

Review

CIRCADIAN RHYTHMS OF PERFORMANCE: NEW TRENDS

Julie Carrier^{1,*} and Timothy H. Monk²

¹Centre d'étude du sommeil et des rythmes biologiques,
Hôpital du Sacré-Cœur de Montréal, Department of Psychology,
University of Montreal

²Sleep and Chronobiology Center, Western Psychiatric Institute and Clinic,
University of Pittsburgh School of Medicine, Pittsburgh, PA 15213

ABSTRACT

This brief review is concerned with how human performance efficiency changes as a function of time of day. It presents an overview of some of the research paradigms and conceptual models that have been used to investigate circadian performance rhythms. The influence of homeostatic and circadian processes on performance regulation is discussed. The review also briefly presents recent mathematical models of alertness that have been used to predict cognitive performance. Related topics such as interindividual differences and the postlunch dip are presented. (*Chronobiology International*, 17(6), 719–732, 2000)

Key Words: Alertness—Circadian rhythms—Homeostatic factor—Performance—Postlunch dip.

As reviewed by Lavie (1980), the search for cycles in mental performance is not a novel interest derived from the recent development of chronobiology as an accepted field. The study of performance rhythms began in the early days of experimental and educational psychology, well before the terms *circadian* and *chronobiology* had even been invented. This work was concerned mainly with determining the optimal time of day for the teaching of an academic subject (e.g., Gates 1916; Muscio 1920; Laird 1925).

It is generally accepted that Nathaniel Kleitman was the investigator who made the link between the early studies and current research on the circadian fluctuation of human behavior (Lavie 1980; Folkard and Monk 1985). Kleitman (1963) showed strong evidence for a parallelism between circadian rhythm in body temperature and time of day

*To whom correspondence should be addressed at: Centre d'étude du sommeil, Hôpital du Sacré-Cœur de Montréal, Department of Psychology, University of Montreal, 5400 boul Gouin Ouest Montréal, Qc, H4J 1C5 Canada. E-mail: j-carrier@crhsc.umontreal.ca

effects in performance for simple repetitive tasks involving motor activity that had a small cognitive load (card sorting, mirror drawing, copying, code substitution, etc.). As with the temperature rhythm, the results showed a well-marked diurnal rhythm of performance, with a maximum at midday and minima early in the morning and late at night. Kleitman and Jackson (1950) went as far as to assert that fluctuations in performance could be inferred from variation in oral temperature, thus avoiding the use of "time consuming performance tests which, in themselves, interfere with, or disrupt, the scheduled activities of the persons studied" (p. 309).

Subsequently, the work of Colquhoun and coworkers, again concerned mainly with simple repetitive tasks, also stressed a parallelism between temperature and performance circadian fluctuations. Colquhoun (1971) studied vigilance tasks (detection of an infrequent signal), simple addition tasks (adding six two-digit numbers), and other simple reaction time tasks. Unlike Kleitman, Colquhoun and coworkers did not infer a *causal* relationship between the performance and body temperature. Instead, they viewed the diurnal fluctuation in performance as being mediated by a circadian rhythm in "basal arousal" (or the inverse of sleepiness).

DIFFERENTIAL TIME-OF-DAY VARIATION FOR DIFFERENT TASKS: OBSERVATIONS UNDER NORMAL DAY-NIGHT CONDITION

Subsequent studies would demonstrate that, under normal day-night conditions, there was no single performance rhythm, but many. Until the mid-1980s, most of the research into circadian fluctuations of performance examined performance over the normal working day (09:00 to 18:00). No attempt was made to distinguish variations in performance due to endogenous circadian factors from those linked to the amount of time since awake. According to this view, the parallelism between temperature and performance observed in early studies seems to hold for only a fairly restricted range of tasks. This heralded a new approach to the study of circadian rhythm in performance, with more emphasis on the differences between performance rhythms than on the similarities. The new approach is epitomized by Folkard (1983): "Perhaps the main conclusion to be drawn from studies on the effects of time of day on performance is that the best time to perform a particular task depends on the nature of that task" (p. 266). Moreover, for the first time, efforts were made to understand the *mechanisms* underlying circadian performance rhythms.

Diurnal fluctuation of working memory well illustrates this attempt to understand heterogeneity between tasks. In general, performance on working memory tasks shows a maximum at about midday (Laird 1925; Folkard 1975). This is later than the peak for immediate memory (which peaks in the morning hours), but earlier than for the tasks involving simple processing, which show a parallelism with body temperature. In addition, other studies have shown different time-of-day effects for working memory depending on the requirements of the task or the particular subject population to be tested. Thus, for example, one study showed an early morning peak of mental arithmetic performance in children (Rutenfranz and Helbruegge 1957), while another study found an evening peak for this type of performance in highly practiced young adults (Blake 1967). Folkard et al. (1976) have shown that the trend of performance for this type of task seems to depend on the precise size of the working memory load. These authors used a serial visual search task in which the working memory load (number of target letters to be remembered) could vary systematically. With a low working memory load, performance

was correlated positively with the circadian rhythm of body temperature. However, as the memory load was increased, the relationship between performance and body temperature broke down and eventually was reversed, with peak performance occurring at the trough of temperature in a high working memory load version. These results suggest that, for a given individual, manipulations of the memory load involved in the performance of a task will affect the timing of the trend over the day.

