Am J Physiol Regul Integr Comp Physiol 283: R1370–R1377, 2002.
First published August 15, 2002; 10.1152/ajpregu.00205.2002.

Relationship between alertness, performance, and body temperature in humans

KENNETH P. WRIGHT, JR., JOSEPH T. HULL, AND CHARLES A. CZEISLER
Division of Sleep Medicine, Department of Medicine, Brigham and Women's Hospital, Harvard Medical School, Boston, Massachusetts 02115

Received 9 April 2002; accepted in final form 12 August 2002

Wright, Kenneth P., Jr., Joseph T. Hull, and Charles A. Czeisler. Relationship between alertness, performance, and body temperature in humans. *Am J Physiol Regul Integr Comp Physiol* 283: R1370–R1377, 2002. First published August 15, 2002; 10.1152/ajpregu.00205.2002.—Body temperature has been reported to influence human performance. Performance is reported to be better when body temperature is high/near its circadian peak and worse when body temperature is low/near its circadian minimum. We assessed whether this relationship between performance and body temperature reflects the regulation of both the internal biological timekeeping system and/or the influence of body temperature on performance independent of circadian phase. Fourteen subjects participated in a forced desynchrony protocol allowing assessment of the relationship between body temperature and performance while controlling for circadian phase and hours awake. Most neurobehavioral measures varied as a function of internal biological time and duration of wakefulness. A number of performance measures were better when body temperature was elevated, including working memory, subjective alertness, visual attention, and the slowest 10% of reaction times. These findings demonstrate that an increased body temperature, associated with and independent of internal biological time, is correlated with improved performance and alertness. These results support the hypothesis that body temperature modulates neurobehavioral function in humans.

sleep homeostasis; circadian phase; neurobehavioral performance; forced desynchrony; core body temperature

CONSIDERABLE EFFORT has been devoted to understanding the relationship between body temperature and human performance (2, 4, 12, 24, 34, 48). Kleitman (32–34) originally proposed that body temperature was an underlying mechanism regulating performance. "Assuming that the effect of temperature indicates that we are dealing with a chemical phenomenon, there are two interpretations of the relationship between temperature and reaction time possible: either *a*, mental processes represent chemical reactions in themselves, or *b*, the speed of thinking depends upon the level of metabolic activity of the cells of the cerebral cortex, and by the raising of the latter through an increase in body temperature we indirectly speed up the thought process" (Ref. 34, p. 501). Kleitman's hypothesis is supported by results from studies using in vitro and in vivo preparations in which it was reported that synaptic function is altered by supraphysiological changes in brain temperature (39, 40, 47) such that higher brain temperatures resulted in faster transmission, whereas lower brain temperature resulted in slower transmission.

Brain mechanisms involved in the regulation of body temperature include the preoptic area and the suprachiasmatic nuclei, both of which are located in the hypothalamus. The preoptic area regulates homeostatic mechanisms to maintain body and brain temperature in mammals within a limited range in response to physiological and environmental conditions, and the suprachiasmatic nuclei regulate the circadian or near-24-h rhythm of temperature (28, 43, 44). Homeostatic and circadian mechanisms influence cutaneous vasodilatation, peripheral vasoconstriction, and basal metabolism, all of which change the rate at which body heat is lost and gained (36). The circadian peak-to-trough range of body temperature, when examined under controlled environmental conditions (e.g., constant ambient temperature, constant dim light, supine posture, restricted activity, and periodic nutrition intake), is ~1°C. The daily pattern of brain temperature is reported to vary with the circadian rhythm of body temperature, although the rhythm in brain temperature was not tested in constant conditions that controlled for changes in wakefulness-sleep state (37). Yet, even under controlled conditions, the amplitude of the body temperature rhythm is reported to be influenced by other factors such as age (8, 11, 16, 21) and menstrual cycle phase (6, 49).

It has long been recognized that there exists a positive relationship between daily rhythms of body temperature and neurobehavioral performance and alertness in humans (4, 32–34, 38). During total sleep deprivation, increased homeostatic sleep drive results in impaired performance, but when examined under constant conditions, body temperature and neurobehavioral performance levels still exhibit a circadian pattern with higher levels during the habitual waking day and lower levels during habitual sleep time at

Address for reprint requests and other correspondence: K. P. Wright, Jr., Dept. of Kinesiology and Applied Physiology, Univ. of Colorado, Boulder, CO 80309-0354 (E-mail: kenneth.wright@colorado.edu).

The costs of publication of this article were defrayed in part by the payment of page charges. The article must therefore be hereby marked "*advertisement*" in accordance with 18 U.S.C. Section 1734 solely to indicate this fact.

night (5). The positive relationship between rhythms in performance and body temperature has been verified by studies that have controlled for factors that can influence body temperature and performance, such as light exposure, activity, posture, nutrition, and drug intake (i.e., constant routine) (5, 31, 41, 49–52). In studies that have manipulated body temperature via external means (e.g., altering ambient temperature, cold water immersion), it has generally been reported that cognitive function is improved by increasing body temperature slightly above the normal temperature of ~37°C and that cognitive function is reduced by decreasing body temperature below normal (3, 23–26, 46, 48).

