

The Human Circadian Clock's Seasonal Adjustment Is Disrupted by Daylight Saving Time

Thomas Kantermann,¹ Myriam Juda,¹ Martha Merrow,² and Till Roenneberg^{1,*}

¹Ludwig-Maximilian-University
Goethestrasse 31
D-80336 Munich
Germany

²Department of Chronobiology
University of Groningen
9750AA Haren
The Netherlands

Summary

A quarter of the world's population is subjected to a 1 hr time change twice a year (daylight saving time, DST). This reflects a change in social clocks, not environmental ones (e.g., dawn). The impact of DST is poorly understood. **Circadian clocks use daylight to synchronize (entrain) to the organism's environment. Entrainment is so exact that humans adjust to the east-west progression of dawn within a given time zone [1].** In a large survey (n = 55,000), we show that **the timing of sleep on free days follows the seasonal progression of dawn under standard time, but not under DST.** In a second study, we analyzed the timing of sleep and activity for 8 weeks around each DST transition in 50 subjects who were chronotyped (analyzed for their individual phase of entrainment [2]). **Both parameters readily adjust to the release from DST in autumn but the timing of activity does not adjust to the DST imposition in spring, especially in late chronotypes.** Our data indicate that **the human circadian system does not adjust to DST and that its seasonal adaptation to the changing photoperiods is disrupted by the introduction of summer time.** This disruption may extend to other aspects of seasonal biology in humans.

Results and Discussion

Despite the fact that ~1.6 billion people experience DST, few studies have investigated the impact of DST transitions on physiology and behavior. One found no effect on psychiatric disorders [3]. Others studied the effect on traffic accidents with inconsistent results [4–7]. Behavioral studies accompanying subjects across DST transitions are rare. The first study (65 subjects; 6 days prior to and 11 days after the autumn change) showed full adjustment of wake-up times after 5 days [8]. The second study recorded sleep EEGs and concluded that sleep architecture adjusts within several days to the spring DST transition [9]. The largest study (101 subjects) found instantaneous adjustment of bedtimes after both transitions, while wake-up times took about 1 week [10]. The longest study, so far (4 weeks around the

spring change), found interindividual differences in adjustment (ranging from 1–2 days up to 2 weeks) [11] but no effects for the autumn change [12]. The first study [13, 14] considering different time-of-day preferences in their subjects (by the morningness-eveningness scale [15]) found a reduction in sleep duration by ~1 hr after the spring transition for morning and evening types. Whereas activity times adjusted immediately, sleep times took a week.

Studying the effects of DST transitions essentially investigates the potential re-entrainment of individuals to a new social schedule and should, therefore, consider chronotype (an individual's phase of entrainment), which differs substantially within a given population [2]. Depending on genotype [16], gender, age [17], and light exposure, our clocks will adopt a different phase relationship to dawn. We have developed a simple tool, the Munich ChronoType Questionnaire (MCTQ; see [Experimental Procedures](#) and [Supplemental Data](#) available online) to assess chronotype in a highly quantitative manner.

Assessment of how the human clock adjusts to DST transitions at nonequatorial latitudes is confounded by the fact that the times of dawn and dusk also change. Dawn times (see gray area in [Figure 1](#)) change rapidly around the spring DST transition (which often occurs close to the March equinox) and change to a lesser extent around the autumn transition (which often occurs more than a month after the September equinox). Given that daylight (including the low light levels at dawn) is the predominant zeitgeber for our circadian system [1, 19, 20], it is unlikely that it readily adjusts to the abrupt and purely social DST transitions.

We investigated the adaptation of the human circadian clock to both season and DST with two approaches. First, we mined the MCTQ database (containing ~55,000 subjects from Central Europe, including the date of entry) for seasonal changes in sleep timing at the population level. Second, we conducted a longitudinal study to describe the adaptation to DST transitions at the individual level (50 subjects investigated for 4 weeks before and 4 weeks after both the autumn and the spring transition in 2006 and 2007, respectively).