Several studies have also demonstrated that change over the day in adopted strategy (Baddeley 1966a, 1966b; Folkard 1979; Monk 1981); hemispheric dominance (Zaidel 1983; Folkard 1990; Corbera et al. 1993; Shub et al. 1997); and ability to suppress incorrect, but strong answers (May and Hasher 1998) are also significant factors when we try to understand the heterogeneity between tasks in the literature on time-of-day effect. Furthermore, individual characteristics influencing these factors (like age, level of practice, morningness-eveningness) have all been shown to give rise to different time-of-day fluctuations. Thus, for example, Horne et al. (1980) showed that when extreme evening types and morning types were compared, not only the phase, but also the shape, of the time-of-day curve differed between the two groups, with the morning-type group showing much more of a postlunch dip (see below). In a similar vein (this time using a simple median split in morningness score), Monk and Leng (1986) showed that the phase difference in performance time-of-day effect between the two groups was amplified when a cognitive task was used rather than a simple repetitive task. With regard to aging, our own work has shown that, especially in men, the circadian performance rhythms of older (>70 years) people are more determined by time since waking (homeostatic) processes than by rhythmic inputs from the endogenous circadian pacemaker (see below). This tends to attenuate the amplitude of the older person's circadian variation in performance (and alertness), especially when the sleep/wake cycle is suspended.

There is still much work to do before one can understand which performance tasks will show different time-of-day effects and what the mechanisms are that underlie these differences. Many of the studies have not yet been replicated using different populations of subjects. In addition, many of the models generated to explain the mechanisms underlying heterogeneity between the different tasks are quite stimulating, but need to be tested more systematically. Furthermore, these conclusions were based largely on studies that sampled data infrequently and/or limited data collection to normal working hours. The question of how performance fluctuates during the normal waking hours is very important for many fields in which optimal performance is obligatory. For example, sports performance has been studied quite extensively (Atkinson and Reilly 1996; Atkinson and Speirs 1998). The majority of components of sports performance (e.g., flexibility; muscle strength; short-term, high-power output) seem to vary with time of day and peak in the early evening close to temperature maximum. However, tests of physical fitness based on heart rate and prolonged submaximal exercise carried out in hot conditions show peak time in the morning. As is the case for cognitive performance, individual differences, such as morningness-eveningness and age, and change of strategy are also reported to play a significant role in daily fluctuation of sport performance efficiency.

CONTEMPORARY MODELS OF PERFORMANCE EFFICIENCY: CIRCADIAN AND HOMEOSTATIC REGULATION

Contemporary models of subjective alertness and performance efficiency view these variables as being determined both by a homeostatic process (amount of hours

since awake) and by an input from the circadian timing system (CTS) (Monk et al. 1983; Monk et al. 1989; Dijk et al. 1992; Folkard and Akerstedt 1992; Johnson et al. 1992). Thus, the time-of-day fluctuations observed in performance are thought to be generated by the interaction of these two processes. For example, performance efficiency on a specific task may decrease over the day because the amount of hours since awakening increases (homeostatic drive), because the input from the CTS produces a less optimal "state" to perform the task, or because of both of these influences. In the same manner, performance efficiency may be stable over the day because the input from the CTS exactly counterbalances the effects of increasing hours awake. To dissect the individual effect of rhythmic and homeostatic factors on performance efficiency is not easy. Some experimental and mathematical approaches have been proposed (e.g., forced desynchrony, mathematical removal of data trends), with each of these having underlying assumptions and limitations. Unless a study adopts a specific approach to separate rhythmic and homeostatic factors, it is not possible to know how they are interacting to influence the observed fluctuation in performance.

SIMILAR TIME-OF-DAY VARIATION FOR DIFFERENT TASKS: RECENT RESULTS FROM CONSTANT ROUTINE AND FORCED DESYNCHRONY PROTOCOLS

Recent studies suggest that intertask differences observed under normal day-night conditions (sleeping at night and being awake during the day) can fail to appear when data collection is extended into the night and when subjects not sleep deprived are tested at all circadian phases (using the forced desynchrony protocol).

Johnson et al. (1992) have replicated the decline in short-term memory over the first 10h of the waking day in a 40h wakeful bed rest protocol. However, when the testing was extended to the entire 40h and the sleep-wake cycle was suspended, a parallelism between short-term memory performance and temperature emerged, with a coincidence in the timing of troughs of temperature and performance. These data were consistent with the results of a 72h sleep deprivation study in which performance on a memory and search task reached a trough between 02:00 and 06:00 (Babkoff et al. 1988). These results raise doubts about a general inversion of short-term memory and body temperature rhythms.

Monk et al. (1997) have studied the circadian fluctuations of performance (speed and accuracy) at serial search, verbal reasoning, and manual dexterity tasks during 36h of unmasking conditions (constant wakeful bed rest, temporal isolation, homogenized "meals"). Figure 1 shows the time-of-day functions for search speed, reasoning speed, vigilance hits, and dexterity speed. The linear trend of each subject's individual time series has been removed to factor out the effect of sleep deprivation. As found by Johnson et al. (1992), the minima of the average performance rhythms were mostly within the 05:00 to 07:00 time window, broadly coincident with the timing of the trough in rectal temperature. Thus, when the sleep-wake cycle is suspended and data collection is extended into the night, circadian performance rhythms appear generally to be predictable from the circadian temperature rhythm. This is true even for reasoning speed, a "working memory" task shown by Folkard (1979) to exhibit a time-of-day effect (under day-night conditions) that is rather different from body temperature (a midday peak versus an evening peak). In the same vein, Monk and Carrier (1997) have shown, after controlling