Low performance associated with low body temperature has also been reported in studies of shift work and continuous night operations (10, 13, 17, 33). In forced desynchrony studies, which experimentally separate circadian and sleep-wake homeostatic influences on neurobehavioral function, it has also been reported that performance tends to be lowest during the biological night near to the minimum of the body temperature rhythm regardless of the duration of prior wakefulness (14, 18, 30, 54). Yet, it has been unclear from prior studies whether performance is directly affected by body temperature or whether both body temperature and performance simply covary with circadian phase. To address the latter, we used a 28-h forced desynchrony protocol to investigate whether higher body temperature levels were associated with higher neurobehavioral performance levels while controlling for both circadian phase and hours awake.

METHODS

Subjects. Fourteen healthy adults, 3 females and 11 males (mean ± SD age 31.6 ± 6.4 yr; range 20–41 yr), participated. Participants each gave informed consent in writing. The Brigham and Women's Hospital/Partners Health Care System Human Research Committee approved the procedures for the protocol. The investigation was conducted according to the principles expressed in the Declaration of Helsinki. Participants were healthy based on medical history, physical and psychological exams, blood and urine chemistries, and electrocardiogram. Toxicology screens for drug use verified that participants were drug free near the beginning of the screening process and on admission to the laboratory.

Experimental procedures. Participants maintained consistent sleep-wake schedules with ~8 h of sleep for 3 wk before admission, verified by call-in times to a time-stamped voice recorder, sleep logs, and for at least 1 wk by wrist actigraphy (Minimitter, Sun River, OR). On *days 35–49* of a 55-day in-patient protocol (53), participants were scheduled to a forced desynchrony protocol (Fig. 1) for 12 consecutive 28-h days (18.66 h of scheduled wakefulness and 9.33 h of scheduled sleep). Subjects were scheduled to sleep in darkness, and during scheduled wakefulness they were exposed to very dim room light. The first subject tested was exposed to ~3 lx in the angle of gaze (<5 lx ambient at ~76 cm and <15 lx maximum at ~183 cm in the direction of the ceiling fixtures) during the forced desynchrony. The remaining 13 subjects were exposed to ~1.5 lx in the angle of gaze (<3 lx ambient and <8 lx maximum). The 28-h day length is known to be outside the range of entrainment of the human circadian clock under these dim light conditions, i.e., the circadian clock cannot adapt to the 28-h day length and instead it continues to oscillate at its near-24-h intrinsic period (15, 53).

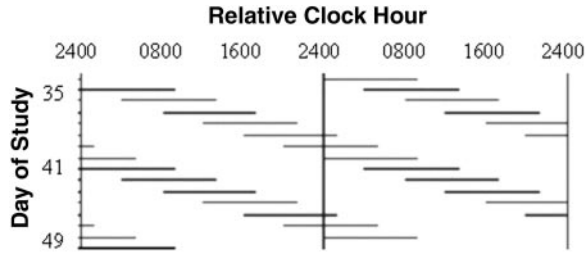

Fig. 1. Raster plot of 28-h forced desynchrony protocol. Data are double plotted such that subsequent days are next to and beneath the other. Horizontal bars represent scheduled sleep episodes. In this forced desynchrony protocol, sleep and wakefulness are scheduled to occur 4 h later each day.

Body temperature was measured every minute by means of a rectal thermistor (Yellow Springs Instruments, Yellow Springs, OH), except during showers and bowel movements, and room temperature was maintained at ~24.5°C as measured with an air thermistor.

Performance tests. Participants performed an ~30-min battery of neurobehavioral function tests every 2 h beginning 2 h after scheduled wake time. Working memory and cognitive throughput were measured with the Digit Symbol Substitution Test (DSST) and a mathematical addition test (ADD). Recall memory was measured with the Probed Recall Memory (PRM) task, and subjective alertness was measured with a visual analog scale (VAS). Visual vigilance/attention was measured with the Psychomotor Vigilance Task (PVT), for which we assessed the number of lapses, median reaction time, and the fastest and slowest 10% reaction time (19). These tests were selected because they are known to vary with the circadian rhythm of body temperature and to be sensitive to sleep loss (9, 18, 19, 54).

Data analysis. The intrinsic circadian period of the body temperature rhythm was estimated using a nonorthogonal spectral analysis technique. That is, temperature data were fitted with periodic components corresponding to both the forced period of the imposed sleep-wake cycle and the sought-for period of the endogenous circadian rhythm, together with their harmonics, using an exact maximum likelihood fitting procedure (7). This technique is described in detail in Ref. 15. Neurobehavioral performance and alertness data were then averaged into 60-degree (4-h) bins with the phase of the body temperature minimum (T_{min}) assigned to 0° and into 2-h bins from *hour 2* through *hour 16* of scheduled wakefulness. Body temperature data were averaged into 1-h bins during scheduled wakefulness and averaged into 15-degree (1-h) bins for the circadian component. Body temperature data are plotted for the hour during which the performance battery occurred. Performance data were transformed into deviation from the forced desynchrony mean to control for individual differences in performance capability. Performance scores were then categorized as being associated with the highest or lowest body temperature value for each separate circadian phase/hours awake bin for each individual. If more than two performance tests and body temperature values occurred at the same bin, only the scores associated with the highest and lowest body temperature level were used in the ANOVA analyses. For example, if three performance batteries, with associated hourly body temperature values of 36.8, 37.5, and 37.8°C, occurred at the 0° circadian phase/2-h hours awake bin, then the performance battery associated with the 37.8°C

Table 1. *Summary of results of repeated-measure ANOVA with factors time and highest vs. lowest body temperature performance*