Mining the MCTQ database shows that midsleep on free days, MSF correlates with dawn under standard time, whereas it is scattered around 3:30 under DST ([Figure 1A](#)). Notably, the onset of DST elicits no significant change in sleep timing, whereas a large delay follows the offset of DST. Self-reported sleep duration changed significantly across seasons (by ~20 min; [Figure 1B](#)).

To understand the dynamics of how individuals respond to DST transitions, we evaluated both the phase of sleep (as midsleep, calculated from sleep logs) and the phase of activity (as center of activity, CoAct, calculated from wrist actimetry; see [Experimental Procedures](#)). [Figure 2](#) shows how an individual's activity profile reflects early or late chronotype. The individual

*Correspondence: roenneberg@lmu.de

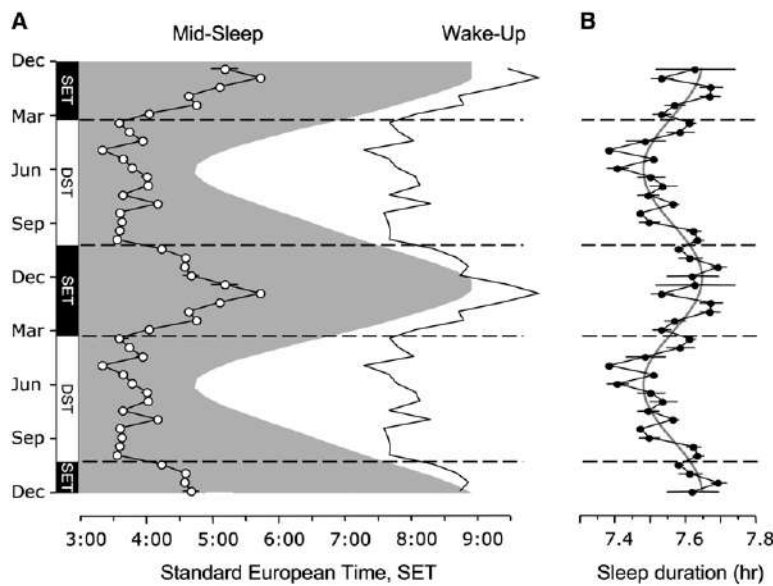


Figure 1. Seasonality in Sleep Timing Taken from the MCTQ Database

Annual time courses are double plotted (the same data are shown sequentially to more easily visualize systematic trends) ($n \approx 55,000$). (A) Half-monthly averages of midsleep times on free days [1], MSF (open circles \pm SEM), and of wake-up times (line). DST periods are indicated by the open boxes and their transitions by dashed horizontal lines; dawn times are shown as a gray to white border. Whereas sleep times track down under standard time, midsleep is scattered around 3:30 (wake-up times around 7:40) under DST. Age and sex ratio were not significantly different in the 24 averages and showed no interactions. (B) Seasonal changes in sleep duration (filled circles; averaged over both free and work days \pm SEM) result in about 20 min more sleep in winter than in summer (cosine fit: $r = 0.75$; $p < 0.0001$).

weekly phase deviations from baseline are averaged for both markers (separately for free and work days) either for the entire cohort (Figure 3A) or for the different chronotype groups (Figure 3B; see legend for statistical analysis). The timing of midsleep and CoAct for all subjects on free days fully adjusted to the release from DST in autumn within 1 week (top left in Figure 3A). On workdays, this acute response of CoAct was less pronounced, followed by a gradual change over the four post-transition weeks (top right in Figure 3A). Whereas both midsleep and CoAct on workdays showed a constant (social) phase before the release from DST, they paralleled dawn thereafter, similar to the results shown in Figure 1A.

The spring transition was anticipated by midsleep on free days (hence, a reduced acute post-transition phase

jump; Figure 3A). This was even more pronounced for the timing of activity (CoAct gradually advanced for 5 consecutive weeks) and indicates that the human clock tracks dawn as photoperiod increases. However, 2 weeks into DST, CoAct delayed again and settled at an advance of less than 30 min (final relative phase; see Experimental Procedures). Both midsleep and CoAct on workdays tracked the social clock before the spring change as they did in autumn. Whereas midsleep fully adjusted on workdays (60% of the subjects indicated using an alarm clock on workdays), the incomplete advance of CoAct on free days was similar for workdays.