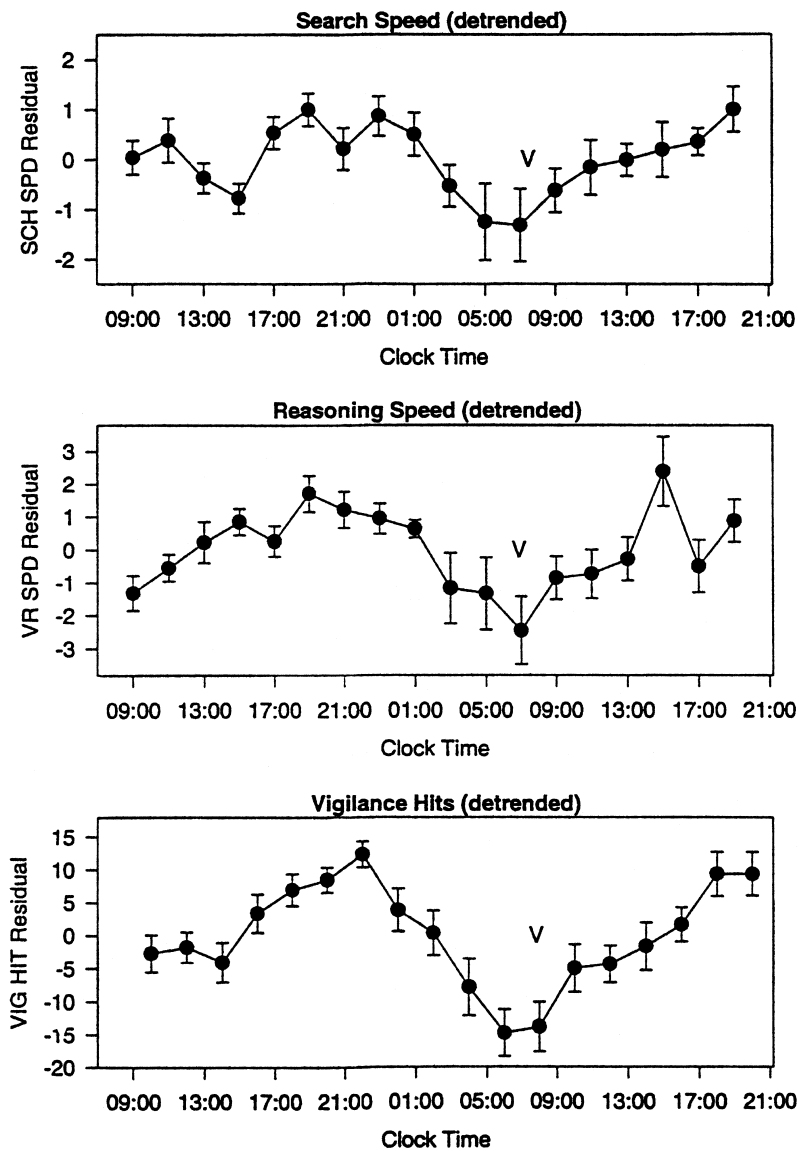


FIGURE 1. Detrended functions for search speed (lines/minute), reasoning speed (lines/minute), and vigilance hits (percentage hits). Plotted is mean \pm SEM from 17 subjects. (From Monk et al. 1997.)

for the effects of microsleep, psychomotor slowing, and inattention, that speed of mental processing seems to slow around the temperature minimum time.

The Johnson et al. (1992) and Monk et al. (1997) studies suggest that intertask differences under a normal day-night condition might be driven more by the homeostatic influence of time since waking than by intertask differences in CTS influence. As mentioned above, it is not easy to separate the homeostatic influence from the drive of the