Neurobehavioral Measure	Highest vs. Lowest Temperature Performance *F*	Time *F*	Highest vs. Lowest Temperature Performance × Time *F*
Body temperature (°C)			
Circadian phase	99.81§	126.27§	1.48(NS)
Hours awake	284.53§	16.65§	1.82(0.094)
DSST (cognitive throughput)			
Circadian phase	23.18‡	20.51§	0.40(NS)
Hours awake	21.49‡	6.53§	0.58(NS)
ADD (cognitive throughput)			
Circadian phase	3.78(0.074)	10.56§	0.65(NS)
Hours awake	3.93(0.069)	3.81‡	0.97(NS)
PRM (no. recalled)			
Circadian phase	5.40*	1.83(NS)	1.09(NS)
Hours awake	5.51*	7.97§	2.47*
VAS (alertness)			
Circadian phase	12.09†	11.40§	2.84*
Hours awake	9.29†	16.58§	0.91(NS)
PVT (no. of lapses)			
Circadian phase	2.36(NS)	14.02§	2.71*
Hours awake	2.09(NS)	8.25§	0.55(NS)
PVT (median reaction time)			
Circadian phase	1.32(NS)	1.82(NS)	0.96(NS)
Hours awake	1.27(NS)	1.42(NS)	1.03(NS)
PVT (fastest 10% reaction time)			
Circadian phase	0.05(NS)	16.21§	1.09(NS)
Hours awake	0.00(NS)	3.26†	0.79(NS)
PVT (slowest 10% reaction time)			
Circadian phase	4.45(0.055)	6.11§	1.42(NS)
Hours awake	4.80*	3.96‡	1.19(NS)

Circadian phase degrees were 0, 60, 120, 180, 240, or 300; hours awake were 2, 4, 6, 8, 10, 12, 14, or 16. DSST, Digit Symbol Substitution Test; ADD, mathematical addition test; PRM, Probed Memory Recall; VAS, visual analog scale; PVT, Psychomotor Vigilance Task. *$P < 0.05$, †$P < 0.01$, ‡$P < 0.001$, §$P < 0.0001$. NS, not significant. Nos. in parenthesis represent trends ($P < 0.10$); df highest vs. lowest temperature performance 1,13; df time and df highest vs. lowest temperature performance × time: hours awake 7,91; circadian phase 5,65.

body temperature level was categorized as the highest body temperature performance and the performance battery associated with the 36.8°C temperature level was categorized as the lowest body temperature performance for that bin. However, there were often only two data points within each individual circadian/time-awake bin. This is the reason we selected a high vs. low and not a high-medium-low analysis structure.

High-low body temperature test categorizations were distributed evenly across the forced desynchrony protocol. Repeated-measures ANOVA with factors highest vs. lowest body temperature and time [circadian phase (degrees 0, 60, 120, 180, 240, 300) or hours awake (*hours 2, 4, 6, 8, 10, 12, 14, 16*)] were analyzed. Modified Bonferonni correction factors were used for determining significance of comparisons when there was a significant interaction effect. Partial correlation techniques were used to examine the relationship between body temperature level and raw performance scores for each individual subject using all the tests performed by that subject, while controlling for both circadian phase and hours awake.

RESULTS

Results for most neurobehavioral performance measures and for body temperature level showed significant main effects of factor time (Table 1). Performance levels were lowest near the body temperature minimum and decreased across scheduled wakefulness (Figs. 2–4). Furthermore, participants performed better when body temperature levels were highest at the same circadian and hours awake bin for cognitive throughput on the DSST (Fig. 3*A*), as evidenced by a significant main effect for the factor highest vs. lowest body temperature (Table 1). Addition performance tended to be better when body temperature was highest within a given circadian and hours awake bin (Table 1, Fig. 3*B*). Recall memory on the PRM task was better when body temperature was highest for the circadian component (Table 1). In addition, an interaction between factors highest vs. lowest body temperature and time revealed better recall memory within a

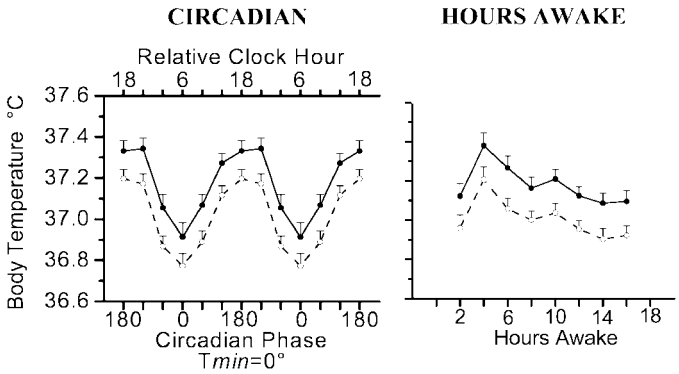

Fig. 2. Average high and low body temperature of 14 subjects across circadian phase (*left*; data double plotted) and hours awake (*right*). Error bars represent ±SE.