Different chronotypes respond differently to time changes. Most people (except for extreme early chronotypes) adjust more readily to delays than to advances, i.e., they suffer less from jet lag after westward than after

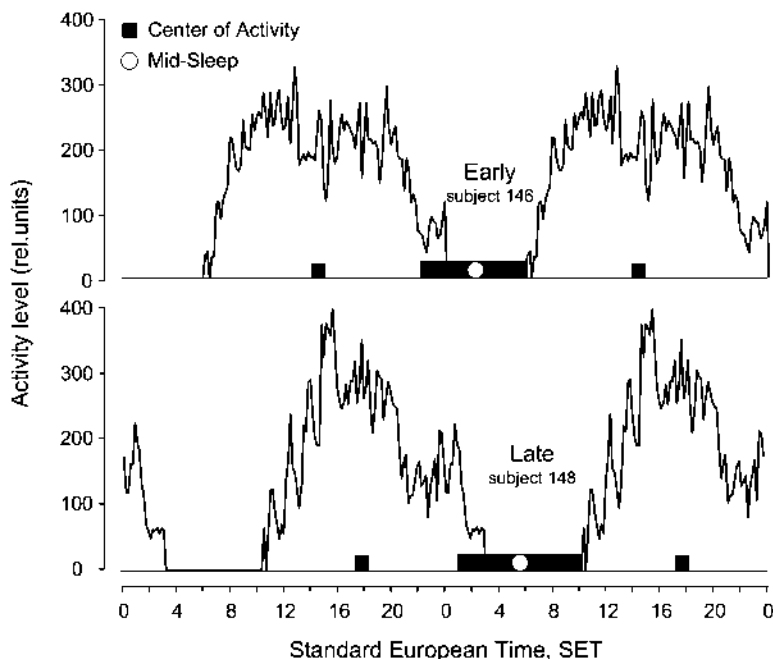


Figure 2. Comparison of Sleep Times and Activity Profiles between Different Chronotypes

Sleep times (black bars) and activity (black lines)—recorded during the two longitudinal studies around the autumn and the spring DST transition—averaged for the free days within the 4 weeks before the autumn change in an early (top) and a late (bottom) chronotype. Sleep onset and offset times are taken from the sleep logs; activity levels were measured by wrist actimetry. The phase of mid-sleep is indicated by an open circle within the sleep bar and the phase of the center of activity (CoAct, see Experimental Procedures) as a black square. Chronotype correlated highly with the CoAct at baseline (see Experimental Procedures; $r = 0.56$, $p < 0.0001$). Sleep log entries also correlated with the sleep times extracted from the activity records similarly for both transitions (for the autumn: $\text{sleep-onset}_{\text{before}}$: $r = 0.38$, $p < 0.001$; $\text{sleep-end}_{\text{before}}$: $r = 0.7$, $p < 0.001$; $\text{sleep-onset}_{\text{after}}$: $r = 0.22$, $p < 0.005$; $\text{sleep-end}_{\text{after}}$: $r = 0.55$, $p < 0.001$).

