$ in the sections with the long periods). The same results are seen when a larger sample of experiments is considered ($n = 21$; not including the 12 experiments in Figure 7): again, there is a significant correlation, between fraction of sleep and range of rectal temperature ($r = .721$; $p < .001$), but there is no other significant correlation, for instance between period and amplitude ($r = -.171$) or period and or period and fraction of sleep ($r = -.425$).

It is apparent from Figure 7 that the correlations between fractions of sleep and amplitude of the temperature rhythm have opposite signs when computed from intra- and inter-individual variations. This apparently contradictory result is, however, in agreement with predictions derived from a simple model of selfsustained oscillations, which also predicts the observed interdependencies between changes in many different rhythm parameters (Wever, 1964, 1965, 1966); here, the 'Threshold-level hypothesis' is relevent. According to this hypothesis, the discontinuous alternation between activity and sleep can be attributed to a continuous oscillation (Wever, 1960). As long as this basic oscillation exceeds a threshold, the subject is active, whereas below this threshold, he is asleep; since in humans, activity-time is always longer than sleep-time, the mean level of the basic oscillation must be higher than the threshold. The diagrams in Figure 8 illustrate these relationships. For intra-individual variations (Figure 8, right), the model postulates an increase in the mean level when the amplitude increases; consequently, the 'sleep fraction' becomes shorter. For inter-individual variations (Figure 8, left), there is no need to assume interconnections between amplitude and mean level; consequently, the 'sleep fraction' becomes longer when the amplitude increases. It has to be emphasized that it is not only the observed results from long-term variations that are in agreement with these theoretical postulates, but also those from the short-term variations that were discussed earlier; i.e., the model also predicts serial correlations of the same type as observed experimentally (cf. Figures 5 & 6).

Freerunning, Internally Desynchronized Rhythms

In our total sample of 155 experiments under constant conditions, 53 of the subjects showed internal desynchronization. In all these cases, the overt rhythms of activity and rectal temperature differed in period (Aschoff, Gerecke, & Wever, 1967b); the periods of the rhythms of rectal temperature remained close to 25 hours, whereas activity-sleep cycles with durations between 12 and 65 hours were observed. Remarkably enough, in none of these cases was the subject aware of his unusual behavior.

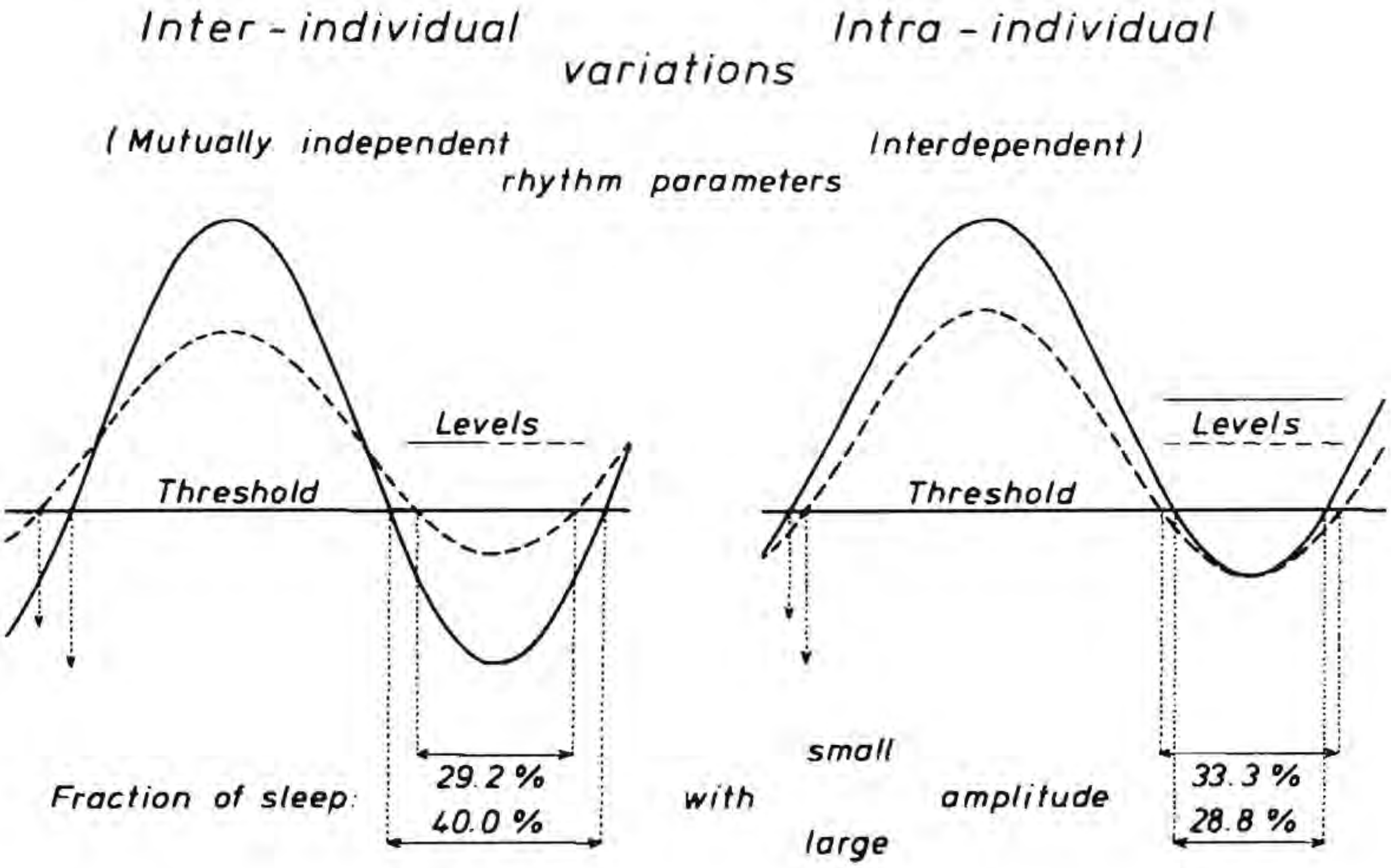

Figure 8. Schematic representations of the relationships between range of oscillation and sleep fraction according to the 'threshold level hypothesis': The oscillation defines 'activity' as long as it is above the threshold, and 'sleep' as long as it is below it. Level and amplitude of the oscillation are correlated intra-individually, but not inter-individually.

In the typical example shown in Figure 9, the activity-sleep cycle has an abnormally long period right from the beginning of the experiment. In other experiments, this lengthening occurred later on; in some cases, the period of the activity rhythm was not lengthened, but in fact drastically shortened. It is characteristic of all these cases of internal desynchronization that the internal phase relationship between different overt rhythms varies from day to day; this means, for instance, that on some days, the subjects sleep when deep body temperature is increasing (as they do with freerunning, internally synchronized rhythms) but on other days when temperature is decreasing (as in the normal 24-hour day). In the particular experiment illustrated in Figure 9, the courses of both rhythms show typical scalloping patterns (left-hand diagram), with repetition periods of about 6 days. The periodogram analyses of the two time series (right-hand diagram) show two peaks in each case. The rectal temperature rhythm has a significant primary period of 25.0 hr, which is obvious in the overt rhythm's course; additionally, there is a secondary, also significant period of 30.2 hr, corresponding to one in the overt activity rhythm. In fact, in the latter, the 30.2 hr period is the primary one, but there is another significant period at 32.5 hr, and a suggestion of one at 25.0 hr,corresponding to the primary period of the overt rectal temperature rhythm (the further peak at 16.25 hr is only due to the fact that this is the first harmonic of 32.5 hr).

The analyses of many other overt rhythms measured in this experiment (e.g., electrolytes in the urine) result in similar peaks. It should be noted that the components of the different rhythms, when the latter are considered separately, keep internal phase relationships which are temporally constant and identical, in contrast to the internal phase relationships between the different overt rhythms themselves, which vary from day to day.

Another example of internally desynchronized rhythms is given in Figure 10, based on data from a subject who had to perform ergometer work during half the duration of the experiment. Each of the two parts presented includes 5 cycles of rectal temperature but only 4 cycles of activity-sleep; the workload had no effect on the period of either rhythm. A few of the activity-times are interrupted by 'naps' which are normally not permissible but could not be avoided by the subject in this experiment. The temporal relationship between the two rhythms changes over time, so that a main sleep occasionally coincides with a temperature maximum; but the naps always coincide with temperature minima. During the section without workload (B), a direct reactive interaction ('masking') between the two variables can be observed: when the subject falls asleep while deep body temperature is high, rather than being at a minimum, the temperature always drops; the magnitude of this 'masking effect', which is nearly independent of the true phase of the rhythm, is roughly a third of the total circadian range. During the section with workload (A), the interactions between the circadian temperature rhythm and the frequent temperature rises due to ergometer sessions are of particular interest. The result is a simple superimposition: the reactive temperature rises can occur even around the temperature minimum without influencing the rhythmicity itself.