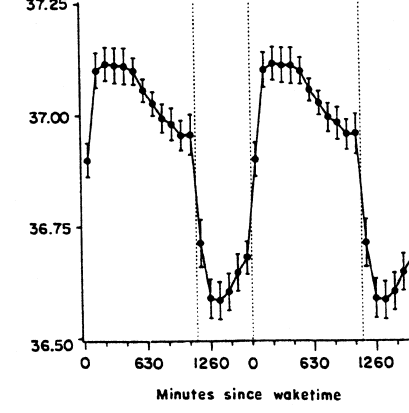
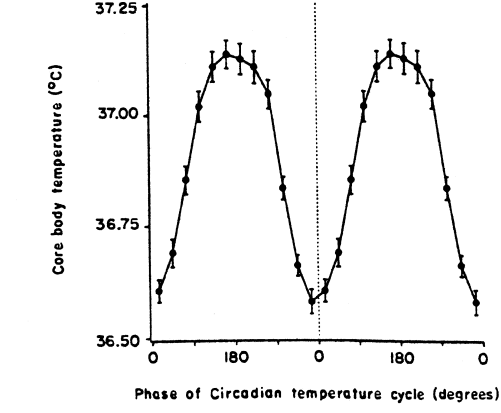
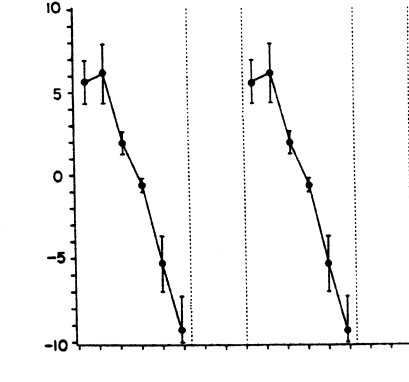
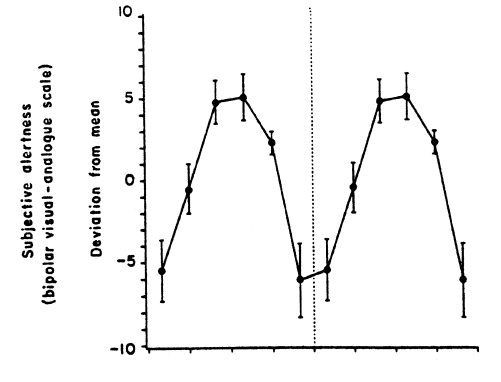
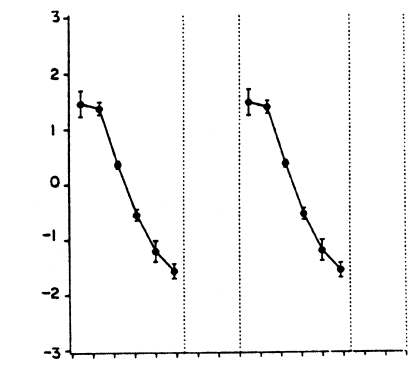
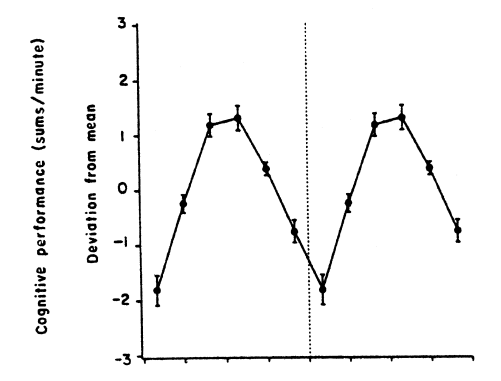
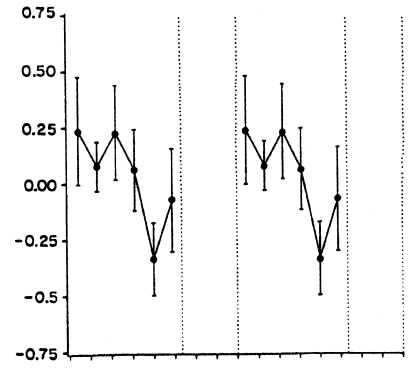
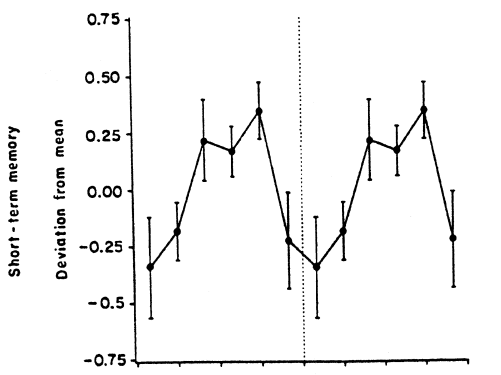
CTS. Monk et al. (1997) suggest that the parallelism observed in their study occurred because the sleep/wake cycle was suspended, and the linear buildup had been factored out by the removal of the linear trend.

The forced desynchrony protocol is one of the techniques often proposed to separate out the homeostatic influence from the drive of the CTS. Using such a protocol, Monk et al. (1983) showed that intertask differences existed in the weight given to homeostatic versus CTS influences in the final circadian performance rhythm. Interestingly, however, when performance is induced at τ (the period length of the CTS), a parallelism between temperature and performance seems to occur for all tasks (Monk et al. 1983; Monk et al. 1989; Dijk et al. 1992; Johnson et al. 1992). Figure 2 illustrates the circadian and the sleep/wake-dependent influences on short-term memory, calculation performance, subjective alertness, and core body temperature in nine subjects experiencing a forced desynchrony protocol (Johnson et al. 1992). Each subject was scheduled to a 28h rest/activity cycle to induce a desynchrony between the body temperature rhythm and the sleep/wake cycle. Rhythms in short-term memory, subjective alertness, and calculation performance clearly varied with circadian phase and paralleled closely the educed waveform of the body temperature rhythm. Figure 2 also shows that short-term memory, subjective alertness, and performance all varied systematically with elapsed time since waking on the 28h day. Thus, Johnson et al. (1992) confirmed the original 1983 assertion of Monk et al. that performance on these three behavioral variables is influenced by two interacting factors: an endogenous circadian process that is coupled to the temperature rhythm and a homeostatic process related to the sleep/wake cycle. Monk and Carrier (1998) extended results obtained with the forced desynchrony protocol and showed that performance on several tasks, including hand dexterity, verbal reasoning, and serial search, show a parallelism with body temperature whether educed at τ (the period of the CTS) or at T (hours since waking). These results have also shown that, at least for these specific tasks, the influence of hours since waking is at least as strong as the influence of the CTS.

CIRCADIAN CORRELATES OF PERFORMANCE: THE PREDICTIVE VALUE OF CORTISOL, MELATONIN, VIGILANCE, AND MOOD RHYTHMS

Allowing that homeostatic ("time since waking") effects also exist, recent studies strongly suggest that endogenous circadian performance rhythms are controlled by the same pacemaker that drives the endogenous circadian rhythm of body temperature. This pacemaker also drives a number of other physiological rhythms, including plasma corti-

FIGURE 2. Circadian and sleep/wake-dependent influences on short-term memory, cognitive performance, subjective alertness, and core body temperature (°C) in 9 subjects during episodes of forced desynchrony between the body temperature and sleep/wake cycles. Data are double plotted. Left panel: All data are referenced to the phase of the endogenous circadian temperature cycle educed at its intrinsic period, with 0 = temperature nadir. Right panel: The same data are referenced to wake time (0 minutes) and educed at the period of the imposed sleep/wake cycle (28h). (From Johnson et al. 1992.)