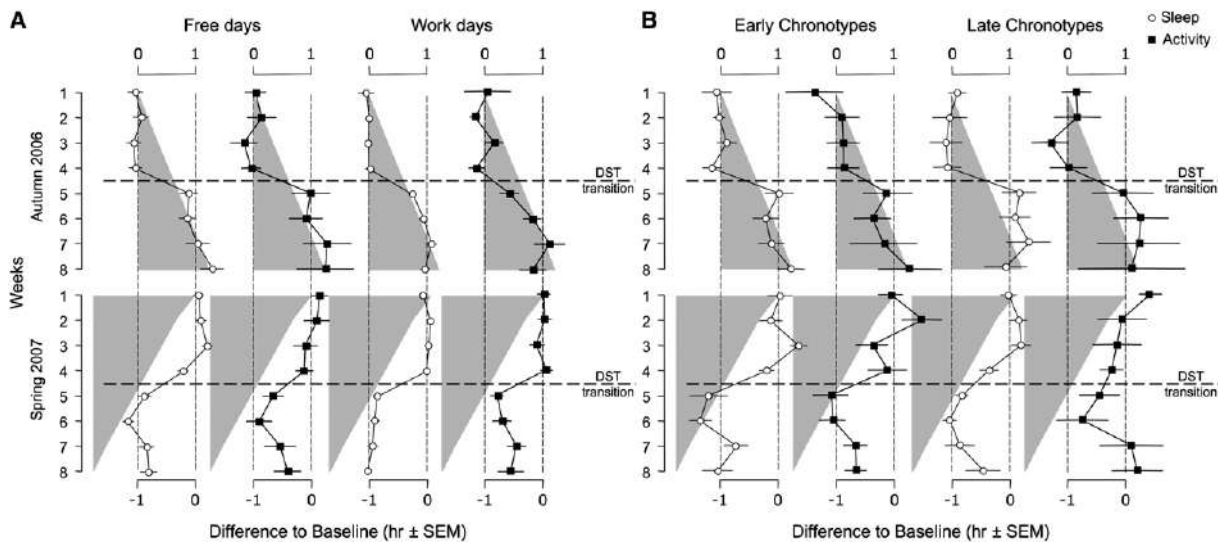


Figure 3. Adjustments to DST Transitions of Sleep and Activity Times Resulting from the Longitudinal Study

(A) Phase adjustments of midsleep (circles) and activity (CoAct, black squares) around the DST transitions expressed as weekly averages relative to each individual's baseline (average phase during the four pretransition weeks, see *Experimental Procedures*). Results are shown for the entire cohort both on free (left) and on work (right) days. The autumn transition is shown in the top panels; the spring transition is in the bottom panels. Horizontal bars connected to the respective symbols represent SEM, which were in most cases smaller than the size of the symbols. $n = 50$. (B) The comparison between early (left) and late (right) chronotypes is shown for free days only (otherwise as in [A]). For the changes of midsleep on free days in autumn, a mixed ANOVA (within-subject design with chronotype [early, intermediate, and late] as a between-subject factor) shows a significant difference between all weeks ($F(4.33;117) = 10.00, p < 0.001$). For both transitions, post-hoc tests show that neither the 4 pre- nor the 4 post-transition weeks differ among each other, whereas they differ significantly across the transitions. In autumn, the CoAct times show no difference between the 8 weeks ($F(3.5; 94) = 1.89, p = .13$). The changes for CoAct of early chronotypes correlates better with dawn than with social time ($r: 0.938$ versus 0.896). In spring, the phase changes of both midsleep and CoAct differ significantly before versus after the transition (mixed-design ANOVA; midsleep: $F(4.57; 128) = 20.26, p \leq .001$; CoAct: $F(4.84;170) = 4.36, p \leq .001$), whereas they are statistically indifferent among the pre- and post-transition weeks. The changes for CoAct of late types between week 1 and 6 correlate better with dawn than with social time ($r: 0.974$ versus 0.774). Whereas post-hoc tests show that the final phases reached in the last two weeks show no significant difference relative to any of the 4 weeks prior to transition for both chronotypes, they differ significantly between early and late types ($t(49) = 2.13, p \leq 0.05$).

eastward flights [21]. A similar pattern is suggested for DST transitions [13, 14]. Our results show that adjustment to DST transitions is chronotype specific (Figure 3B). We present results only for early and late chronotypes here ("larks" and "owls;" those for intermediate chronotypes lie predictably in between the two extremes) and concentrate on the less socially influenced free days. Midsleep in both larks and owls showed a large phase jump in response to the autumn delay (compare with Figure 1A); the response of the CoAct suggests that owls delay more readily than larks (at a level below significance). The chronotype-specific differences are more marked after the spring change. Again, both midsleep and CoAct moved with dawn before the transition to DST (compare with Figure 1A), most prominently in the late chronotypes who gradually advanced their CoAct for five consecutive weeks (compare with Figure 3A). Midsleep of larks readily adjusted while an apparent full adjustment in owls was transient. Whereas larks advanced their CoAct by only 40 min, owls failed to adjust their CoAct to the advance of the social clock.