From results like those shown in Figures 9 and 10, together with computer simulations, a consistent multi-oscillator model of the human circadian system has been established (Wever, 1975a). It assumes, in essence, two basic oscillators which normally run in synchrony with each other but which can, in spe-

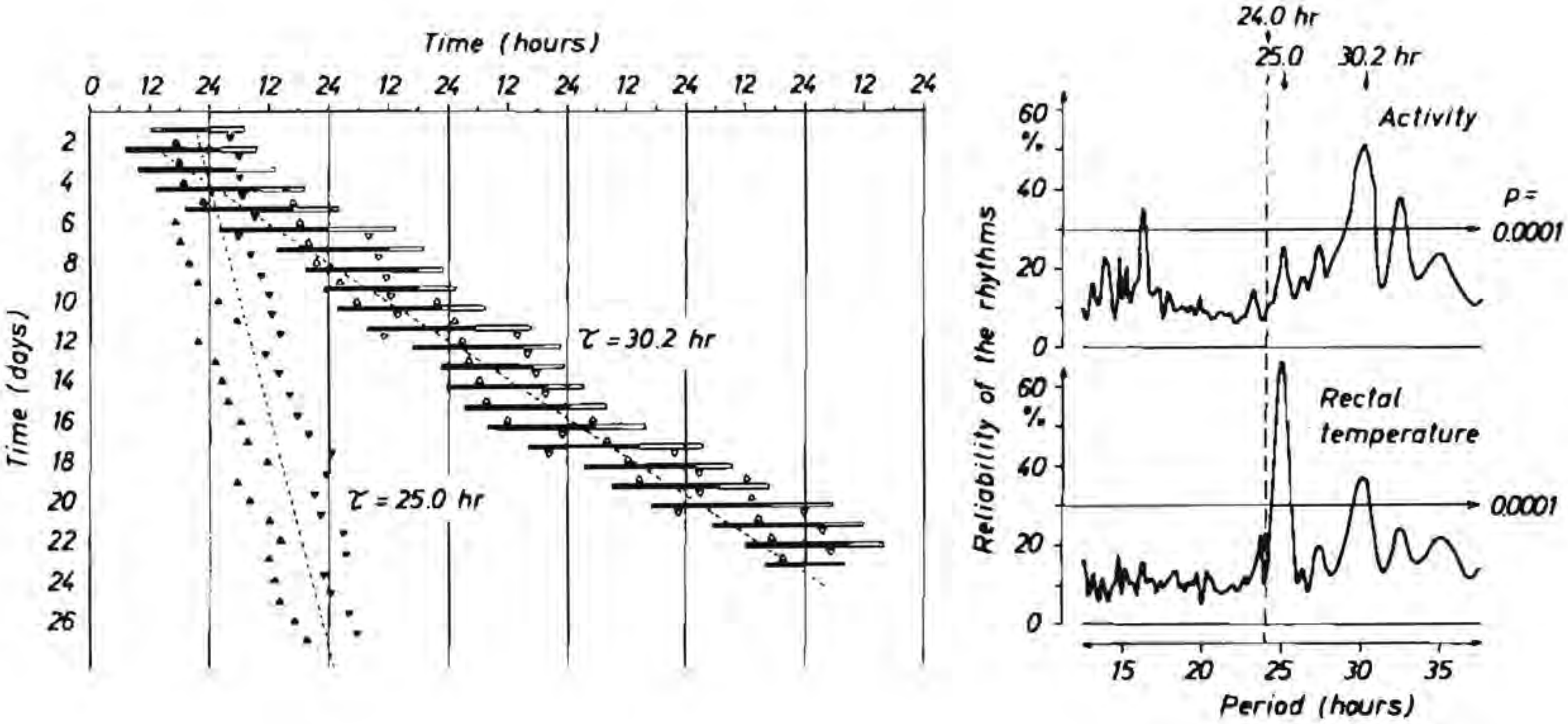

Figure 9. Autonomous rhythms of a subject (A.F., ♂ 24y) living under constant conditions without environmental time cues. Left: rhythms of activity and rectal temperature, graphed as for Figure 1 (the white triangles are the temporally correct placings of the corresponding black triangles). Right: periodograms of the two time series (for details of the analyses, see Wever, 1979a).

cial conditions, have different periods in the steady state. Each of these oscillators contributes to the control of all overt rhythms; or, in other words, every overt rhythm is controlled simultaneously by both basic oscillators, though in proportions varying from rhythm to rhythm. The two basic oscillators are matched in all relevant properties except strength, or degree of persistence: the oscillator that predominantly controls the overt rectal temperature rhythm is about 12 times stronger than the one that predominantly controls the overt activity rhythm. Normally, i.e., in the case of internal synchronization, the overt rhythms behave outwardly as though they are controlled by only one oscillator. In the case of internal desynchronization, every overt rhythm is composed of two or more components with different periods superimposed on each other. As a result, beat phenomena occur, which appear outwardly as a scalloping pattern (cf. Figure 9, left) and as a periodic change in amplitude (cf. Figure 10); the repetition period of the beats is determined by the two contributing rhythm periods. Another consequence of the contribution of two components to every overt rhythm is that the negative serial correlations, which in other time series indicate that the data have an oscillatory origin, are obscured. Actually, these correlations would, in fact, be expected to be present in each of the contributing rhythm components separately and independently; but it is exactly for this reason that they cannot be seen in the composite of these components. Indeed, in the overt rhythms, small positive serial correlations can be expected to show up due to the beats, and, for the same reason, only higher order negative serial correlations.

In the discussions of Figures 9 and 10, it was mentioned that subjects, in a state of internal desynchronization, sometimes sleep with an increasing and sometimes with a decreasing deep body temperature. These variations can be used to test the hypothesis of a direct connection between trends in deep body temperature and sleep structure. Sleep-times with predominantly increasing and with predominantly decreasing temperatures were identified in the data from the experiment shown in Figure 9 and analysed separately. In the upper diagram of Figure 11, the mean duration of REM sleep as a percent of total sleep is shown for the two types of sleep-time, in each third of the sleep (to standardize the evaluation, each sleep-time was divided into three equidistant intervals, independent of its absolute duration). It can be seen that, in those sleep-times where body temperature increases (as it usually does with freerunning, internally synchronized rhythms), REM sleep propensity decreases during the sleep, again in agreement with what is observed with internally synchronized rhythms (cf. Figure 4). In sleep-times where body temperature decreases REM sleep propensity increases, a pattern resembling that seen when rhythms are synchronized to 24 hours. The difference in slope between the two curves shown in the upper part of Figure 11 is statistically significant; as is also the difference in mean absolute duration of the first REM phase in the two types of sleep-time (cf. Zulley, 1979). These differential relationships support the hypothesis of a dependency of the structure of sleep on the rhythm of deep body terperature.

The lower diagram of Figure 11 shows the actual values of rectal temperature recorded during the two types of sleep. It is clear that sleep-times coinciding with decreasing deep body temperature are longer than sleep-times coinciding with increasing deep body terperature. Bearing in mind the correlation between variations in REM sleep propensity and rectal temperature, it fol-

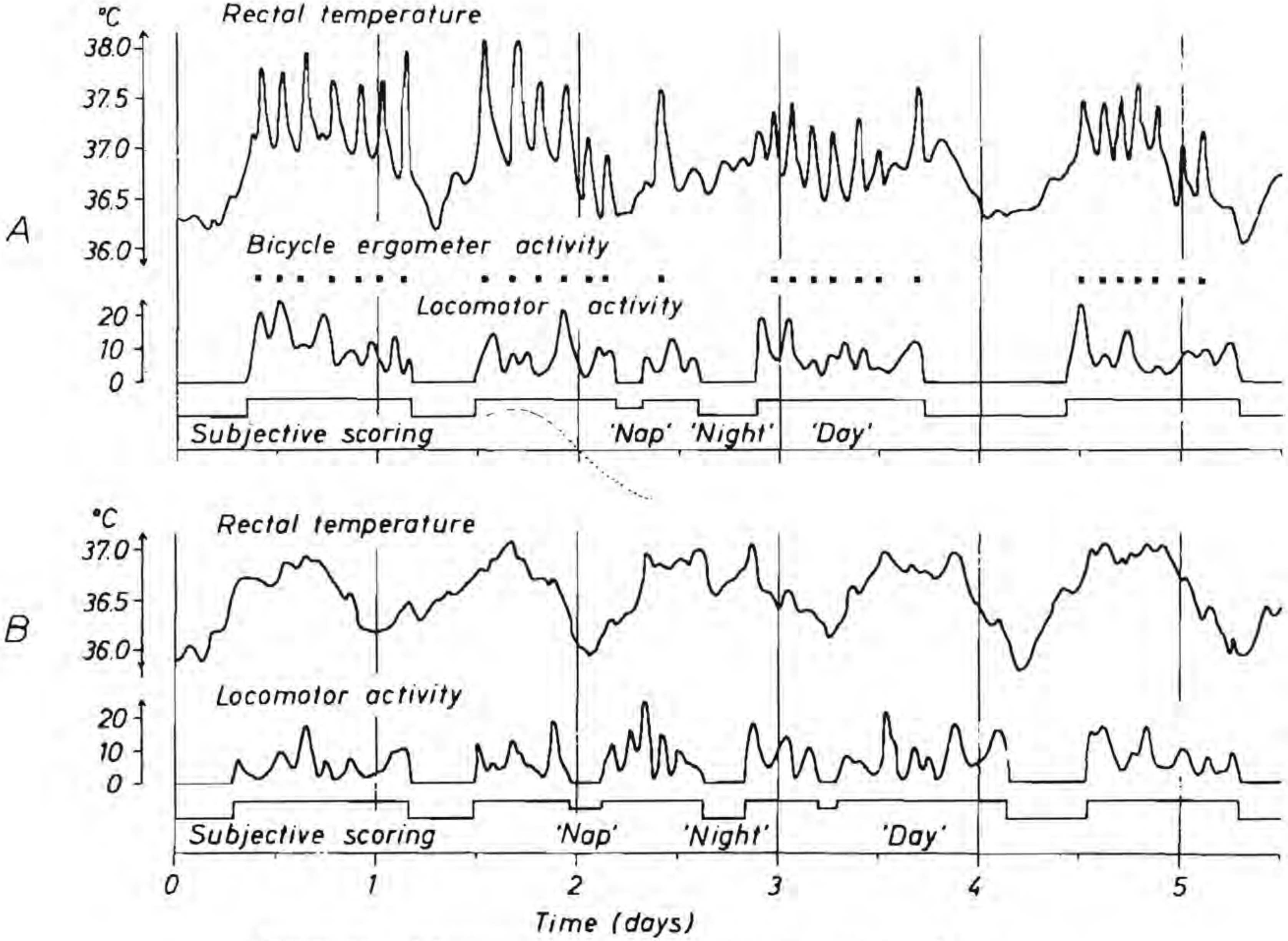

Figure 10. Autonomous rhythms of a subject (P.C., ♂ 24y) living under constant conditions without environmental time cues, and during the first section (A) with a heavy ergometer workload (100 W for about 20 min, 7 times per activity cycle). Rectal temperature, locomotor activity, subjective scorings of 'day' and 'night', and interposed 'naps' are shown in the same manner as in Figure 3. For clarity, only short parts (days 3 to 7 and 22 to 26) of the two-week sections of the experiment are illustrated. From Wever (1979b).

