Interdependence between locomotor activity and duration of wakefulness in humans during isolation

J. Aschoff

Max-Planck-Institut für Verhaltensphysiologie, D-8138 Andechs (Federal Republic of Germany)
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Summary. Locomotor activity was recorded in 14 subjects who lived singly in an isolation unit for 16 to 88 days. Their free-running circadian rhythms had a mean period of 25.9 h, with individual means in the duration of wakefulness (α) ranging from 12.1 to 22.9 h. Intraindividually, the hourly means of activity were negatively correlated with α to such a degree that the total amount of activity per 'day' remained constant irrespective of large variations in α.
Key words. Circadian rhythms; activity; wakefulness; humans; homeostatic control; isolation.

Human subjects who live in isolation without temporal cues continue to have a regular sleep-wake cycle, but lose synchrony with the 24-h day. The period of the 'free-running' circadian rhythm is often close to 25 h[1]. Sometimes, however, the sleep-wake cycle is lengthened to more than 28 h, or shortened to less than 20 h. In those instances, the rhythms of other functions such as body temperature become uncoupled from the sleep-wake cycle and continue to free-run with a period of about 25 h[2]. During such a state of 'internal desynchronization' subjects may be awake for up to 30 h (long desynchronization), or for only 10 h (short desynchronization) without noticing it[3]. In spite of these drastic changes, the subjects adhere to their usual number of (mostly 3) meals; the intervals between meals are stretched or compressed proportionally to the duration of wakefulness[4]. The caloric intake per meal remains more or less constant[5], and the subjects neither gain weight during short, nor lose weight during long desynchronization[6,7]. From these observations it must be concluded that the subjects somehow adjust their energy expenditure to the duration of wakefulness. This report demonstrates that the mean hourly activity is negatively correlated with the duration of wakefulness. As a consequence, the total amount of activity remains almost the same on short and long 'days'.

Data were collected from 14 subjects (4 females, 10 males) who lived singly in an underground isolation unit for an average time span of 32 days (range 16 to 88 days). The subjects could prepare their meals in the kitchenette, and were allowed to turn the lights in the room on and off at will. As a measure for the duration of wakefulness the interval between two signals was taken that were given by the subjects immediately after waking up and at the time of turning off their bedside reading lamp. The room had a base of 15 m^2, with about 10 m^2 free walking space. Across this space, 18 plates (0.25×0.25 m^2) were installed below the carpet at an average distance of 0.48 m. Steps on the plates triggered electric contacts which were recorded continuously outside the isolation room. For further analysis, the contacts were summed in hourly bins.

The results of a typical experiment are summarized in figure 1. They come from a male subject (No. 118) who was in the unit for 32 days. He was temporarily desynchronized and went through 35 cycles with a mean period of 22.5 h. Due to technical failures, only 32 cycles could be analyzed. The two diagrams in figure 1A illustrate the pattern of activity on two non-consecutive 'days'. On one of these 'days', wakefulness lasted 12.1 h (left), on the other one 20.9 h (right); the means of hourly activity (dashed horizontal lines) were 104.1 and 59.8, respectively. (High initial values of activity could occur on short as on long 'days'; their distribution did not affect the out-

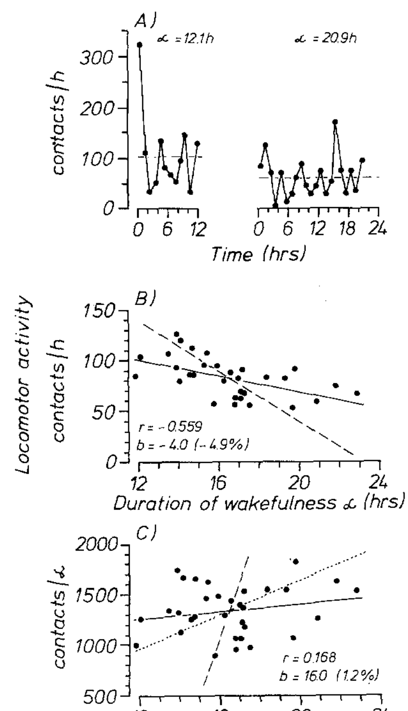

Figure 1. Locomotor activity of a male subject in the isolation unit. *A* Patterns of activity on a short (left) and on a long 'day' (right). α = duration of wakefulness. Dashed horizontal lines: mean activity per α. *B* Mean hourly activity drawn as a function of the duration of wakefulness. r = coefficient of correlation. b = slope of the solid regression line representing the dependence of activity on α (in brackets expressed in percent of the overall mean of activity). *C* Amount of 'daily' activity, drawn as a function of the duration of wakefulness. Regression lines, r and b as in *B*. Short-dashed line: amount of activity to be expected when the mean hourly activity remains constant.