The similarity between the longitudinal study (50 individuals followed across the DST transitions) and those found in the database is remarkable (compare Figures 3A and 3B with Figure 1A). In both cases, the human circadian clock tracks dawn under standard time but not under DST. Whereas the human clock (as measured by

the CoAct) predictably advances from autumn to spring (15:54 SET, averaged between Nov 19 and Dec 3, compared to 15:14 SET, averaged between Mar 24 and Apr 21), it remains locked to the same time between spring and autumn (14:36 SET for both, averaged between Apr 15-29 and Oct 3-28, respectively). These results, in combination with those from the database, suggest that the incomplete adjustment of activity in larks and the nonadjustment in owls continues beyond the four recorded post-transition weeks and throughout the months of DST. Our results also suggest that the circadian clock does not adjust to the DST transition in spring—especially in late types. Notably, the strongest reduction of average sleep duration (for 8 consecutive weeks; Figure 1B) follows the spring transition.

What could trigger the severe effect of DST on seasonal adaptation of the human clock? It is unlikely that midsleep tracks dawn throughout the summer, especially at higher latitudes. It is, however, equally unlikely that the abrupt cessation of dawn tracking, shown here, reflects a threshold beyond which the clock cannot advance (corresponding to a wake-up time around 7:30 SET, 8:30 DST). We have previously shown that the human clock is predominantly entrained to the natural light-dark cycle ($zeitgeber_N$) and that social time affects this entrainment [1]. Behaviorally induced light-dark cycles (e.g., by sleeping in a dark room with our eyes closed; $zeitgeber_B$) may compete with $zeitgeber_N$,

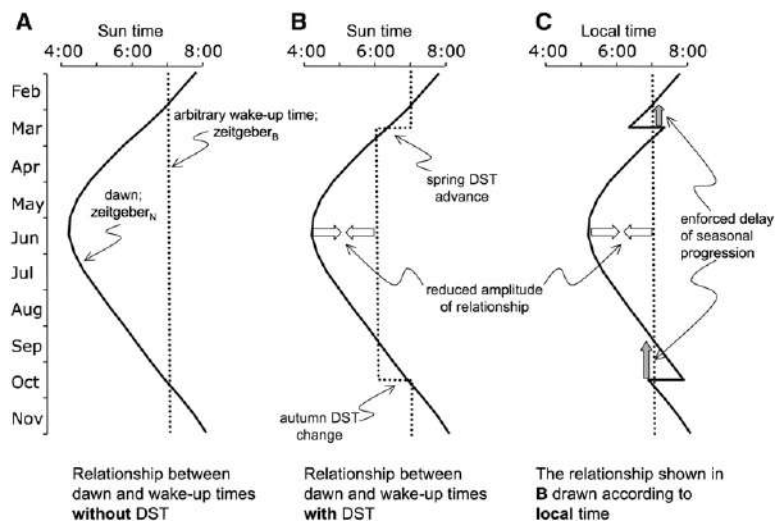


Figure 4. Relationship between Natural and Behavioral Light-Dark Cycles with and without DST

The relationship between the natural light-dark cycle (dawn, zeitgeber_N; solid curve) and the behavioral light-dark cycle (created by the use of artificial light and sleeping in dark rooms with closed eyes, zeitgeber_B, exemplified by an arbitrary wake-up time at 7 a.m.; dotted line) changes systematically with season (A). DST affects only zeitgeber_B by advancing the social clock by 1 hr in spring and delaying it in autumn (B). The 1 hr advance corresponds to traveling 15° westward within the same time zone. DST transitions have large effects on the seasonal relationship between the two zeitgebers. This phenomenon becomes more apparent if natural dawn is drawn with respect to local time (consistent with social wake-up times) (C). The seasonal progression of the phase relationship between the two zeitgebers is delayed

by 4 weeks in the spring and by 6 weeks in the autumn (vertical gray arrows). Hence, we repeat almost 20% of the seasonal progression of the two zeitgebers every year. In addition, DST artificially changes the amplitude of the phase relationship in summer (horizontal white arrows in [B] and [C]), which mimics a translocation of 17° latitude. The diagrams are drawn for the dawn times in Frankfurt/Main (50° 7' N/8° 41' E), which roughly corresponds to the average coordinates of the 50 subjects' places of residence. In this case, the longitudinal and latitudinal translocations would mean moving from Frankfurt to Morocco in spring and back in autumn. The amplitude of the relationships as well as the degree of their perturbations by DST increase with latitude.