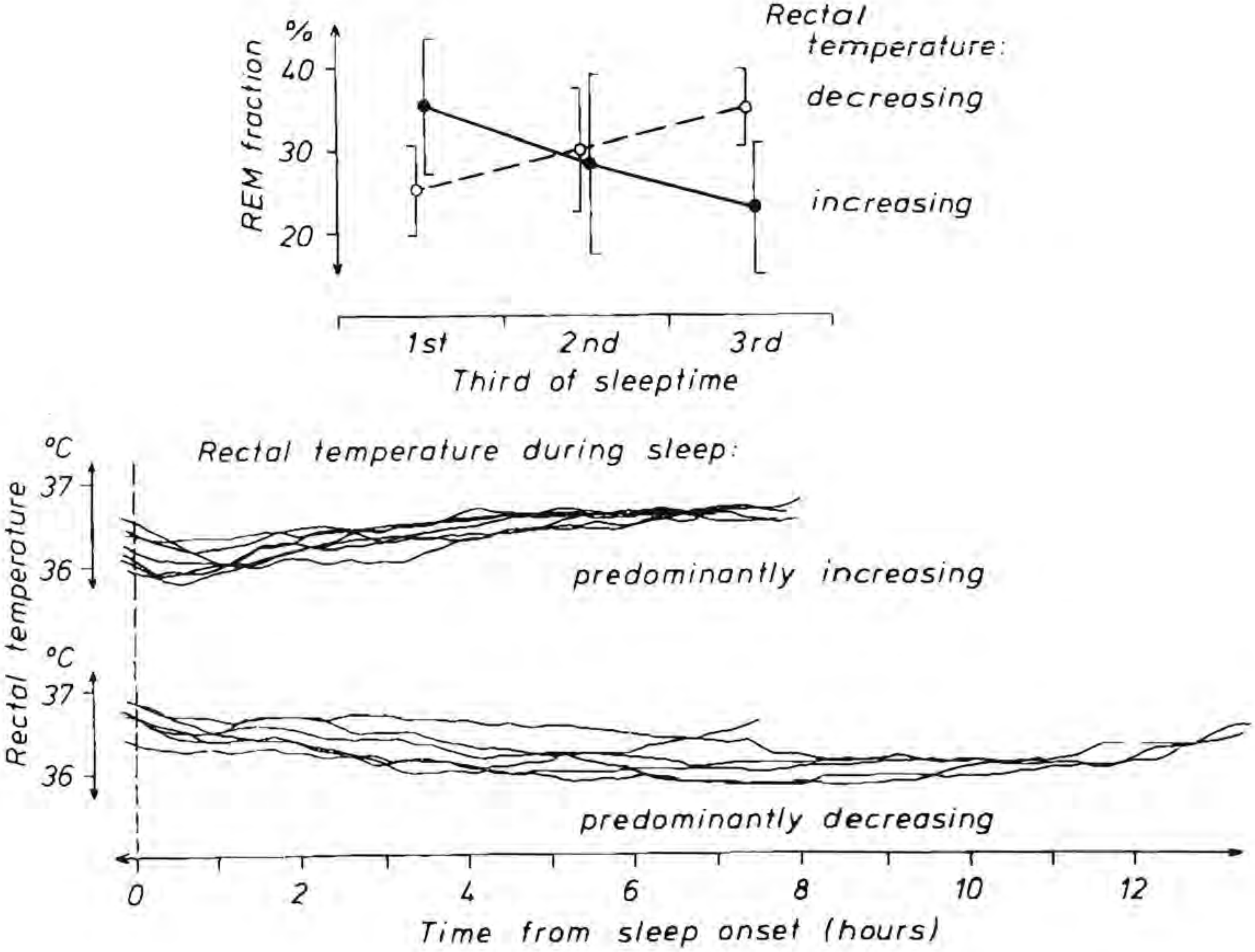

Figure 11. Parameters of sleep, as determined by polygraphic recordings from the subject in the experiment shown in Figure 9. Above: mean fractions of sleep time spent in Stage REM, computed for each third of the sleep-time, and averaged separately for sleeps with (a) predominantly increasing and (b) predominantly decreasing rectal temperature. Brackets indicate SDs. Below: records of rectal temperature during sleeps of type (a) and (b). Data from Zulley (1979).

lows that a correlation exists between structure and duration of sleep: if there is a high fraction of REM at the beginning of sleep and a decrease in REM sleep propensity later on, the sleep will tend to be short; if there is a low REM fraction at the beginning and subsequent increase in REM sleep propensity, the sleep will tend to be long.

The state of internal desynchronization as discussed so far in this paper is mainly characterized by continuously changing internal phase relationships between the overt rhythms of activity and deep body temperature. There is another rhythm state where, although these two rhythms again show different period values, they have a temporally constant internal phase relationship. This happens when one period is an integral fraction of the other. The most frequent type of this state of 'apparent internal desynchronization' is one where there is a 'circa-bi-dian' activity rhythm that is internally synchronized to the rhythm of deep body temperature with a ratio of 2:1, i.e., a state in which two cycles of rectal temperature (period about 25 hr) are coordinated with one alternation between activity and sleep (period about 50 hr). In such a state, the phase relationship between the two rhythms is bivalent but temporally constant. As an example, Figure 12 presents a section of a 29-day experiment performed under constant conditions, showing the polygraphic records of the sleep behavior of the subject, together with the course of his rectal temperature. The presentation corresponds to that shown in Figure 4, apart from the fact that all parts of the cycle are about twice as long, the mean values being: period 49.2 hr, sleep-time 14.3 hr, and activity-time 34.9 hr. The sleep profiles thus appear, as a function of local time, only every other day. It is obvious from Figure 12 that there is a consistent relationship between the trend in deep body temperature, which has a minimum at about the middle of sleep-time, and sleep structure; note that there are 10 REM-phases per sleep-time instead of the typical 5 or thereabouts. The subject did not consciously perceive the long duration of his activity period; possibly due to this unawareness, his behavior was quite normal, although wakefulness of such a long duration would be ordinarily expected to produce symptoms of sleep deprivation.

Internal desynchronization, whether it occurs by a lengthening or by a shortening of the activity-sleep cycle, affects both wakefulness and sleep equivalently. Close examination shows, however, that, during internal desynchronization, the fraction of sleep is smaller than when rhythms are internally synchronized. This conclusion is based on experiments from which the freerunning rhythms remained internally synchronized during one section but became internally desynchronized during another section. In 17 experiments where the activity-sleep cycle lengthened spontaneously during the experiments (from a mean of 25.55 to 34.04 hr), the mean sleep fraction decreased by 3.78% (SD 5.08%), i.e., from a mean of 32.21% to 28.43% (in only two of the experiments did the sleep fraction increase); this mean decrease in the sleep fraction was significant ($p < .01$). This result implies that the lengthening of the activity-sleep cycle during the transition to internal desynchronization concerns the activity fraction more than the sleep fraction. However, it could be argued that undetected naps during the very long lasting apparent wakefulness could give rise to the reduction in the observed sleep-time fraction. Apart from the fact that naps are normally detected, and thus included in the calculations (cf. Figure 10), this argument is refuted by the data of 11 other experiments in which the activity-sleep cycle was shortened from a

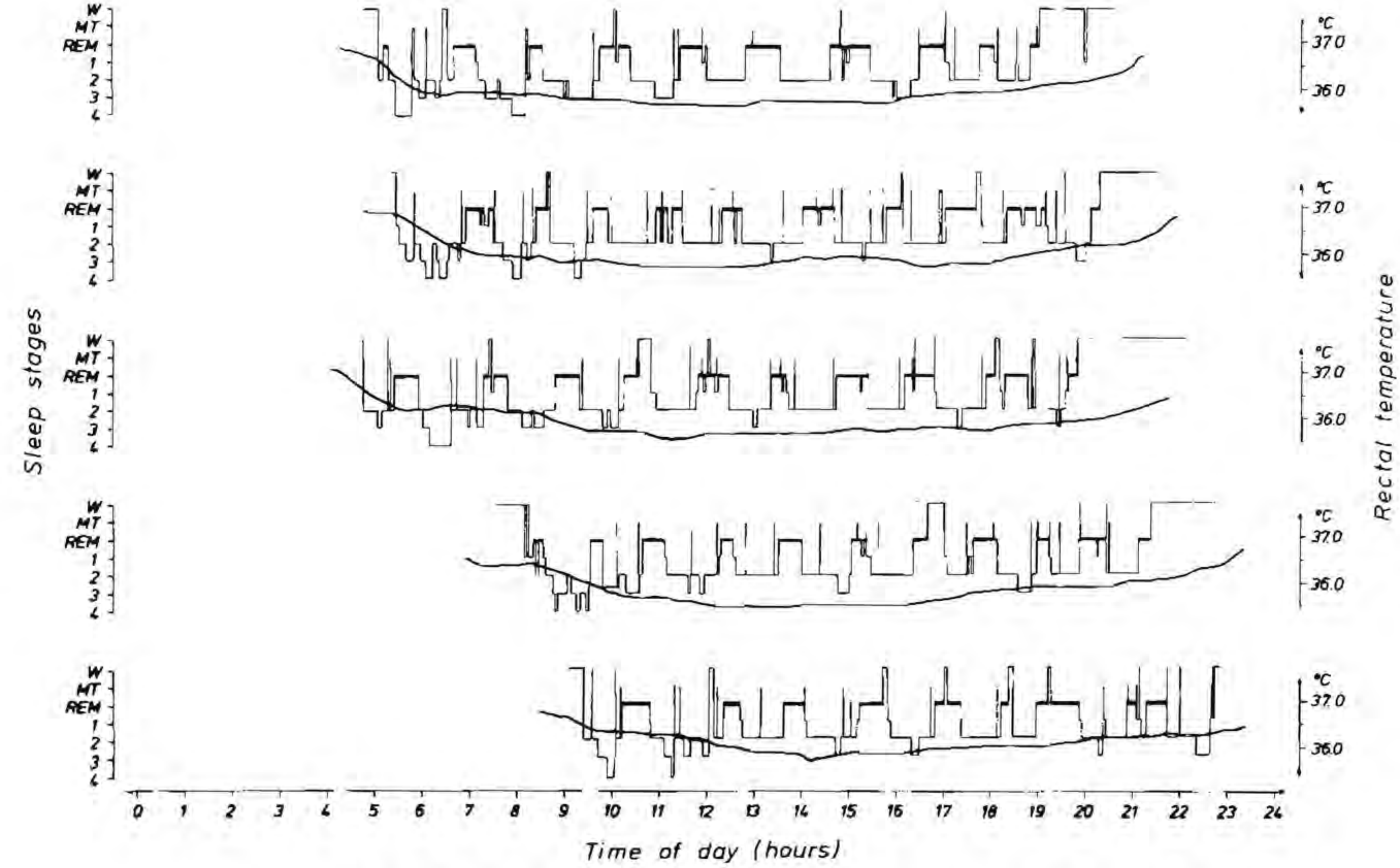

Figure 12. Parts of the autonomous rhythms of a subject (M.K., ♂ 28y) living under constant conditions without environmental time cues. Sleep stages (from polygraphic sleep recordings) and rectal temperature during successive sleeps are shown as related to local time. For clarity, only days 4 to 13 of the 29-day experiment are illustrated. Note: due to the extremely long duration of the sleep-activity cycle, sleep occurs only every second day.

mean of 24.47 to 17.91 hr. Here the fraction of sleep decreased in all experiments; the mean reduction was 4.03% (SD 2.37%), i.e., from 36.27% to 32.24%, and was statistically significant (p <.001). Although in this case the sleep-time is affected by the change more than the activity-time, the shortened activity-time affords less time for naps than the "cycle-lengthening" state of internal synchronization.