sol and plasma melatonin. The body temperature rhythm is the “gold standard” for human circadian rhythms, much as the running wheel is for hamster studies (Wever 1979), at least partly because it is so easy to measure. However, there is no conceptual or mechanistic advantage to using body temperature as an index of the activity of the CTS. Only one recent study has looked at how performance rhythms are correlated with cortisol and melatonin circadian rhythms (Monk et al. 1997). Results showed that temperature and cortisol rhythms correlated with slightly more performance measures than did melatonin. Within subjects, predominantly positive correlations emerged between good performance and higher temperatures and better subjective alertness; predominantly negative correlations emerged between good performance and higher plasma levels of cortisol and melatonin. While all three physiological rhythms were reasonably well correlated with performance, the parallelism was far from compelling, with mean intrasubject correlations accounting for a rather small proportion of variance (<10%). Thus, extreme care should be exercised in asserting, for any physiological variable, a universal parallelism between circadian rhythms in performance and physiology resulting from some posited causal relationship between the two. Instead, it would be more parsimonious to assert that performance rhythms are driven independently by the CTS (and time since waking), with a pattern that happens to yield a positive relationship with temperature and a negative one with cortisol and melatonin, without necessarily being *directly* mediated by *any* particular physiological rhythm. It is noteworthy that, in the same study, global vigor (subjective alertness) correlated about as well with performance as did body temperature. Thus, although it may seem more rigorous to anchor performance rhythms to an objective index such as body temperature, in terms of predictability, a simple rating of alertness may work just as well.

MATHEMATICAL MODELS OF PERFORMANCE

Mathematical models of alertness have been proposed recently (Folkard and Akerstedt 1992; Achermann and Borbély 1994; Folkard et al. 1999; Jewett and Kronauer 1999), and attempts have been made to use them to predict cognitive performance. All these models include three processes: a homeostatic process that increases during sleep and decreases with the amount of hours since awake, a circadian process controlled by the circadian pacemaker, and an inertia process on transitions between sleep and waking states (sleep inertia alone or sleep and wake inertia). These models have been useful for predicting alertness in various research protocols, and efforts have been made recently to refine them to predict alertness in real night shift environments (Folkard et al. 1999).

While some models imply that the homeostatic and circadian processes are independent and additive (Folkard and Akerstedt 1992; Achermann and Borbély 1994), the model of Jewett and Kronauer (1999) implies a nonlinear interaction between the homeostatic and the circadian processes. Jewett and Kronauer (1999) based their assumption on detailed analyses of forced desynchrony data. Those results have shown that the amplitude of the circadian modulation on both alertness and cognitive throughput (number of mathematical additions performed) fluctuates with the amount of hours since awake. According to these results, the circadian influence on alertness and performance is low on awakening, increases during the first 15h of wakefulness, and remains quite constant up to 50h of sleep deprivation (Dijk et al. 1992; Jewett and Kronauer 1999; Wyatt et al. 1999).

It has been suggested, however, that possible nonlinearity in the neurobehavioral metrics used (e.g., floor or ceiling effects) may explain such an interaction (see Achermann 1999 and Dijk et al. 1999 for further discussion). This later argument points out the importance of testing these models with other performance tasks.

In that vein, given the recent suggestion that their model of alertness (Akerstedt and Folkard 1997) may be generalized to predict measures of performance, Owens et al. (1998) examined the hypothesis that alertness can be used to predict time-of-day effects of performance between 08:00 and midnight. While alertness was a reasonably good “predictor” of the simple perceptual-motor speed measures in this study, it predicted less well some of the other performance measures, like accuracy from a low and high memory search task. The authors concluded that the three-process model of alertness could not be generalized to predict successfully all measures of mood and performance.

In conclusion, we need to be very cautious in assertions regarding the mechanism by which circadian performance rhythms occur. While undoubtedly driven by the CTS and the effects of time since waking, performance rhythms do not appear to be the simple *direct* result of circadian changes in either mood or physiology. The understanding of the mechanisms underlying different diurnal fluctuations during waking hours (without suspending the sleep/wake cycle) will require dissection of the individual effects of homeostatic and circadian influences on performance efficiency. This will not be a simple task since current research suggests that these processes vary with task parameters (e.g., cognitive load) and individual characteristics (age, chronotype, level of practice).

ULTRADIAN RHYTHMS OF PERFORMANCE: THE POSTLUNCH DIP

The afternoon siesta is an integral part of many different cultures (Dinges and Broughton 1989). A broad base of empirical evidence suggests that there is a general increase in human sleep propensity during the midafternoon hours (Richardson et al. 1982; Campbell 1984; Lavie 1986; Carskadon and Dement 1992). To account for the postlunch dip phenomenon, Broughton (1975, 1988) initially proposed the existence of a circasemidian rhythm of vigilance and slow-wave sleep (SWS) propensity having 12h and 24h components. In a new model of sleep/wake cycle regulation, Broughton proposes that the afternoon nap zone is due to increasing homeostatic sleep propensity after morning awakening (Borbély's Process-S) being overwhelmed by a circadian arousal process that will become maximal later in the evening (Broughton 1998). Many studies of performance have also reported a short-lived decrement of performance during the midafternoon hours; the postlunch dip was one of the first exceptions found to the parallelism between performance and temperature circadian rhythms. Blake's (1967) classic studies of performance and time of day showed a clear postlunch dip in measures of simple reaction times, serial search, and signal detection. Although the postlunch dip can be exacerbated by a heavy high-carbohydrate lunch (Craig et al. 1981), it can occur even when no lunch is taken (Blake 1971; Monk et al. 1996). Interestingly, postlunch dips are also apparent in “real-life” studies of the frequency of “nodding off” while driving (Prokop and Prokop 1955), missing warning signals as a train driver (Hildebrandt et al. 1974), and the traffic accident statistics of Israel (Lavie 1991) and the United States (Mitler et al. 1985). However, some laboratory studies have failed to find evidence for a postlunch dip, even when very similar measures of performance were considered (Christie and

McBrearty 1979). Likewise, there was little evidence of a clear postlunch dip when a meta-analysis of time-of-day effects in various measures of laboratory performance efficiency, and subjective activation was performed by Folkard and Monk (1987).