especially in large cities where people efficiently shield themselves from environmental signals. We show here that zeitgeber_B (sleep time, represented by midsleep) adjusts to DST, and therefore the “small” 1 hr time change induced by DST may have a much larger effect on our biological timing system (Figure 4). The seasonal progression in phase relationship between the two zeitgebers is pushed back by the equivalent of 4 and 6 weeks in spring and autumn, respectively. The large autumn setback is reflected in the sudden, strong delay (Figures 1A, 3A, and 3B). Assuming that the clock tracks dawn similarly in spring and autumn, the current transition from DST to standard time in late October is scheduled 1 month too late. In addition, DST reduces the seasonal amplitude of the relationship between the two zeitgebers (Figures 4B and 4C). DST-induced changes are theoretically equivalent to geographical translocations. The amplitude of the relationships as well as the degree of their perturbations by DST increase with latitude (notably, all equatorial countries either never introduced or abandoned DST). The examples shown in Figure 4 are based on the location of Frankfurt. The 1 hr DST advance in spring corresponds to traveling 15° westward and the reduction of amplitude corresponds to traveling 17° latitude southward. Thus, DST translocates the inhabitants of Central Germany to Morocco in spring and back in autumn, without changing time zone or climate.

In some animals, the circadian clock adopts a fixed phase in long photoperiods under laboratory conditions while they track dawn in short photoperiods [22, 23]. The interruption of seasonal adjustment in summer shown here, however, exactly coincides with the DST transitions and, therefore, suggests an additional effect of DST rather than a purely natural phenomenon. This would mean that DST severely affects our seasonal timing. Like other animals, humans are seasonal [24, 25]

(in birth rates, mortality, suicide rates, etc.). However, seasonality in humans has drastically declined in industrialized countries over the last 60 years [26]. The main reason for this is probably increased shielding from natural zeitgebers, but DST might constitute an additional factor for the dissociation of human biology from the seasons.

Experimental Procedures

Subjects, Study Design, and Instruments

The study included the autumn DST transition (night of Oct 28/29, 2006; study period, Oct 3–Dec 3) and the spring DST transition (night of Mar 24/25, 2007; study period, Feb 19–Apr 29). Volunteers (autumn: n = 51, 34 F/29 M; spring: n = 49, 32 F/17 M; age: 18–59 yr, mean 34.5 yr) were recruited by word of mouth from Germany, Italy, Switzerland, France, Slovakia, The Netherlands, and Luxembourg. 43 subjects participated in both transitions and 6 new subjects were recruited for the spring study. Prerequisites were informed consent, regular daytime employment, no diagnosed psychiatric diseases or sleep disorders, and no traveling during the study periods. Delivery of questionnaires, logs, and actimeters were scheduled 1 week prior to the actual start of each study period, so that all participants were able to complete the full 8 weeks in autumn and spring. As a reward, subjects participated in a lottery, whereby any subject could win 250 EUR in each study period.

At the onset, participants completed an abbreviated version of the Munich ChronoType Questionnaire [2] (MCTQ; see Supplemental Data), which we developed to assess chronotype in a highly quantitative manner. The questionnaire contains questions about sleep times on both work and free days. Chronotype is then expressed as the time of midsleep on free days (MSF) because free-day schedules are less confounded by social obligations such as regimented work. The MSF is corrected for sleep debt accumulated over the work week (MSF_{sc}). MSF_{sc} is a reliable marker for chronotype and correlates significantly with the daily rhythms of activity and physiology (e.g., melatonin, cortisol, or body temperature, recorded in constant routines) [18].