The general conclusion from the above set of findings is that rhythm disorders reduce the fraction of sleep within the total sleep-wake cycle. It must be emphasized again that, in the experimental conditions pertaining in the studies, the subjects have complete control over when they sleep; though they have no idea about the duration of their sleeps, nor the value of the sleep fraction in any cycle. When, at the beginning of an experiment, a subject thinks he can remember his previous sleep habits, he usually has a tendency to overestimate the duration of his sleep-times in the isolation chamber: most subjects judge their first sleep-time to be longer than normal, whereas, in reality, it is usually shorter. On the other hand, there is a tendency to underestimate the duration of naps, and this is the reason why naps are normally inadmissable. Thus, in some of the experiments where internal desynchronization occurs by a lengthening of the activity period, the sleep-time subjectively scored to be the 'night-sleep' is not lengthened, but is supplemented by a 'nap; such a 'nap' which mostly is subjectively scored as lasting 15 to 30 minutes, actually lasts for up to 15 hours.

From all the foregoing considerations, it must be concluded that the sleep fraction under constant conditions really reflects the need for sleep, and need is obviously reduced under internal desynchronization. So, in other words, the need for sleep is less than normal when the circadian system is in a disintegrated state.

Externally Synchronized Rhythms

In the laboratory, circadian rhythms can be synchronized by means of artificial zeitgebers. The application of periodic stimuli with different modalities and varying properites (e.g., period) is one of the tools to test the effectiveness of zeitgebers. Figure 13 (left) shows the course of an experiment where a subject was exposed to an artificial light-dark cycle (but with reading lamps available) which was changed at intervals,and which was complemented by regular gong signals calling the subject to give a urine sample and to perform certain tests (Wever, 1970). The right diagram of Figure 13 shows the mean rhythms averaged from all but the first two cycles in each of the three sections. From the left-hand diagram, it can be seen that the subject's rhythm is synchronized to all three zeitgeber periods used. [It has been shown in further experiments of the same type that synchronization is only possible within about the limits used here, and the zeitgebers with periods longer than 27 hours or shorter than 23 hours have not the capacity to synchronize human circadian rhythms (see Aschoff, Poeppel, & Wever, 1969).] However, the right-hand diagram shows that some changes occur when the zeitgeber period is shortened: (1) The activity fraction becomes shorter and the sleep fraction longer; i.e., the subject changes from a "short" to a "long" sleeper. (2) The rhythm's phases shift to later points in the cycle, to a greater extent in rectal temperature than in activity; this means that the subject changes from a "morning type" to an "evening type" (Wever, 1969b). [Note that

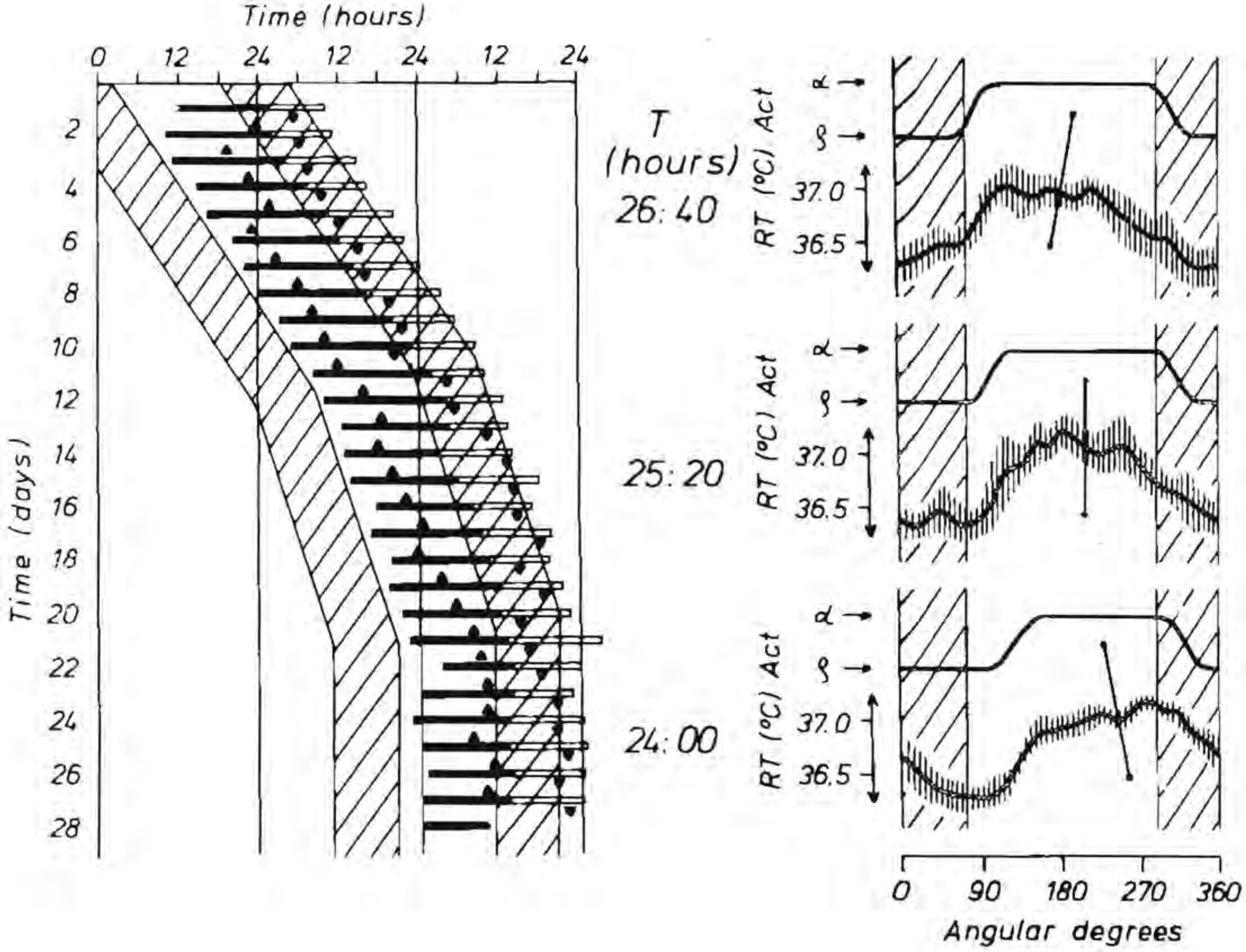

Figure 13. Circadian rhythms of a subject (M.O., ♂ 24y) living without environmental time cues but under the influence of an artificial zeitgeber (light-dark cycle with reading lamps available during the dark-time, and gong-signals at regular intervals calling the subject for urine samples and certain tests), with two alterations of the zeitgeber period. Left: rhythms of activity and rectal temperature, graphed as in Figure 1; hatched areas: dark-time of the zeitgeber. Right: longitudinal representations of the rhythms, averaged separately from the three sections with different zeitgeber periods (omitting the first two cycles of each section). Hatched areas: dark-time of the zeitgeber. Arrowed lines indicate standard deviations computed from the successive cycles within each section; the other lines join the acrophases of the two rhythms.

the subject, although he was aware of his changed behavior, did not realize the reason for it, i.e., the alteration in the duration of his day.] Since the two rhythms are phase shifted by different amounts, the internal phase relationship between the two rhythms changes with the zeitgeber period. This means that the subject sleeps predominantly during a period of increasing deep body temperature when the zeitgeber period is long (first section) but with one of decreasing temperature when it is short (third section); it is known that this can be expected to influence the duration of sleep-time (cf. Figure 11). During the second section, the minimum of deep body temperature would be expected to occur near the midpoint of the sleep-time; however, the average cycle actually shows a split minimum, indicating that this intermediate position of the minimum is not so stable as are positions near the beginning and near the end of sleep-time. This impression is confirmed by inspection of the original data (Figure 13, left), where it can be seen that, during the middle section, the position of the minimum varies between locations near the beginning and near the end of sleep.

The same type of artificial zeitgeber can be used to simulate time-zone shifts accompanying transmeridian flights. In a typical experiment (Figure 14), a subject was exposed to an artificial 24-hour day; on the 8th day, an eastward flight across 6 time-zones was simulated and on the 16th day a 6 time-zone westward flight. The subject did not consciously perceive any change in the experimental conditions; on the contrary, he was convinced that during the whole experiment, he had lived in temporal agreement with the outside environment. When, at the end of the experiment, he observed that he was, in fact, living in accordance with local time, he was reconfirmed in his conviction that nothing special had happened, and was very surprised to learn that, during a substantial part of the experiment, he had been out of phase with local time by 6 hours. As can be seen in the left-hand diagram of Figure 14, the subject's activity rhythm adjusts to the changes in the zeitgeber in about two days, and the rhythm of deep body temperature in a few more days, but more slowly after the delay shift than after the advance shift. The right-hand diagram shows the mean rhythms in each of the three sections (the first two days of each section were again excluded in calculating these averages). The diagrams confirm the general adjustment of the rhythms to the shifted zeitgeber in the second and third sections; even the characteristic individual shape of the rectal temperature rhythm is maintained. Only the phasing of the temperature rhythm suggests that re-entrainment is not totally complete; but this is due to the inclusion in the averaged curves of days where the re-entrainment process is still in progress. The diagrams do not include the data obtained from psychomotor performance tests; however, measurements of computation speed show a clear rhythm which, even during the re-entrainment process, follows the rhythm of deep body temperature. Disregarding the underlying practice effect, there is a clear decrement in performance following the advance shift, but no detectable alteration in level following the delay shift.