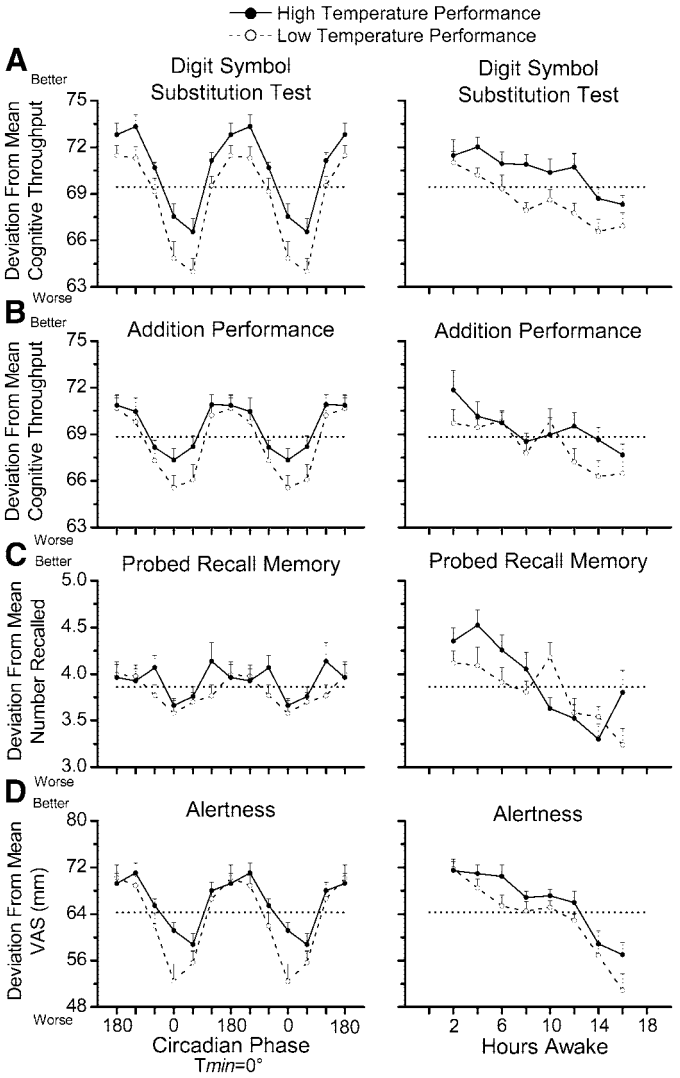

Fig. 3. Circadian phase-dependent (*left*; data double plotted) and hours awake-dependent variation (*right*) of cognitive throughput/working memory [Digit Symbol Substitution Test (*A*) and addition performance (*B*)], recall memory [Probed Recall Memory (*C*)], and subjective alertness (*D*) associated with high vs. low body temperature. Neurobehavioral data are expressed in deviation from individual subject's mean. Scores in the upward direction represent better performance. The group mean (n = 14) is added to the high-low deviation scores to indicate the amount of change in performance. Error bars represent ±SE. Dotted line represents the group mean. VAS, visual analog scale.

bin near the middle of scheduled wakefulness when body temperature was lowest (*hour awake 10*; P = 0.0234) and at the end of scheduled wakefulness (*hour awake 16*; P = 0.0212) when body temperature was highest (Fig. 3*C*, *right*). Across hours awake, alertness was rated higher when body temperature was high whereas a significant interaction between highest vs. lowest body temperature and time showed alertness to be higher at the phase of the body temperature minimum (circadian phase = 0°, P = 0.00002; Fig. 3*D*). The number of lapses in attention on the PVT was fewer when body temperature was highest within a given bin but only during the biological night (circadian phase = 300° and 0°, P = 0.0279 and P = 0.0026, respectively; Fig. 4*A*, *left*) as demonstrated by a significant interaction between factors highest vs. lowest body temperature and time (Table 1). Median reaction time and fastest 10% reaction time performance on the PVT did not significantly differ based on highest vs. lowest temperature. The large variability in performance for median reaction times during the circadian bin 60 degrees was due to poor performance in one individual at that time. However, an analysis of the slowest 10% reaction time showed a significant difference for highest vs. lowest body temperature for circadian phase and hours awake (Table 1; Fig. 4*D*).

Significant main effects for high-low temperature performance (Table 2) revealed that regardless of time