Some studies have suggested that individual characteristics may be linked to the probability of showing an afternoon dip, which might explain some of the inconsistencies found in the literature. For example, Lavie and Segal (1989), using the ultrashort sleep/wake paradigm, have shown a much clearer postlunch dip in sleep length for morning types than for evening types after sleep deprivation. Along the same vein, Monk et al. (1996) hypothesized that physiological characteristics of the biological clock may indicate who will, and who will not, show a postlunch performance dip. To test this, they

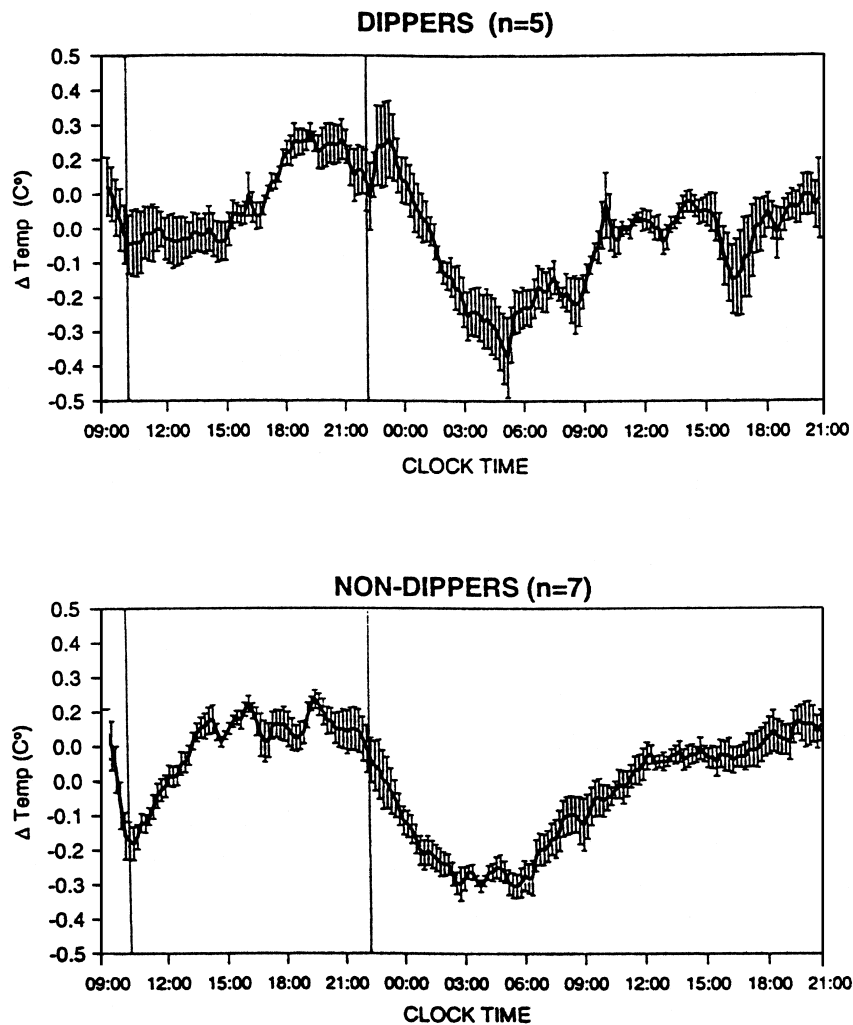


FIGURE 3. Mean 36h rectal temperature (\pm SEM) plotted by time of day for "dippers" and "non-dippers." Each value is expressed as deviation from that subject's 36h mean. The two lines indicate the time interval 10:00 to 22:00 on day 1. (From Monk et al. 1996.)

studied rectal temperature rhythms in groups of subjects who either did or did not show a clear postlunch dip at a monotonous (25–30 minute) vigilance task (Mackworth visual vigilance task; Mackworth 1948). Performance was tested every 2h for the 36h unmasking protocol. During the protocol, the subject was kept in wakeful bed rest in a temporal isolation environment. Meals were replaced by hourly food supplement comprised of 1/24th the subject's daily caloric requirement. Figure 3 shows vigilance performance (% signals correctly detected \pm SEM) as a function of time of day for "dippers" and "nondippers." Subjects showing the postlunch performance dip had a higher amplitude and later peaking 12h component of rectal temperature rhythm than those not showing the performance dip. This resulted in a flat, rather than rising, function in body temperature over the 10:00–15:00 time interval (see Fig. 3). These results suggest that the postlunch dip is linked to an endogenous phenomenon that is individually determined and is related to the strength of the (12h) harmonic of the temperature circadian system.

CONCLUSIONS

"It's as different as night and day" is an apt summary of how human performance ability fluctuates over the 24h. Importantly, these fluctuations are nontrivial and are predictable, given knowledge of the status of the circadian system and the amount of prior wakefulness. Because both of these factors combine to influence performance, circadian performance rhythms do not *always* parallel the body temperature rhythm, although they invariably do so when the sleep/wake cycle is suspended.