The results of the zeitgeber experiments illustrated in Figure 13 (varying period) and in Figure 14 (phase shift) have been confirmed in a sufficient number of additional experiments to be generalized as follows. When the duration of an artificial day is shortened, a subject changes from being a "morning" to being an "evening" type and the rectal temperature rhythm also shifts to a later phase of the sleep-wake cycle; simultaneously, the fraction of sleep increases. When the phase of an artificial day is shifted, different

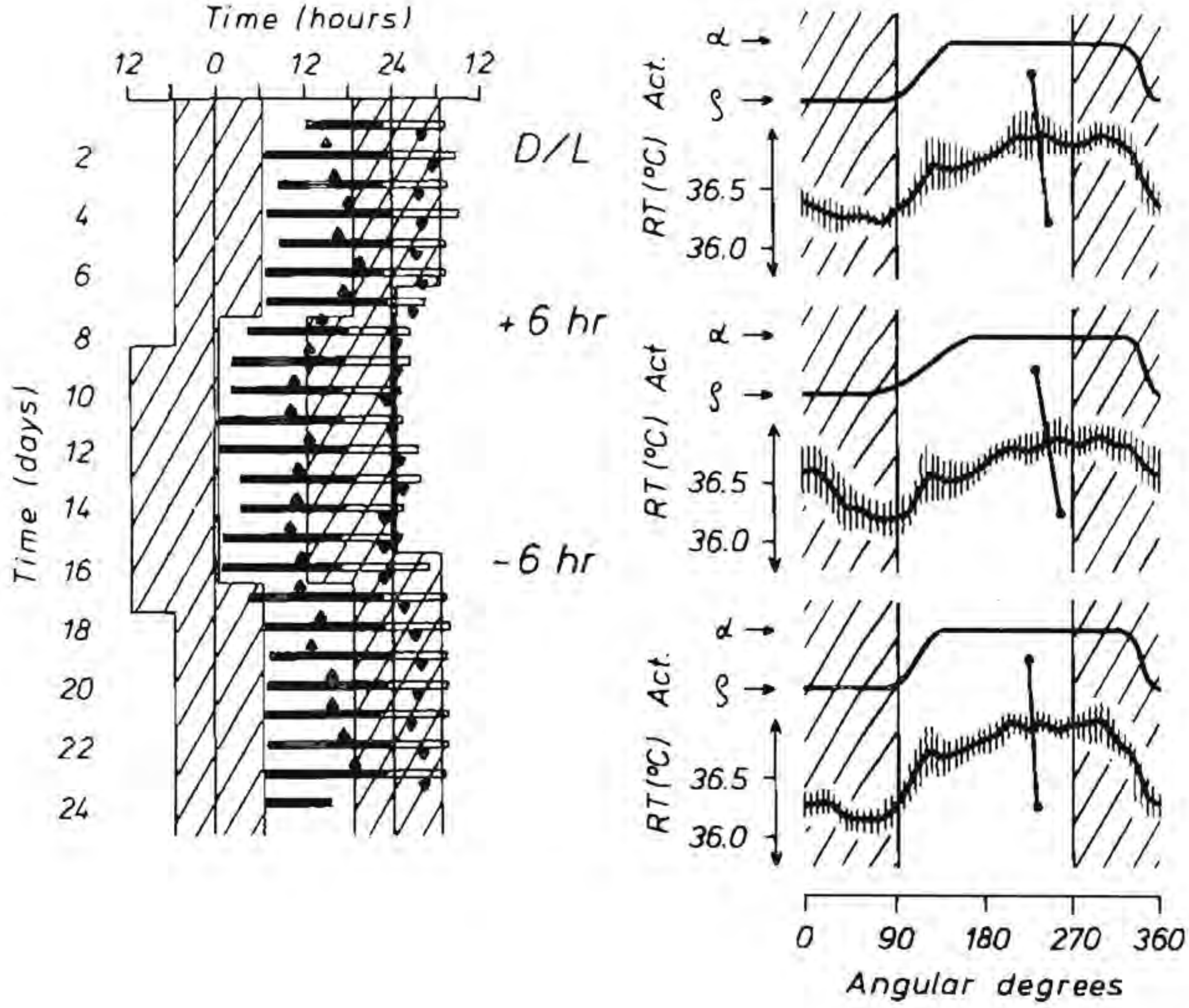

Figure 14. Circadian rhythms of a subject (G.L., ♂ 26y) living without environmental time cues but under the influence of an artificial 24-hour zeitgeber of the same type as in Figure 13, with two phase shifts of the zeitgeber. Left: rhythms of activity and rectal temperature, graphed as in Figure 1; hatched areas; dark-time of the zeitgeber. Right: Longitudinal representations of the rhythms, graphed as in Figure 13.

rhythms re-entrain at different rates, the rhythm of activity always faster than that in physiological functions; after an advance shift, the duration of re-entrainment is shorter than after a delay shift of the same amount, but both the number of subjective complaints and the decrements in psychomotor performance are greater. All these results are in agreement with those from real flight experiments (as long as the different time-shifts are performed under comparable conditions; see Sonderfeld, 1977). The existence of significant inter-individual correlations enables the duration of re-entrainment and the amount of behavioral impairment resulting from a time-shift to be predicted. Both of these predictions are independent of each other: (1) the larger the amplitude of the basic rectal temperature rhythm of a particular subject, the more persistent the rhythm, and the longer will its re-entrainment take after a zeitgeber shift; (2) the earlier the acrophase of the rhythm, the greater the behavioral impairment of the subject after an advance shift (Wever, 1980).

In the freerunning rhythms situation where the subject had no time reference to estimate the duration of his total sleep-wake cycle, or the value of the sleep fraction, there was a clear correlation between the fraction of sleep and the amplitude of the rectal temperature rhythm (cf. Figure 7). It is of interest to determine whether the same correlation exists in the case of externally synchronized rhythms; since here the sleep fraction also depends on the zeitgeber period, only those values obtained in a 24-hour day situation have been considered. There are 15 experiments which include at least one 24-hour section (cf. Figures 13 & 14). In Figure 15, mean sleep fraction in this section is plotted against mean rectal temperature range for these 15 subjects. The resulting positive correlation is weaker than that seen in freerunning rhythms (cf. Figure 7); the parametric and non-parametric coefficients are barely statistically significant. For comparison, Figure 15 (right) shows the regression of fraction of sleep on duration of the artificial day, assessed from experiments of the type shown in Figure 13. As can be seen, there is a strong relationship: the sleep fraction clearly decreases when the zeitgeber period is lengthened ($p < .001$) (it has been shown earlier in this paper that, simultaneously, the sleep shifts to a later phase of the rectal temperature rhythm).

Partially Synchronized Rhythms

The previous discussion of externally synchronized rhythms considered only those experiments in which all overt rhythms followed the zeitgeber synchronously. This is the case if the zeitgeber has a 'normal' strength, and if its periodicity does not deviate too much from 24 hours. However, of greater practical interest, in the present context, is a state of the rhythmic system where some of the overt rhythms follow a zeitgeger while others freerun, or where different overt rhythms follow different competing zeitgebers which deviate from each other in phase or period. This state of 'partial synchronization' is always combined with internal desynchronization, and it is only possible because of the multi-oscillatory set-up of the circadian system.

Since the two oscillators that constitute the human circadian system have different strengths (Wever, 1975a), they also differ in their ranges of entrainment: the weaker oscillator that predominantly controls the activity rhythm has a larger range of entrainment than the stronger oscillator that