Every morning, directly after awakening, the following items were estimated and entered into the supplied sleep logs (see Supplemental Data): time spent outside during the prior day, bedtime, time of

preparing for sleep, sleep latency, subjective alertness at bedtime (0 to 10), time of wake up, time of getting up, use of an alarm clock, subjective sleep quality (0 to 10), subjective alertness at wake up (0 to 10), and whether it was the morning of a work or a free day. Time spent outside did not significantly contribute to DST adjustment, possibly because no significant differences were found in time spent outside among the subjects. All subjects continually wore waterproof actimeters (DaqtoMeter by Daqtix GbR, Oetzen Germany) around their wrists, storing movement accelerations every minute. Subjects kept a protocol indicating when not wearing the actimeter.

Data Analysis

Sleep and activity data were analyzed separately for work and free days (in many subjects, free days were not restricted to weekends, and some subjects also worked on Saturday or Sunday). Data were also analyzed separately for three chronotype groups based on mid-sleep on free days corrected for sleep debt (MSF_{sc}) as determined by the MCTQ (early: $MSF_{sc} < 3.5$, $N_{autumn}/N_{spring} = 11/12$; intermediate: $n = 20/16$; late: $MSF_{sc} > 4.5$, $n = 19/15$) [1]. As a single reference point for sleep, daily mid-sleep times were calculated from the sleep logs and were averaged for each week. Activity data, from wake up to sleep onset (as determined by the activity profiles), were consolidated to 10 min bins and also averaged for each week (the Sunday after the actual time change was excluded). For the determination of the activity's phase, we chose the center of gravity method [27] (CoAct), which is independent of the individual shape of the activity profile (see gray areas and squares in Figure 2). For further analysis, the weekly phases of both mid-sleep and CoAct for each subject were expressed as deviation from their average over the 4 weeks preceding each of the transitions (baseline). An additional average was calculated for weeks 7 and 8 in each study period (final relative phase). Figure 3A shows the averaged deviations from baseline of the entire cohort, and Figure 3B shows those for the three groups of chronotypes.

Supplemental Data

Two figures are available at <http://www.current-biology.com/cgi/content/full/17/22/1996/DC1/>.

Acknowledgments

We are indebted to the subject volunteers. We thank H. Distel for helpful discussions, S. Troppmann for office management, and C. Weigert and G. Hoffmann for data input. This work is supported by the research networks EULOCK (the European Commission) and CLOCKWORK (the Daimler-Benz-Stiftung).