ACKNOWLEDGMENT

This research was supported by a research scholarship (Carrier) and grant MT-14999 from the Medical Research Council of Canada (Carrier), AG-13396 (Monk), AG-15136 (Monk), Research Scientist Development Award MH-01235 (Monk), and NASA grant NAG9-1036 (Monk).

REFERENCES

- Achermann P. 1999. Technical note: a problem with identifying nonlinear interactions of circadian and homeostatic processes. *J Biol Rhythms*. 14:602–3.
- Achermann P, Borbély AA. 1994. Simulation of daytime vigilance by the additive interaction of a homeostatic and a circadian process. *Biol Cybern*. 71:115–21.
- Akerstedt T, Folkard S. 1997. The three-process model of alertness and its extension to performance, sleep latency and sleep length. *Chronobiol Int*. 14:115–23.
- Atkinson G, Reilly T. 1996. Circadian variation in sports performance. *Sports Med*. 21:292–312.
- Atkinson G, Speirs L. 1998. Diurnal variation in tennis service. *Percept Motor Skills*. 86:1335–38.
- Babkoff H, Mikulincer M, Caspy T, et al. 1988. The topology of performance curves during 72 hours of sleep loss: a memory and search task. *Q J Exp Psychol*. 737–56.

- Baddeley AD. 1966a. The influence of acoustic and semantic similarity on long-term memory for word sequences. *Q J Exp Psychol.* 18:302–9.
- Baddeley AD. 1966b. Short-term memory for word sequences as a function of acoustic, semantic and formal similarity. *Q J Exp Psychol.* 18:362–65.
- Blake MJF. 1967. Time of day effects on performance in a range of tasks. *Psychonom Sci.* 9:349–50.
- Blake MJF. 1971. Temperament and time of day. In: Colquhoun WP, editor. *Biological rhythms and human performance.* London: Academic, pp. 109–48.
- Broughton R. 1975. Biorhythmic variations in consciousness and psychological functions. *Can Psychol Rev.* 16:217–39.
- Broughton R. 1988. The circasemidian sleep rhythm and its relationship to the circadian and ultradian sleep-wake rhythms. In: Kalba R, Oval R, Schulz H, et al., editors. *Sleep '86.* New York: Gustav Fisher Verlag, pp. 41–43.
- Broughton RJ. 1998. SCN controlled circadian arousal and the afternoon “nap zone.” *Sleep Res Online.* 1:166–78.
- Campbell SS. 1984. Duration and placement of sleep in a “disentrained” environment. *Psychophysiology.* 21:106–13.
- Carskadon MA, Dement WC. 1992. Multiple sleep latency tests during the constant routine. *Sleep.* 15(6):396–99.
- Christie MJ, McBrearty EMT. 1979. Psychophysiological investigations of post lunch state in male and female subjects. *Ergonomics.* 22:307–25.
- Colquhoun WP. 1971. *Biological rhythms and human performance.* London: Academic.
- Corbera X, Grau C, Vendrell P. 1993. Diurnal oscillations in hemispheric performance. *J Clin Exp Neuropsychol.* 15:300–10.
- Craig A, Baer K, Diekmann A. 1981. The effects of lunch on sensory-perceptual functioning in man. *Int J Occup Environ Health.* 49:105–14.
- Dijk DJ, Duffy JF, Czeisler CA. 1992. Circadian and sleep/wake dependent aspects of subjective alertness and cognitive performance. *J Sleep Res.* 1:112–17.
- Dijk D-J, Jewett ME, Czeisler CA, et al. 1999. Reply to technical note: nonlinear interactions between circadian and homeostatic processes: models or metrics. *J Biol Rhythms.* 16:604–5.
- Dinges DF, Broughton R. 1989. *Sleep and alertness: chronobiological, behavioral, and medical aspects of napping.* New York: Raven.
- Folkard S. 1975. Diurnal variation in logical reasoning. *Br J Psychol.* 66:1–8.
- Folkard S. 1979. Time of day and level of processing. *Mem Cogn.* 7:247–52.
- Folkard S. 1983. Diurnal variation in human performance. In: Hockey GRJ, editor. *Stress and fatigue in human performance.* Chichester, England: Wiley, pp. 245–72.
- Folkard S. 1990. Circadian performance rhythms: some practical and theoretical implications. *Phil Trans R Soc Lond.* 327:543–53.
- Folkard S, Akerstedt T. 1992. A three-process model of the regulation of alertness-sleepiness. In: Broughton RJ, Ogilvie RD, editors. *Sleep, arousal, and performance: a tribute to Bob Wilkinson.* Boston: Birkhauser, pp. 11–26.
- Folkard S, Akerstedt T, MacDonald I, et al. 1999. Beyond the three-process model of alertness: estimating phase, time on shift, and successive night effects. *J Biol Rhythms.* 14:577–87.
- Folkard S, Knauth P, Monk TH, et al. 1976. The effect of memory load on the circadian variation in performance efficiency under a rapidly rotating shift system. *Ergonomics.* 19:479–88.