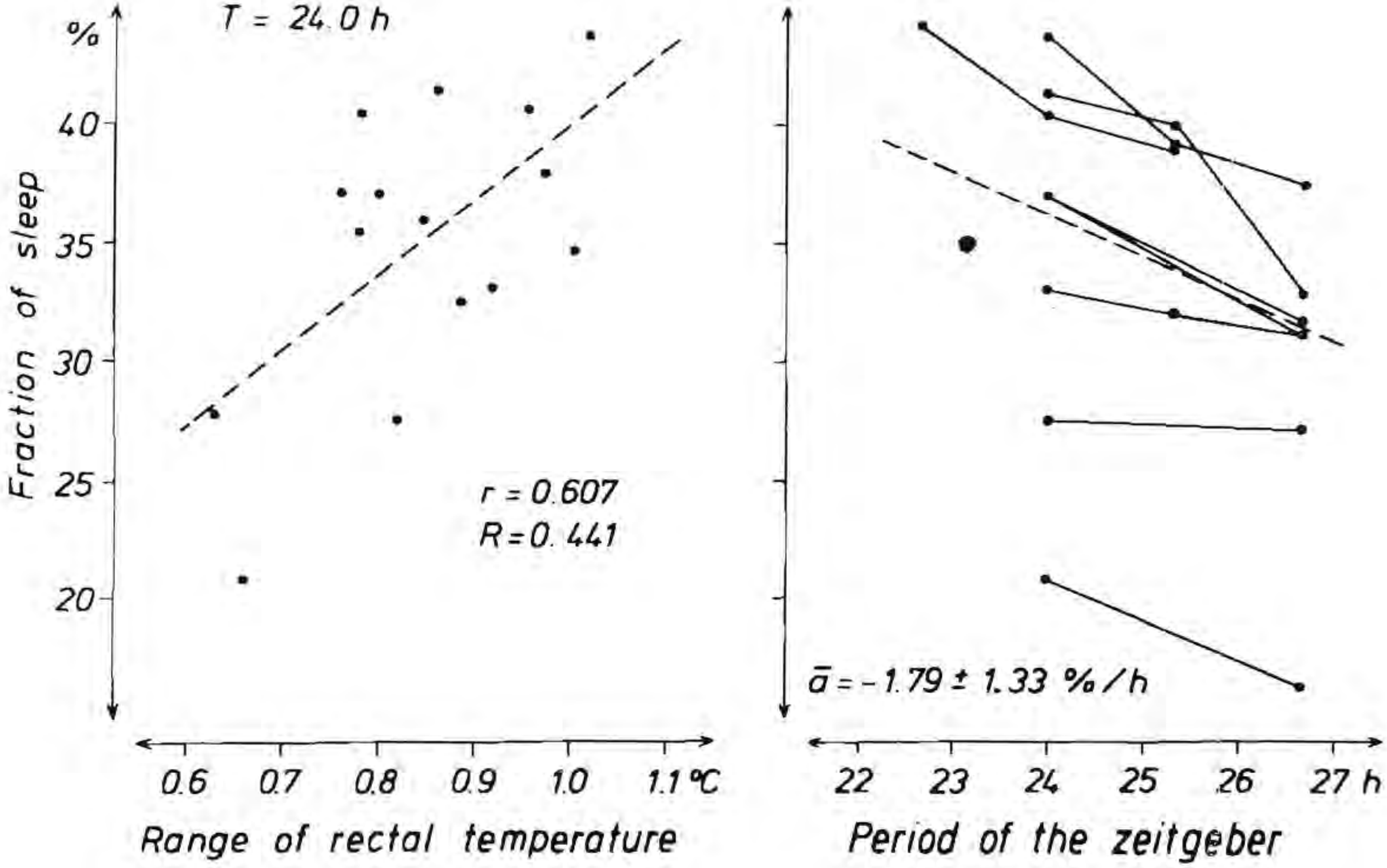

Figure 15. Fraction of sleep, measured in experiments performed without environmental time cues but with an artificial zeitgeber of the same type as in Figure 13; plotted on the left, as a function of the range of the rectal temperature rhythm (from 15 experiments with a 24-hour zeitgeber); and on the right, as a function of the zeitgeber period (from 8 experiments with varying zeitgeber period). In the left graph, r is the parametric and R the non-parametric inter-individual correlation coefficient; in the right graph, the mean and standard deviation of the individual regressions computed from the different sections in individual experiments are shown.

predominantly controls the rhythm of rectal temperature. This means that, under the influence of a zeitgeber with a period that deviates sufficiently from 24 hours, the overt activity rhythm can remain synchronized while the overt rhythm of rectal temperature freeruns. In the experiment shown in Figure 16, the subject was exposed to a strong zeitgeber (with no reading lamps available; Wever, 1975c), the period of which was successively increased from 24 to 28 and eventually to 32 hours. The activity-rest cycle of the subject was synchronized to the zeitgeber during all three sections without conscious perception by the subject of the changes in the duration of his days. The overt rhythm of rectal temperature, however, was synchronized to the zeitgeber only during the first section (24 hours), while it showed the typical freerunning period of 24.8 hours during the two subsequent sections; i.e., during the latter,it was not synchronized either to the zeitgeber or to the activity-rest cycle. Of special interest is the performance rhythm (computation speed): during the first section, this rhythm was synchronized with the zeitgeber and with all other rhythms; during the second section, it was synchronized with the rhythm of deep body temperature but not with the zeitgeber or with the activity-rest cycle; and during the third section, it was synchronized with the zeitgeber and the activity-rest cycle but not with the rhythm of deep body temperature. [It is generally true that the rhythm of performance, like other behavioral rhythms, does not, under varying conditions, consistently follow either the activity rhythm or the rhythm of deep body temperature.]

The findings mentioned above are confirmed by the results of periodogram analyses (Figure 16, right). In the first section, all three time series show one period which coincides with the zeitgeber period. In the two other sections, the activity rhythm again shows only one peak, which is at the appropriate zeitgeber period; and the rectal temperature rhythm shows two significant periods in each section, with the dominant one at 24.8 hours in both sections, and a secondary peak at the appropriate zeitgeber period. The performance rhythm periodogram in the second section is very similar to that of the rectal temperature rhythm; however, during the third section, there is only one significant period which coincides with that of the zeitgeber.

The opposite case, synchronization of the rectal temperature rhythm while the activity rhythm freeruns, has been observed under the influence of a weak zeitgeber. It has been shown in many experiments that a light-dark cycle with reading lamps available, and without any 'gong' signals to the subject, is almost completely ineffective as a zeitgeber (Wever, 1970). Since, under such a weak zeitgeber, rhythms freerun as they do under constant conditions, spontaneous occurrence of internal desynchronization can be expected in at least a part of the experiment (Wever, 1978). Figure 17 shows the courses of three experiments where internal desynchronization occurred after a preliminary period of freerunning internally synchronized rhythms. After the disintegration of the rhythms, the course deviates in each case from that observed under constant conditions, since following its separation from the activity rhythm, the rhythm of deep body temperature runs in synchrony with the zeitgeber. By some additional independent arguments (including e.g., their phase relationships with the zeitgeber), it can be proved that there are not, by chance, any periods of the freerunning temperature rhythms that are very close to 24 hours (Wever, 1979a). This is particularly evident in the third example, where the temperature rhythm loses entrainment by the zeitgeber at the beginning of the last week.

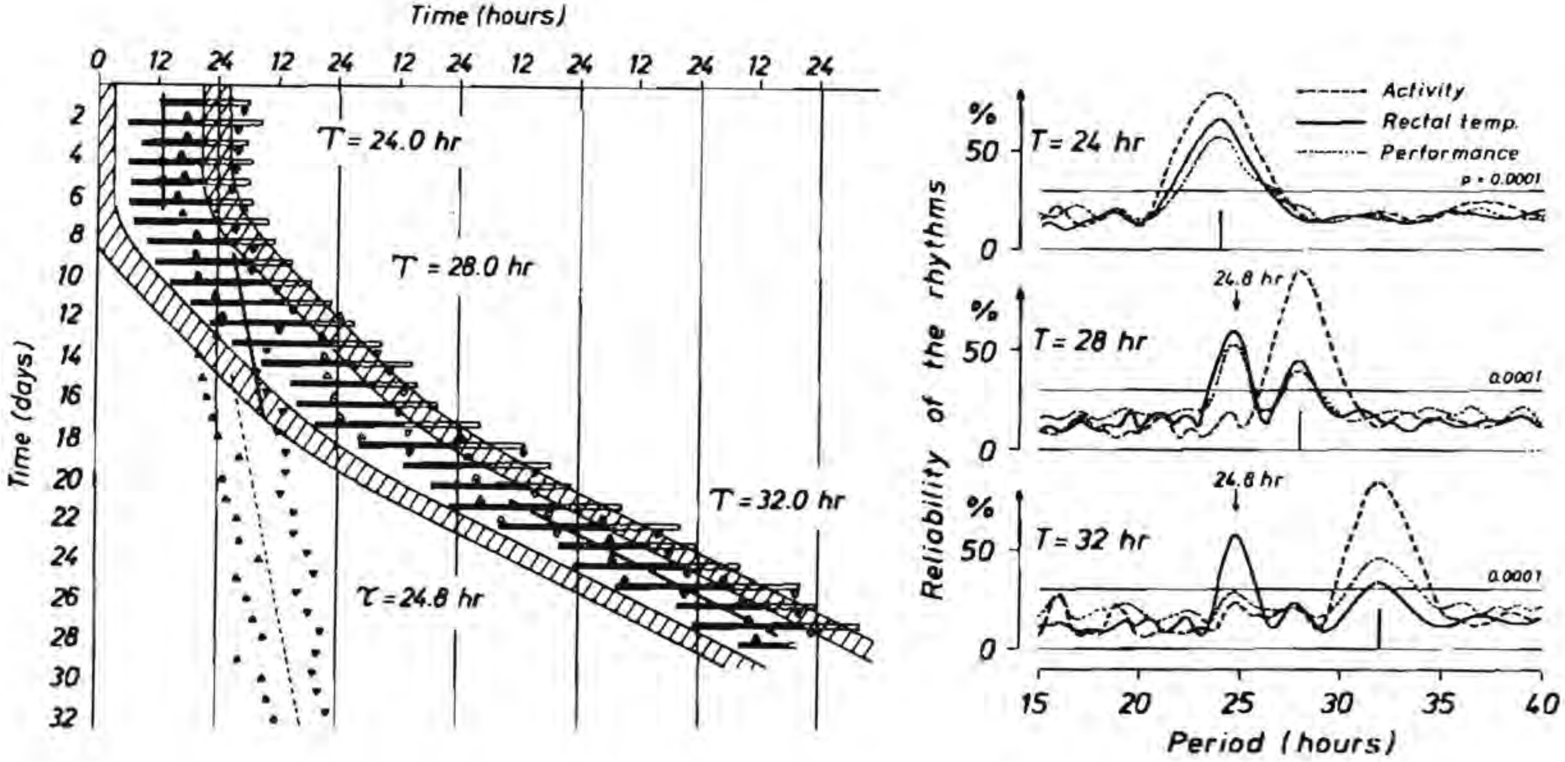

Figure 16. Circadian rhythms of a subject (I.P., ♂ 31y) living without environmental time cues but under the influence of a strong artificial zeitgeber (light-dark cycle without reading lamps available, and gong-signals at regular intervals calling the subject for urine samples and certain tests), with two alterations of the zeitgeber period. Left: rhythms of activity and rectal temperature, graphed as in Figure 1 (for meaning of white and black triangles, see Figure 9); the rhythm of computation speed (Paulitest) is indicated by the solid lines joining successive acrophases within each of the three sections; hatched areas: dark-time of the zeitgeber. Right: periodograms of the three time series, computed separately from the three sections with different zeitgeber periods.