Received: September 17, 2007

Revised: October 7, 2007

Accepted: October 9, 2007

Published online: October 24, 2007

References

1. Roenneberg, T., Kumar, C.J., and Mellow, M. (2007). The human circadian clock entrains to sun time. *Curr. Biol.* **17**, R44–R45.
2. Roenneberg, T., Wirz-Justice, A., and Mellow, M. (2003). Life between clocks—daily temporal patterns of human chronotypes. *J. Biol. Rhythms* **18**, 80–90.
3. Shapiro, C.M., Blake, F., Fossey, E., and Adams, B. (1990). Daylight saving time in psychiatric illness. *J. Affect. Disord.* **19**, 177–181.
4. Varughese, J., and Allen, R.P. (2001). Fatal accidents following changes in daylight savings time: the American experience. *Sleep Med.* **2**, 31–36.
5. Ferguson, S.A., Preusser, D.F., Lund, A.K., Zador, P.L., and Ulmer, R.G. (1995). Daylight saving time and motor vehicle crashes: the reduction in pedestrian and vehicle occupant fatalities. *Am. J. Public Health* **85**, 92–95.
6. Lambe, M., and Cummings, P. (2000). The shift to and from daylight savings time and motor vehicle crashes. *Accid. Anal. Prev.* **32**, 609–611.
7. Pfaff, G., and Weber, E. (1982). More accidents due to daylight savings time? A comparative study on the distribution of accidents at different times of day prior to and following the introduction of Central European Summer Time (CEST) (author transl.). *Int. Arch. Occup. Environ. Health* **49**, 315–323.
8. Monk, T.H., and Folkard, S. (1976). Adjusting to the changes to and from Daylight Saving Time. *Nature* **261**, 688–689.
9. Nicholson, A.N., and Stone, B.M. (1978). Adaptation of sleep to British Summer Time. *J. Physiol.* **275**, 22P–23P.
10. Monk, T.H., and Aplin, L.C. (1980). Spring and autumn daylight saving time changes: studies of adjustment in sleep timings, mood, and efficiency. *Ergonomics* **23**, 167–178.
11. Valdez, P., Ramírez, C., and Nevárez, C. (1991). Efectos psicofisiológicos del horario de verano en una población nunca antes expuesta. In *La Neuropsicología: Una Nueva Rama del Conocimiento Psicológico*, E. Cairo, ed. (Havana, Cuba: ENPES), pp. 135–170.
12. Ramírez, C., Nevárez, C., and Valdez, P. (1994). Efectos psicofisiológicos de la eliminación del horario de verano en una población nunca antes expuesta a éste. *Salud Ment.* **17**, 25–30.
13. Lahti, T.A., Leppamäki, S., Lonnqvist, J., and Partonen, T. (2006). Transition to daylight saving time reduces sleep duration plus sleep efficiency of the deprived sleep. *Neurosci. Lett.* **406**, 174–177.
14. Lahti, T.A., Leppamäki, S., Ojanen, S.M., Haukka, J., Tuulio-Henriksson, A., Lonnqvist, J., and Partonen, T. (2006). Transition into daylight saving time influences the fragmentation of the rest-activity cycle. *J. Circadian Rhythms* **4**, 1.
15. Home, J.A., and Östberg, O. (1976). A self-assessment questionnaire to determine morningness-eveningness in human circadian rhythms. *Int. J. Chronobiol.* **4**, 97–110.
16. Toh, K.L., Jones, C.R., He, Y., Eide, E.J., Hinz, W.A., Virshup, D.M., Ptacek, L.J., and Fu, Y.H. (2001). An *hPer2* phosphorylation site mutation in familial advanced sleep phase syndrome. *Science* **291**, 1040–1043.
17. Roenneberg, T., Kuehne, T., Pramstaller, P.P., Ricken, J., Havel, M., Guth, A., and Mellow, M. (2004). A marker for the end of adolescence. *Curr. Biol.* **14**, R1038–R1039.
18. Roenneberg, T., Kuehne, T., Juda, M., Kantermann, T., Allebrandt, K., Gordijn, M., and Mellow, M. (2007). Epidemiology of the human circadian clock. *Sleep Med. Rev.*, in press.
19. Danilenko, K.V., Wirz-Justice, A., Krauchi, K., Weber, J.M., and Terman, M. (2000). The human circadian pacemaker can see by the dawn's early light. *J. Biol. Rhythms* **15**, 437–446.
20. Boivin, D.B., Duffy, J.F., Kronauer, R.E., and Czeisler, C.A. (1996). Dose-response relationships for resetting of human circadian clock by light. *Nature* **379**, 540–542.
21. Waterhouse, J., Edwards, B., Nevill, A., Carvalho, S., Atkinson, G., Buckley, P., Reilly, T., Godfrey, R., and Ramsay, R. (2002). Identifying some determinants of "jet lag" and its symptoms: a study of athletes and other travellers. *Br. J. Sports Med.* **36**, 54–60.
22. Pittendrigh, C.S., and Daan, S. (1976). A functional analysis of circadian pacemakers in nocturnal rodents. IV. Entrainment: pacemaker as clock. *J. Comp. Physiol. [A]* **106**, 291–331.
23. Boulos, Z., and Macchi, M.M. (2005). Season- and latitude-dependent effects of simulated twilights on circadian entrainment. *J. Biol. Rhythms* **20**, 132–144.
24. Roenneberg, T., and Aschoff, J. (1990). Annual rhythm of human reproduction: I. Biology, sociology, or both? *J. Biol. Rhythms* **5**, 195–216.
25. Roenneberg, T., and Aschoff, J. (1990). Annual rhythm of human reproduction: II. Environmental correlations. *J. Biol. Rhythms* **5**, 217–240.
26. Roenneberg, T. (2004). The decline in human seasonality. *J. Biol. Rhythms* **19**, 193–195.
27. Kenagy, G.J. (1980). Center of gravity of circadian activity and its relation to free-running period in two rodent species. *J. Interdisc. Cycle Res.* **11**, 1–8.