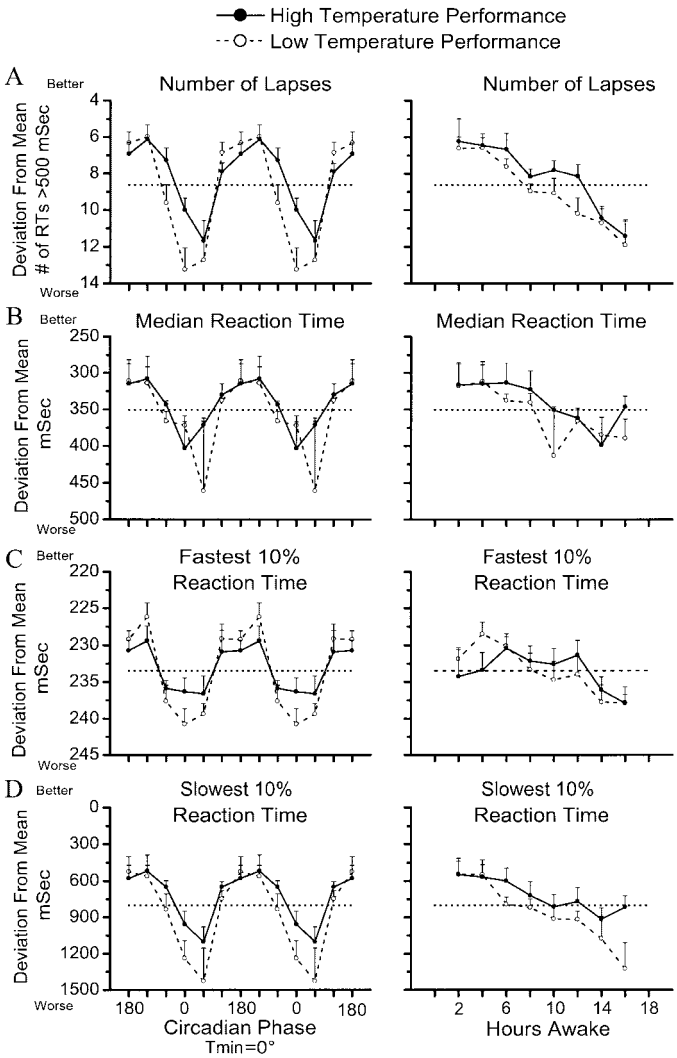

Fig. 4. Circadian phase-dependent (*left*; data double plotted) and hours awake-dependent variation (*right*) of Psychomotor Vigilance Task (PVT) performance associated with high vs. low body temperature [number of lapses (*A*), median reaction time (*B*), fastest 10% reaction time (*C*), and slowest 10% reaction time (*D*)]. Neurobehavioral data are expressed in deviation from individual subject's mean. Scores in the upward direction represent better performance. The group mean (n = 14) is added to the high-low deviation scores to indicate the amount of change in performance. Error bars represent ±SE. Dotted line represents the group mean. RT, reaction time.

Table 2. *Summary of results for individual subject partial correlation analysis (n = 14) between body temperature and neurobehavioral function while controlling for circadian phase and hours awake*

Neurobehavioral Measure	Number of Subjects With Significant Partial Correlations	Average ± SD Individual Subject Correlation
DSST (cognitive throughput)	10	0.27 ± 0.09
ADD (cognitive throughput)	10	0.21 ± 0.14
PRM (no. recalled)	1	0.07 ± 0.11
VAS (alertness)	9	0.29 ± 0.15
PVT (no. of lapses)	9	−0.25 ± 0.16
PVT (median reaction time)	10	−0.31 ± 0.20
PVT (fastest 10% reaction time)	10	−0.25 ± 0.18
PVT (slowest 10% reaction time)	9	−0.24 ± 0.13

awake or circadian phase, an increase in core body temperature of ~0.17°C was associated with an improvement in performance for working memory and cognitive throughput on the DSST of approximately two correct answers and on the ADD of approximately one correct answer; an improvement of recall memory performance of only 0.12 words recalled; an improvement in subjective alertness of approximately three points; and a speeding of the 10% slowest reaction time by ~150 ms.

We next calculated individual subject partial correlations between body temperature level and neurobehavioral function level using all available tests conducted during the forced desynchrony protocol [90.93 ± 4.45 (mean ± SD), range 80–94 tests per subject], while controlling for the factors circadian phase and hours awake. We recognize that circadian phase is a circular variable, and therefore we computed the partial correlations assigning circadian phase both negative and positive (negative 180 to positive 180 degrees) and only positive (0–360 degrees) phase assignments. We observed a negligible difference between the two analyses (mean correlation difference of 0.003 ± 0.026 and the number of significant individual subject partial correlations were very similar). Most participants showed significant relationships between body temperature level and neurobehavioral function level while partialing out the influence of circadian phase and hours awake (Table 2). With the exception of recall memory (PRM), higher body temperature was significantly associated with better performance and alertness. As body temperature increased, working memory improved (DSST, ADD), subjective alertness increased (VAS alertness), visual attention lapses decreased (PVT number of lapses), and reaction time quickened (PVT median reaction time, PVT fastest l0% reaction time, PVT slowest l0% reaction time).

DISCUSSION

Overall, the current results demonstrate that changes in body temperature are associated with changes in human performance even after controlling for the effects of circadian phase and hours awake. Cognitive performance on the DSST, a measure of working memory requiring matching symbols and numbers, was better when body temperature was higher at the same circadian phase and hours awake. Cognitive performance on a two-digit mathematical addition test, as well as the slowest 10% reaction time performance on a 10-min version of the PVT, tended to be better when body temperature was higher at the same circadian phase and hours awake. Although we observed a main effect for highest vs. lowest body temperature performance and no interaction with time, it appears that the slowest 10% reaction time performance is best only during the biological night. The number of lapses in attention was fewer when body temperature was higher but only during the biological night. Recall memory on a six-word pair version of the PRM task was better when body temperature was higher at the same circadian phase, but results for hours awake were mixed. The reason for the mixed results for the PRM task for the high-low temperature performance analysis is unclear, but the task may not be sensitive to differences in body temperature since this was the only performance task that was not better when temperature was higher as assessed with the partial correlation analysis. Subjective alertness on the VAS was higher when body temperature was higher across hours awake and during the biological night at the phase of the body temperature minimum. Median reaction time and the fastest 10% reaction time performance on the PVT were, however, not significantly different between high and low body temperature at any circadian phase or hours awake bin. In general, these results indicate that a higher body temperature within the normal circadian range is associated with better performance regardless of circadian phase or hours awake. However, with respect to highest vs. lowest body temperature performance across circadian phase for subjective alertness and lapses in attention, neurobehavioral function was better when body temperature was higher during the biological night but not the biological day.