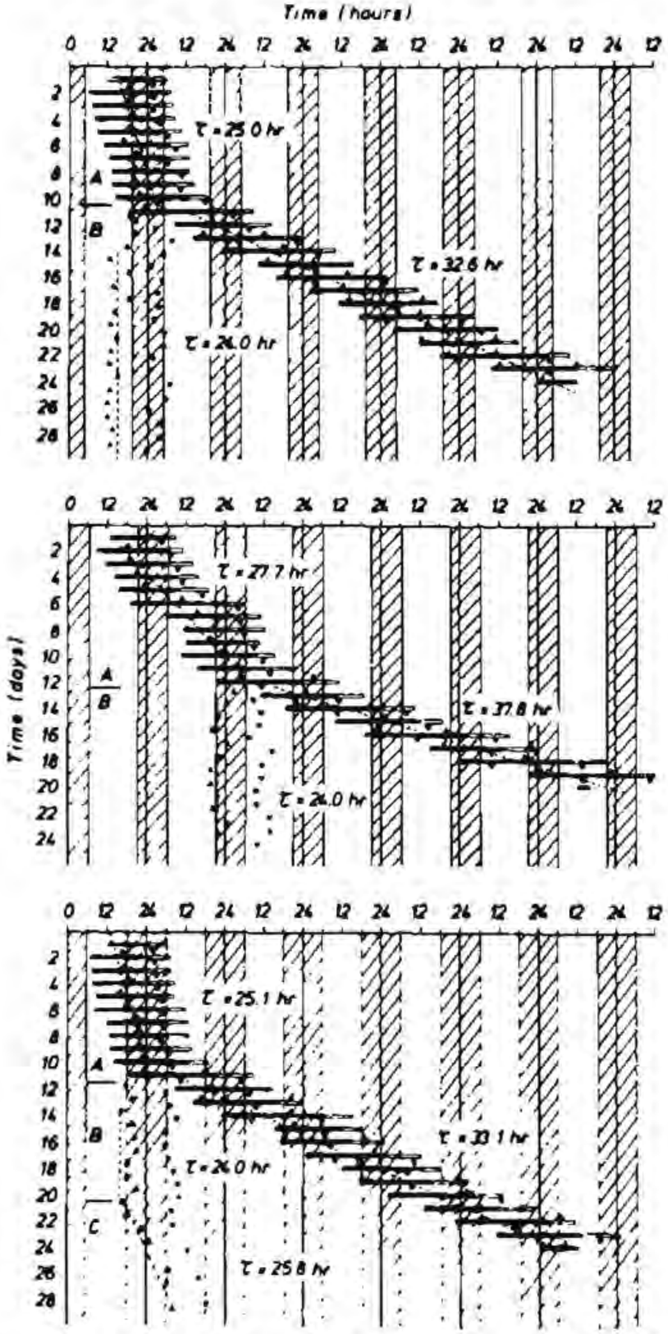

Figure 17. Circadian rhythms of three subjects (G.G., ♂ 25y; R.A., ♂ 27y; H.A., ♂ 25y) living without environmental time cues but under the influence of a weak artificial 24-hour zeitgeber (light-dark cycle with reading lamps available during dark-time); rhythms of activity and rectal temperature are graphed as in Figure 1 (for meaning of white and black triangles, see Figure 9). Hatched areas: dark-time of the zeitgeber. Sections with internally synchronized rhythms are indicated as A; sections after spontaneous occurrence of internal desynchronization as B (and C).

The synchronization found in these experiments is the more remarkable since no subject had consciously perceived the drastic lengthening of his activity-sleep cycle; at the same time, they all considered the light-dark cycle to have been very short and irregular. Nevertheless, the (consciously) imperceptible rhythm of deep body temperature was synchronized to this cycle.

It would, of course, be of particular interest to know whether, during the state of desynchronization, the performance rhythm follows the activity-sleep rhythm or the rhythm of deep body temperature. Unfortunately, the design of these experiments does not allow the measurement of performance rhythms, since in order to ensure the necessary weakness of the zeitgeber, it is not possible to awaken the subject from sleep for tests (as in other zeitgeber experiments); and rhythms cannot be evaluated meaningfully when there are consistent night-gaps in the data (Wever, 1981).

Cases of partial synchronization, as exemplified in Figure 17, have been observed only occasionally. It is only after the spontaneous occurrence of internal desynchronization in subjects who have a predisposition for rhythm disintegration in isolated conditions (Lund, 1974; Wever, 1975c) that a weak zeitgeber can "capture" the rhythm of rectal temperature, while, at the same time, the period of the activity rhythm differs too greatly from that of the zeitgeber to become synchronized (in spite of its larger range of entrainment). On the other hand, cases of partial synchronization of the type illustrated in Figure 16 can be forced in all subjects, including those who have no predisposition for spontaneous rhythm disintegration. In all experiments where the period of the strong zeitgeber is either 22 hours or less, or 28 hours or more, internal desynchronization is forced. The one exception to this occurs when the zeitgeber period is close to 48 hours; here, there is not only a 1:1 synchronization of the activity-sleep cycle, but also a 2:1 synchronization of the physiological rhythms. In most of the experiments that have been conducted with this extremely long zeitgeber period, the subjects have never been consciously aware of the great deviation of their subjective day from 24 hours (this ignorance would even appear to be a necessary condition of the success of such experiments).

The aim of the experiments with only partial external synchronization (and, hence, forced internal desynchronization) is the systematic study of the interactions between disintegrated overt rhythms, and of the effects of such rhythm disintegration on the behavior of the subjects. Preliminary results suggest that there is less need for sleep during sections of experiments with forced internal desynchronization than during sections with intact rhythms (Wever, 1979a), just as is the case with spontaneous internal desynchronization; and that the effects of rhythm disintegration on objectively measurable performance (e.g., computation speed) and on the subject's well-being (as assessed by self-rating scores; Wever, 1981) are advantageous. However, the extent to which these apparently paradoxical but significant results can be applied to practical situations is still an open question.

The capacity of different overt rhythms to become synchronized by external zeitgebers separately and independently of each other suggests the possibility that some zeitgebers are more effective than others for particular rhythms. In conclusion, therefore, two experiments will be described as examples of cases where zeitgebers with different modalities and different periods have been presented simultaneously. The first example is shown in Figure 18, which gives data from a subject who, in an experiment in which the sleep of another subject under constant conditions was being recorded polygraphically, had the job of monitoring the complex recording equipment. Consequently, he had to be awake when the subject was sleeping, and hence, his own activity rhythm was controlled by the subject's freerunning rhythm. On the other hand, he had precise knowledge of the objective time of day, and he also had sufficient contacts with the outside environment. Thus, he was exposed to two competing zeitgebers: (1) the "watchkeeping" schedule imposed by the rhythm of the monitored subject, and (2) local time. As Figure 18 demonstrated, his activity rhythm, as would be expected, deviated from 24 hours, coinciding with the freerunning rhythm of the subject; however, his rhythms of rectal temperature and of other physiological variables were clearly synchronized to local time. This twofold control by two different zeitgebers can be deduced both from the course of the rhythms (Figure 18, left) and from the periodogram analyses (Figure 18, right).

The second example (Figure 19) shows results from an experiment in which four subjects lived together in an artificial 30-hour day (without reading lamps). The strong zeitgeber collectively synchronized the activity-sleep cycles of all the subjects; none of them consciously perceived that this common cycle deviated from 24 hours. On the other hand, the zeitgeber period was too long to synchronize the physiological rhythms which, in consequence, freeran. But instead of showing the inter-individual differences in period that might have been expected due to slight differences in natural frequency, the four temperature rhythms, and also other physiological rhythms, were mutually synchronized. There are good arguments for excluding the possibility that the temperature rhythms of the different subjects had, by chance, exactly equal periods. Thus, it must be assumed that the consciously imperceptible rectal temperature rhythms acted mutually as a zeitgeber; the only feasible way in which this zeitgeber could have acted is by affecting mutual social contacts. Therefore, in this experiment also, each subject must be assumed to have been exposed (although unexpectedly) to two competing zeitgebers: (1) the deliberately introduced 30-hour day, and (2) the rectal temperature rhythm (and other physiological rhythms) of the other subjects. And again, both of these zeitgebers were effective, but with different strengths for the different overt rhythms.

Conclusions

In this brief survey of biological rhythm perspectives, the main emphasis has been on experiments performed under constant conditions, despite an awareness that such conditions are not directly relevant to real life. However, it is only under such conditions, where all time references are excluded, that the influences of social habits, and of consequent variations in motivation, are eliminated, thus ensuring that activity-sleep behavior is determined only by biological necessities. These necessities can indeed be modified by the conditions of modern industrial society, but they cannot be entirely neglected. Thus when, for practical reasons, it is necessary to establish work-rest schedules, it is obviously preferable that these be chosen to fit in, as far as possible, with the known regularities of human circadian rhyhtms.

When freerunning rhythms are internally synchronized, there are certain negative serial correlations between successive cycles and between successive