- Folkard S, Monk TH. 1985. Circadian performance rhythms. In: Folkard S, Monk TH, editors. *Hours of work—temporal factors in work scheduling*. New York: John Wiley and Sons, pp. 37–52.
- Folkard S, Monk TH. 1987. The measurement of circadian rhythms in psychological functioning. In: Scheving LE, Halberg F, Ehret CF, editors. *Chronobiotechnology and chronobiological engineering*. Dordrecht, The Netherlands: Martinus Nijhoff, pp. 189–201.
- Gates AI. 1916. Variations in efficiency during the day, together with practice effects, sex differences, and correlations. *Univ Calif Pub Psychol*. 1:1–156.
- Hildebrandt G, Rohmert W, Rutenfranz J. 1974. Twelve and 24 hour rhythms in error frequency of locomotive drivers and the influence of tiredness. *Int J Chronobiol*. 2:175–80.
- Horne JA, Brass CG, Pettit AN. 1980. Circadian performance differences between “morning” and “evening” “types.” *Ergonomics*. 23:129–36.
- Jewett ME, Kronauer RE. 1999. Interactive mathematical models of subjective alertness and cognitive throughput in humans. *J Biol Rhythms*. 14:588–97.
- Johnson MP, Duffy JF, Dijk DJ, et al. 1992. Short-term memory, alertness and performance: a reappraisal of their relationship to body temperature. *J Sleep Res*. 1: 24–29.
- Kleitman N. 1963. *Sleep and wakefulness*. Chicago: University of Chicago Press.
- Kleitman N, Jackson DP. 1950. Body temperature and performance under different routines. *J Appl Physiol*. 3:309–28.
- Laird DA. 1925. Relative performance of college students as conditioned by time of day and day of week. *J Exp Psychol*. 8:50–63.
- Lavie P. 1980. The search for cycles in mental performance from Lombard to Kleitman. *Chronobiologia*. 7:247–56.
- Lavie P. 1986. Ultrashort sleep-waking schedule. III. Gates and “forbidden zones” for sleep. *Electroencephalogr Clin Neurophysiol*. 63:414–25.
- Lavie P. 1991. The 24-hour sleep propensity function (SPF): practical and theoretical implications. In: Monk TH, editor. *Sleep, sleepiness and performance*. Chichester, England: John Wiley and Sons, pp. 65–93.
- Lavie P, Segal S. 1989. Twenty-four-hour structure of sleepiness in morning and evening persons investigated by ultrashort sleep-wake cycle. *Sleep*. 12(6):522–28.
- Mackworth NH. 1948. The breakdown of vigilance during prolonged visual search. *Q J Exp Psychol*. 1:6–21.
- May CP, Hasher L. 1998. Synchrony effects in inhibition control over thoughts and actions. *J Exp Psychol Hum Percept Perform*. 24:363–79.
- Mitler MM, Hajdukovic RM, Hahn PM, et al. 1985. Circadian rhythm of death time: cause of death versus recorded death time in New York City [abstract]. *Sleep Res*. 14:306.
- Monk TH. 1981. The interaction between the edge effect and target conspicuity in visual search. *Hum Factors*. 23:615–25.
- Monk TH, Buysse DJ, Reynolds CF, et al. 1996. Circadian determinants of the post-lunch dip in performance. *Chronobiol Int*. 13:135–45.
- Monk TH, Buysse DJ, Reynolds CF, et al. 1997. Circadian rhythms in human performance and mood under constant conditions. *J Sleep Res*. 6:9–18.
- Monk TH, Carrier J. 1997. Speed of mental processing in the middle of the night. *Sleep*. 20:399–401.

- Monk TH, Carrier J. 1998. A parallelism between human body temperature and performance independent of the endogenous circadian pacemaker. *J Biol Rhythms*. 13: 113–22.
- Monk TH, Leng VC. 1986. Interactions between inter-individual and inter-risk differences in the diurnal variation of human performance. *Chronobiol Int*. 3:171–77.
- Monk TH, Moline ML, Fookson JE, et al. 1989. Circadian determinants of subjective alertness. *J Biol Rhythms*. 4:393–404.
- Monk TH, Weitzman ED, Fookson JE, et al. 1983. Task variables determine which biological clock controls circadian rhythms in human performance. *Nature*. 304: 543–45.
- Muscio B. 1920. Fluctuations in mental efficiency. *Br J Psychol*. 10:327–44.
- Owens DS, MacDonald I, Tucker P, et al. 1998. Diurnal trends in mood and performance do not parallel alertness. *Scand J Work Environ Health*. 24:109–14.
- Prokop O, Prokop L. 1955. Ermüdung und Einschlafen am Steuer. *Zentralbl Verkehrs-Medizin, Verkehrs-Psychologie angrenzende Gebiete*. 1:19–30.
- Richardson GS, Carskadon MA, Orav EJ, et al. 1982. Circadian variation of sleep tendency in elderly and young adult subjects. *Sleep*. 5:S82–S94.
- Rutenfranz J, Helbruegge T. 1957. Über Tageschwankungen der Rechengeschwindigkeit bei 11-jährigen Kindern. *Z Kinderheilk*. 80:65–82.
- Shub Y, Ashkenazi IE, Reinberg A. 1997. Differences between left- and right-hand reaction time rhythms: indications of shifts in strategies of human brain activity. *Cogn Brain Res*. 6:141–46.
- Wever RA. 1979. *The circadian system of man: results of experiments under temporal isolation*. New York: Springer-Verlag.
- Wyatt JK, Ritz-DeCecco A, Czeisler CA, et al. 1999. Circadian temperature and melatonin rhythms, sleep, and neurobehavioral function in humans living on a 20-h day. *Am J Physiol: Regulative, Integrative Comp Physiol*. 277:R1152–63.
- Zaidel E. 1983. Disconnection syndrome as a model for laterality effects in the normal brain. In: Hellige JB, editor. *Cerebral hemisphere asymmetry*. New York: Praeger, pp. 95–151.

Copyright of Chronobiology International: The Journal of Biological & Medical Rhythm Research is the property of Taylor & Francis Ltd and its content may not be copied or emailed to multiple sites or posted to a listserv without the copyright holder's express written permission. However, users may print, download, or email articles for individual use.