In the current study, individual subject correlations between neurobehavioral performance and body temperature, while partialing out the influence of circadian phase and hours awake, also showed that most neurobehavioral functions were better when body temperature was high than when it was low. This result in individual subjects is consistent with previous work that did not control for circadian phase and hours awake (23, 24) and is also consistent with the highest vs. lowest group analysis of the current study.

The current result showing that body temperature was low during the biological night, increased near habitual wake time, and was high during the biological day is consistent with previous work showing that body temperature is strongly influenced by internal biological time (6, 14, 49). The hours awake component showed body temperature to be low near scheduled wake time with an evoked increase in body temperature likely due to the shower and a decrease in body temperature thereafter. As noted in the introduction,

the results from previous forced desynchrony studies indicated that neurobehavioral function decreased across the day as a function of hours awake and was worst during the biological night near the minimum of the body temperature rhythm (14, 18, 30, 54). The present results are consistent with these past findings. However, in these aforementioned studies and in our study, performance was not evaluated immediately on awakening from sleep; therefore, the reported pattern of decreased performance across the day does not include the influence of sleep inertia (impaired performance on awakening from sleep). Additional research is necessary to examine the influence of circadian phase and sleep inertia on human performance.

The current results for the highest vs. lowest body temperature performance are also consistent with results from studies in which performance was examined during and after extreme body cooling and heating (3, 23–26, 46, 48). For example, Giesbrecht and colleagues (26) immersed participants in cold water that was 8°C for 55–80 min until participants' body temperature was reduced from ~37.0 to 33.0–34.8°C, as measured in the esophagus at heart level. Compared with their performance before and immediately on immersion when body temperature was near normal, participants performed significantly worse on cognitive tasks such as backward digit span and the Stroop interference test. Little effect of the reduced body temperature was observed for auditory attention or visual recognition. In general, results from other studies using similar methodologies support the finding that tasks with a high cognitive load are most affected by extreme changes in body temperature (12, 48). The current study also found no effect of high vs. low body temperature on median reaction time and the fastest 10% reaction time performance. However, when the slowest 10% reaction times were analyzed, significant effects of high vs. low body temperature were observed. These vigilance/attention results suggest that even tasks with a small cognitive load are also sensitive to changes in body temperature when examined in greater detail, specifically when the slowest reaction times are examined.

In other related studies, body temperature was raised and changes in performance reported (1, 2, 24, 29, 48). Wilkinson and colleagues (48) raised subjects' body temperature from the normal temperature of ~37.0°C, up to 37.3–38.5°C, by exposing subjects to a hot 43°C humid climate. Auditory vigilance performance improved as body temperature rose, whereas addition performance improved when body temperature was increased to 37.3°C but worsened when body temperature was increased to 38.5°C. These results suggest that different types of brain function may have different zones of thermal sensitivity with respect to performance. In the current analysis of high-low body temperature performance, we found that a higher average body temperature of only ~0.15°C was associated with higher performance, suggesting that small changes in body temperature can influence human performance.

Reports from other areas of research provide evidence that altering body temperature level through pharmacological agents (melatonin, caffeine, modafinil) and bright light exposure also influenced neurobehavioral performance. For example, melatonin administration during the biological day decreased body temperature and reduced performance and alertness (20, 27, 35, 45). Exposure to bright light and/or the ingestion of caffeine increased nocturnal body temperature level and improved performance when examined under controlled constant-routine conditions (5, 22, 50, 51). While these pharmacological, physiological, and environmental stimuli are likely to affect performance via mechanisms other than body temperature (e.g., blocking of adenosine receptors by caffeine), the findings from the current study suggest that the change in body temperature that was associated with these stimuli may have contributed to the change in performance that was observed.

Although there are many factors that can influence body temperature, the mechanism underlying the variation in high vs. low body temperature at the same circadian phase/hours wake bin is unknown and requires further study. However, it is evident that the spontaneous high vs. low variations in body temperature at the same circadian phase and hours awake were not due to *1*) ambient temperature, because subjects were maintained in a comfortable constant temperature environment; *2*) ambient light exposure, because subjects were maintained in very dim light during scheduled wakefulness; *3*) changes in sleep-wakefulness state (28), because napping was proscribed and because performance and body temperature were assessed during wakefulness beginning 2 h after scheduled wake time; *4*) nutrition intake, because the timing of meals was regularly scheduled; and *5*) drug intake or exercise, because they were both proscribed.

Overall, our present findings demonstrate the relationship between body temperature and performance while controlling for circadian phase and hours awake; they indicate that within the normal circadian range of body temperature a higher body temperature represents physiological arousal that enhances human performance; and they provide strong support for Kleitman's hypothesis (32–34) that body temperature is an underlying mechanism modulating neurobehavioral performance. In other studies it has been reported that extreme body temperature heating or cooling resulted in impaired human performance. Whether body temperature and arousal influence performance independent of each other is unclear from the present data and requires further study. However, taken together, these results are consistent with an arousal hypothesis asserting that within an optimal thermal zone a higher body temperature will be associated with a higher performance in humans.