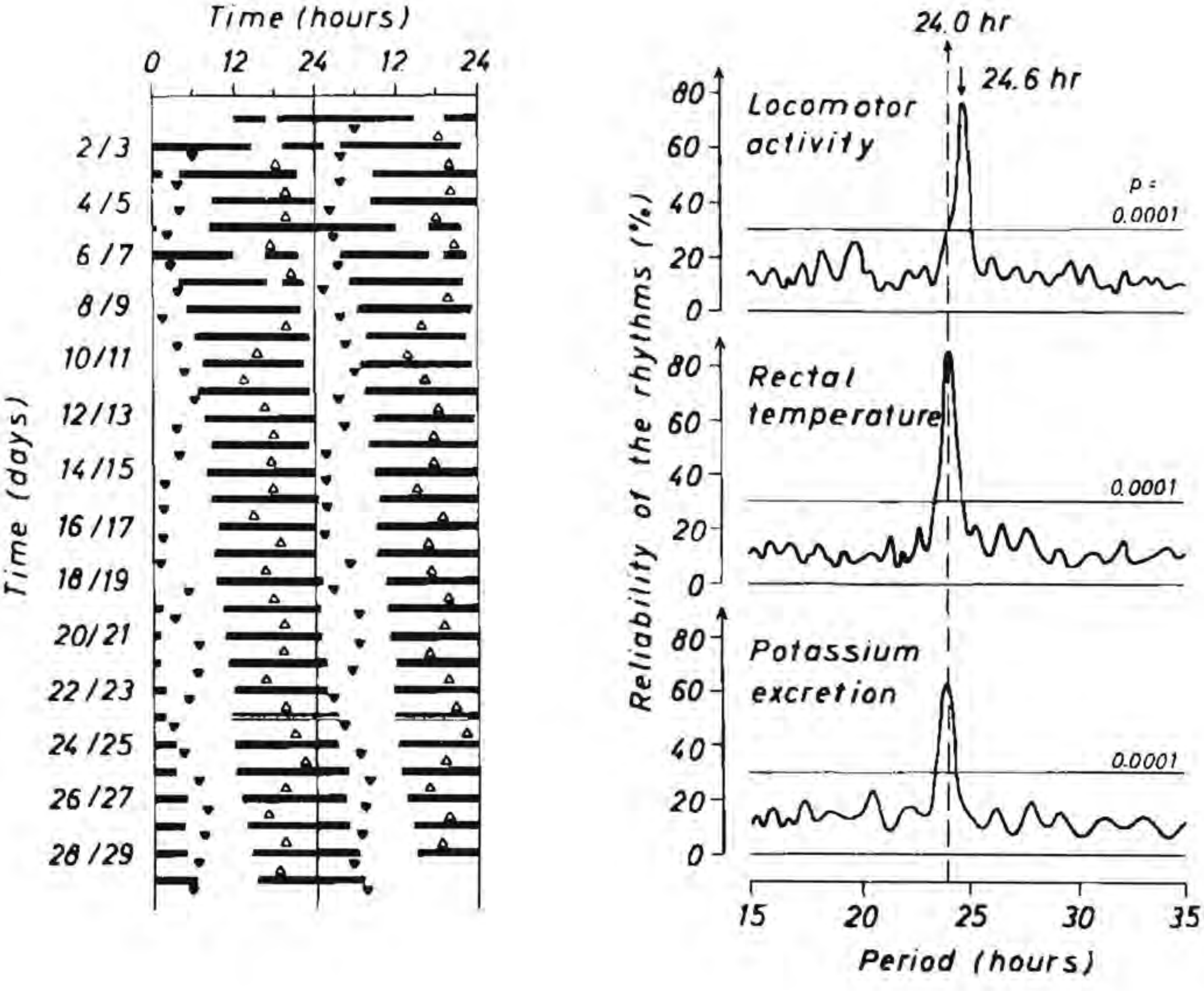

Figure 18. Circadian rhythms of a subject (J.Z., ♂ 29y) who was monitoring the equipment recording polygraphically the sleep of another subject under constant conditions. Left: states of wakefulness (bars) and extreme values of the rectal temperature rhythm (triangles), as functions of local time. Right: periodograms of the time series of activity, rectal temperature, and urinary potassium excretion.

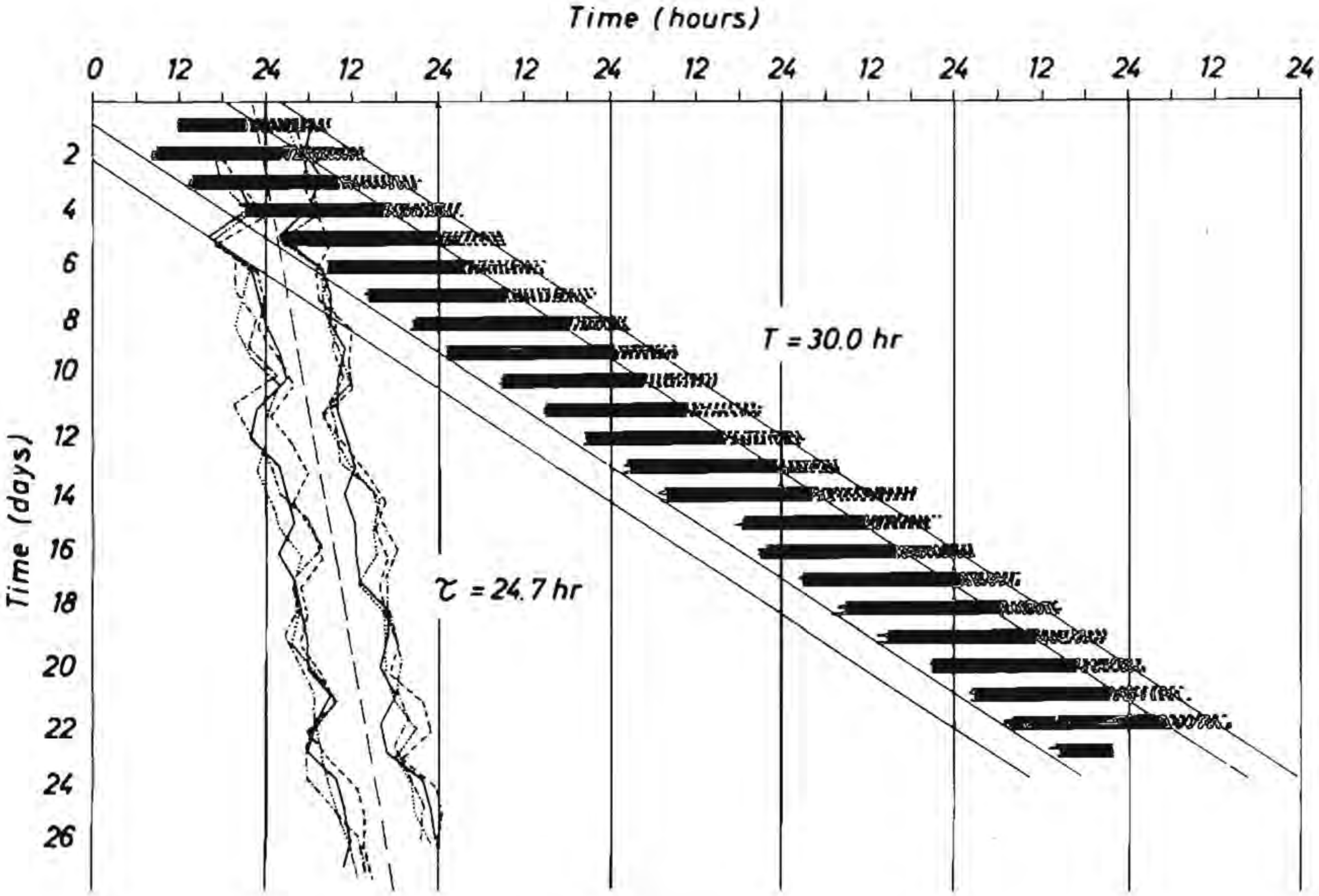

Figure 19. Circadian rhythms of a group of four subjects living together without environmental time cues but under the influence of a strong artificial 30-hour zeitgeber of the same type as in Figure 16. Activity-sleep rhythms indicated by bars (solid: activity; broken: rest). Rhythms of rectal temperature represented by lines joining the temporal positions of successive maxima (left) and minima (right); framed areas: dark-time of the zeitgeber. From Wever (1979a).

elements of each cycle. All these correlations seem to indicate that the system is attempting to achieve stabilization of the cycle at a certain period value; and the negative correlations between activity and sleep seem to demonstrate a preference for stabilization of the full cycle rather than for keeping the durations of the separate sections of activity and sleep constant. Of course, under the influence of a zeitgeber with steady properties, all these negative correlations are self-evident; here they are nothing more than reflections of synchronization. However, the presence of the same correlations under constant conditions demonstrates certain fundamental mechanisms of the circadian system, consideration of which may assist in the solution of practical problems like shiftwork.

Many different investigations show that the amplitude of the rhythm of deep body temperature is one of the most important parameters of the circadian rhythmicity. This means that the amplitude of the rhythm is an index of its degree of resistance to change by external and internal factors: the larger the amplitude, the smaller are the changes in the rhythm induced by a given external stimulus, and the smaller is the tendency towards spontaneous occurrence of internal desynchronization. But, secondly, the amplitude of the rhythm of deep body temperature is also strongly correlated with the need for sleep. This particular correlation is a good example of the mutual interaction between different overt rhythms: the influence of the sleep-wake cycle on physiological rhythms coexists with an even stronger influence of the latter (e.g., the rhythm of deep body temperature) on the former, because of the greater strength of the oscillator that predominantly controls the physiological rhythms. This interaction is directly expressed in the dependence of both the duration and the structure of sleep on the course of rectal temperature during the sleeping period.

The characteristics of the temperature rhythm amplitude mentioned have been determined under constant conditions. They are, however, also applicable to synchronized rhythms; here an advantage of the rectal temperature rhythm is that it is less dependent on socially forced habits than is the activity rhythm. Hence, the amplitude of the rhythm of deep body temperature indicates the need for sleep under natural conditions in the 24-hour day, as it does under constant conditions. Likewise, it is again an index of the degree of resistance of the rhythm to zeitgeber changes; this is expressed, for instance, in the duration of re-entrainment after a particular phase shift of the zeitgeber. The latter characteristic may be of practical interest, since it allows the suitability of a person for time shifts (Wever, 1979b) or shiftwork (Reinberg, Vieux, Ghata, Chaumont, & Laporte, 1978) to be predicted.

In the experiments in the isolation room, disintergration of the rhythmic system, whether it occurs spontaneously or is forced by manipulations of the experimental conditions, reduces the need for sleep, and produced increases in psychomotor performance and in subjective well-being (Wever, 1979a, 1981). However, advantageous effects cannot be generalized outside the laboratory situation; it must rather be assumed that they arise because of the relative lack of external stimuli in the latter. This lack does not, in fact, lead to conscious feelings of lack of well-being in the subjects; but it is assumed that when the number of stimuli to be processed is increased by the addition of the internal stimuli resulting from disintegration of the circadian system, the total input reaches a level which is optimal for inducing a favorable behavioral state.

If the foregoing argument is correct, it follows that in normal life, where the input of external stimuli is considerable, any additional stimuli from the internal system would lead to stress. This conclusion is based on the assumption that the rhythm disintegration which occurs in situation like shiftwork, is, as a stimulus, equivalent to a stimulus emanating from an external source. This hypothesis, the application of which might help to make unavoidable rhythm disorders more tolerable, requires further confirmation; but the results discussed here at least prove that rhythm disintegration need not necessarily lead to loss of well-being.

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