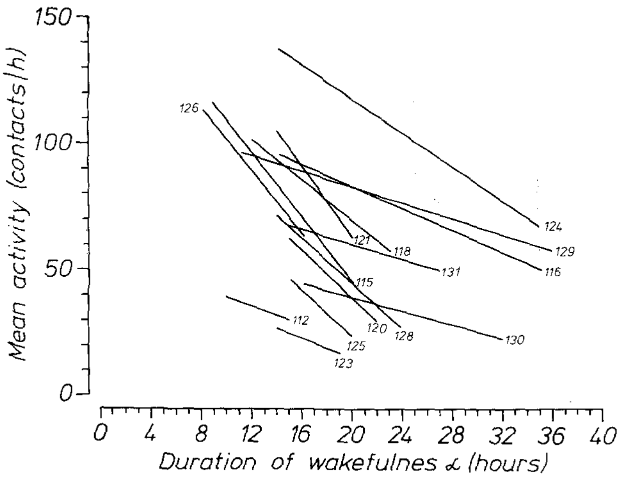

Figure 2. Mean hourly activity per α drawn as a function of the duration of α. Regression lines for the dependence of activity of α are computed from the data of 14 subjects (numbers at lines).

come of the analysis in a systematic manner as shown below.) Figure 1B shows the dependence of the mean hourly activity on the duration of wakefulness (α) for all 32 cycles. The slope (b) of the solid regression line (indicating the dependence of activity on α) has a value of -4.0 contacts/h^2 which, in relative units, amounts to -4.9 % of the overall mean of hourly activity per h increase in α. Due to this negative correlation with α, the total amount of activity per 'day' remained virtually constant over a range of α-values from 12 to 22 h. As shown in part C of figure 1, the 'daily' amount of activity increased (non-significantly) by only 1.2 % when α was lengthened by 1 h.

All 14 subjects developed free-running rhythms which for some time underwent either short or long desynchronization. The individual means of α ranged from 12.1 to 22.9 h. In all subjects, the hourly means of activity were negatively correlated with the duration of α (fig. 2). The coefficients of correlation ranged from -0.239 to -0.559. The mean of the slopes b of the regression lines was -3.5 contacts/h^2, corresponding to -5.4 % of the mean hourly activity (range -2.5 % to -12.5 %).

The regression lines plotted in figure 2 are based on all hourly values within each α. If one uses only the activity data of the first 3 h per 'day', one gets almost the same regression lines as shown in figure 2, with a mean slope b of -3.7 contacts/h^2. This means that the organism 'knows' already at the time of waking up for how long α will last on that particular 'day'. This result agrees with two other findings published elsewhere; the interval between waking-up time and breakfast, and the first few estimates of 1-h intervals made every 'day', were found to be positively correlated with α[3,4].

The correlation between α and the total amount of activity (part C of figure 1) was slightly positive in 10 subjects (r-values ranging from 0.026 to 0.641), and negative in four subjects (r-values from -0.030 to -0.316); the mean coefficient of correlation, computed by z-transformation, was 0.121. The mean of the slopes (b) of all regression lines corresponded to 0.2 % of the overall mean of activity. In other words; when α was lengthened from 10 to 20 h, the daily amount of activity increased on the average only by 2 %. Hence a doubling of the time a subject stays awake is compensated by a decrease in mean locomotor activity. However, under the living conditions provided in the isolation unit, only about 36 % of the total energy expenditure can be attributed to muscular work (and heat increment by feeding), whereas 64 % represent basal metabolic rate[8]. Therefore, in spite of the decrease in activity, an increase in energy demands should be expected on long 'days'. As subjects apparently remained in energy balance without altering their food habits, this raises the question of whether basal metabolic rate is also related to α. The answer will require measurements of basal metabolic rate in subjects whose circadian rhythms are free-running. In any event, the present results demonstrate that the amount of spontaneous locomotor activity per circadian sleep-wake cycle is homeostatically conserved even for large variations in the period of this cycle.

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