REFERENCES

1. **Allan JR and Gibson TM.** Separation of the effects of raised skin and core temperature on performance of a pursuit rotor task. *Aviat Space Environ Med* 50: 678–682, 1979.
2. **Allan JR, Gibson TM, and Green RG.** Effect of induced cyclic changes of deep body temperature on task performances. *Aviat Space Environ Med* 50: 585–589, 1979.
3. **Allnutt MF and Allan JR.** The effects of core temperature elevation and thermal sensation on performance. *Ergonomics* 16: 189–196, 1973.
4. **Åkerstedt T, Fröberg JE, Friberg Y, and Wetterberg L.** Melatonin excretion, body temperature, and subjective arousal during 64 hours of sleep deprivation. *Psychoneuroendocrinology* 4: 219–225, 1979.
5. **Badia P, Myers B, Boecker M, Culpepper J, and Harsh JR.** Bright light effects on body temperature, alertness, EEG and behavior. *Physiol Behav* 50: 583–588, 1991.
6. **Baker FC, Waner JI, Vieira F, Taylor SR, Driver HS, and Mitchell D.** Sleep and 24 hour body temperatures: a comparison in young men, naturally cycling women and women taking hormonal contraceptives. *J Physiol* 530: 565–574, 2001.
7. **Brown EN and Czeisler CA.** The statistical analysis of circadian phase and amplitude in constant-routine core-temperature data. *J Biol Rhythms* 7: 177–202, 1992.
8. **Cagnacci A, Soldani R, and Yen SSC.** Hypothermic effect of melatonin and nocturnal core body temperature decline are reduced in aged women. *J Appl Physiol* 78: 314–317, 1995.
9. **Cajochen C, Khalsa SBS, Wyatt JK, Czeisler CA, and Dijk DJ.** EEG and ocular correlates of circadian melatonin phase and human performance decrements during sleep loss. *Am J Physiol Regul Integr Comp Physiol* 277: R640–R649, 1999.
10. **Campbell SS.** Effects of timed bright-light exposure on shift-work adaptation in middle-aged subjects. *Sleep* 18: 408–416, 1995.
11. **Carrier J, Monk TH, Buysse DJ, and Kupfer D.** Amplitude reduction of the circadian temperature and sleep rhythms in the elderly. *Chronobiol Int* 13: 373–386, 1996.
12. **Coleshaw SRK, Van Someren RNW, Wolff AH, Davis HM, and Keatinge WR.** Impaired memory registration and speed of reasoning caused by low body temperature. *J Appl Physiol* 55: 27–31, 1983.
13. **Colquhoun WP and Folkard S.** Scheduling watches at sea. In: *Hours of Work: Temporal Factors in Work-Scheduling*, edited by Folkard S and Monk TH. New York: Wiley, 1985, 253–261.
14. **Czeisler CA, Dijk DJ, and Duffy JF.** Entrained phase of the circadian pacemaker serves to stabilize alertness and performance throughout the habitual waking day. In: *Sleep Onset: Normal and Abnormal Processes*, edited by Ogilvie RD and Harsh HR. Washington, DC: American Psychological Assoc., 1994, 89–110.
15. **Czeisler CA, Duffy JF, Shanahan TL, Brown EN, Mitchell JF, Rimmer DW, Ronda JM, Silva EJ, Allan JS, Emens JS, Dijk DJ, and Kronauer RE.** Stability, precision, and near-24-hour period of the human circadian pacemaker. *Science* 284: 2177–2181, 1999.
16. **Czeisler CA, Dumont M, Duffy JF, Steinberg JD, Richardson GS, Brown EN, Sánchez R, Ríos, CD, and Ronda JM.** Association of sleep-wake habits in older people with changes in output of circadian pacemaker. *Lancet* 340: 933–936, 1992.
17. **Czeisler CA, Johnson MP, Duffy JF, Brown EN, Ronda JM, and Kronauer RE.** Exposure to bright light and darkness to treat physiologic maladaptation to night work. *N Engl J Med* 322: 1253–1259, 1990.
18. **Dijk DJ, Duffy JF, and Czeisler CA.** Circadian and sleep/wake dependent aspects of subjective alertness and cognitive performance. *J Sleep Res* 1: 112–117, 1992.
19. **Dinges DF, Pack F, Williams K, Gillen KA, Powell JW, Ott GE, Aptowicz C, and Pack AI.** Cumulative sleepiness, mood disturbance, and psychomotor vigilance performance decrements during a week of sleep restricted to 4–5 hours per night. *Sleep* 20: 267–277, 1997.
20. **Dollins AB, Zhdanova IV, Wurtman RJ, Lynch HJ, and Deng MH.** Effect of inducing nocturnal serum melatonin concentrations in daytime on sleep, mood, body temperature, and performance. *Proc Natl Acad Sci USA* 91: 1824–1828, 1994.
21. **Duffy JF, Zeitzer JM, Rimmer DW, Klerman EB, Dijk DJ, and Czeisler CA.** Peak of circadian melatonin rhythm occurs later within the sleep of older subjects. *Am J Physiol Endocrinol Metab* 282: E297–E303, 2002.
22. **Foret J, Daurat A, and Tirilly G.** Effect of bright light at night on core temperature, subjective alertness and performance as a function of exposure time. *Scand J Work Environ Health* 24: 115–120, 1999.
23. **Fort A, Gabbay JA, Jackett R, Jones MC, Jones SM, and Mills JN.** The relationship between deep body temperature and performance on psychometric tests. *J Physiol* 219: 17P–18P, 1971.
24. **Fort A, Harrison MT, and Mills JN.** Psychometric performance: circadian rhythms and effect of raising body temperature. *J Physiol* 231: 114P–115P, 1973.
25. **Giesbrecht GG.** Cold stress, near drowning and accidental hypothermia: a review. *Aviat Space Environ Med* 71: 733–752, 2000.
26. **Giesbrecht GG, Arnett JL, Vela E, and Bristow GK.** Effect of task complexity on mental performance during immersion hypothermia. *Aviat Space Environ Med* 64: 206–211, 1993.
27. **Gilbert SS, van den Heuvel CJ, and Dawson D.** Daytime melatonin and temazepam in young adult humans: equivalent effects on sleep latency and body temperatures. *J Physiol* 514: 905–914, 1999.
28. **Glotzbach SF, and Heller HC.** Thermoregulation. In: *Principles and Practice of Sleep Medicine*, edited by Kryger MH. Philadelphia, PA: Saunders, 1989, p. 300–309.
29. **Holland RL, Sayer JA, Keatinge WR, Davis HM, and Peswani R.** Effects of raised body temperature on reasoning, memory, and mood. *J Appl Physiol* 59: 1823–1827, 1985.
30. **Hull JT, Wright KP Jr, and Czeisler CA.** Variation in self-rating of performance and motivation to perform during a 28-hr forced desynchrony protocol. *Sleep* 23, *Suppl* 2: A191–A192, 2000.
31. **Johnson MP, Duffy JF, Dijk DJ, Ronda JM, Dyal CM, and Czeisler CA.** Short-term memory, alertness and performance: a reappraisal of their relationship to body temperature. *J Sleep Res* 1: 24–29, 1992.
32. **Kleitman N.** *Sleep and Wakefulness*. Chicago, IL: Univ. of Chicago Press, 1963.
33. **Kleitman N and Jackson DP.** Body temperature and performance under different routines. *J Appl Physiol* 3: 309–328, 1950.
34. **Kleitman N, Titelbaum S, and Feiveson P.** The effect of body temperature on reaction time. *Am J Physiol* 121: 495–501, 1938.
35. **Kräuchi K, Cajochen C, and Wirz-Justice A.** A relationship between heat loss and sleepiness: effects of postural change and melatonin administration. *J Appl Physiol* 83: 134–139, 1997.
36. **Kräuchi K and Wirz-Justice A.** Circadian rhythm of heat production, heart rate, and skin and core temperature under unmasking conditions in men. *Am J Physiol Regul Integr Comp Physiol* 267: R819–R829, 1994.
37. **Landolt HP, Moser S, Wieser HG, Borbély AA, and Dijk DJ.** Intracranial temperature across 24-hour sleep-wake cycles in humans. *Neuroreport* 6: 913–917, 1995.
38. **Lavie P.** The search for cycles in mental performance from Lombard to Kleitman. *Chronobiologia* 7: 247–256, 1980.
39. **Masino SA and Dunwiddie TV.** Temperature-dependent modulation of excitatory transmission in hippocampal slices is mediated by extracellular adenosine. *J Neurosci* 19: 1932–1939, 1999.
40. **Masino SA and Dunwiddie TV.** A transient increase in temperature induces persistent potentiation of synaptic transmission in rat hippocampal slices. *Neuroscience* 101: 907–912, 2000.
41. **Monk TH, Buysse DJ, Reynolds CF III, Berga SL, Jarrett DB, Begley AE, and Kupfer DJ.** Circadian rhythms in human performance and mood under constant conditions. *J Sleep Res* 6: 9–18, 1997.
42. **Monk TH and Carrier J.** A parallelism between human body temperature and performance independent of the endogenous circadian pacemaker. *J Biol Rhythms* 19: 113–122, 1998.

43. **Moore-Ede MC.** Physiology of the circadian timing system: predictive versus reactive homeostasis. *Am J Physiol Regul Integr Comp Physiol* 250: R735–R752, 1986.
44. **Refinetti R.** Homeostasis and circadian rhythmicity in the control of body temperature. *Ann NY Acad Sci* 813: 63–70, 1997.
45. **Rogers NL, Phan O, Kennaway DJ, and Dawson D.** Effect of daytime oral melatonin administration on neurobehavioral performance in humans. *J Pineal Res* 25: 47–53, 1998.
46. **Vaughan JA, Higgins EA, and Funkhouser GE.** Effects of body thermal state on manual performance. *Aerospace Med* 39: 1310–1315, 1968.
47. **Volgushev M, Vidyasagar TR, Chistiakova M, and Eysel UT.** Synaptic transmission in the neocortex during reversible cooling. *Neuroscience* 98: 9–22, 2000.
48. **Wilkinson RT, Fox RH, Goldsmith R, Hampton IFG, and Lewis HE.** Psychological and physiological responses to raised body temperature. *J Appl Physiol* 19: 287–291, 1964.
49. **Wright KP Jr and Badia P.** Effects of menstrual cycle phase and oral contraceptives on alertness, cognitive performance, and circadian rhythms during sleep deprivation. *Behav Brain Res* 103: 185–194, 1999.
50. **Wright KP Jr, Badia P, Myers BL, and Plenzler SC.** Combination of bright light and caffeine as a countermeasure for impaired alertness and performance during extended sleep deprivation. *J Sleep Res* 6: 26–35, 1997.
51. **Wright KP Jr, Badia P, Myers BL, Plenzler SC, and Hakel M.** Caffeine and light effects on nighttime melatonin and temperature levels in sleep-deprived humans. *Brain Res* 747: 78–84, 1997.
52. **Wright KP Jr, Badia P, Plenzler SC, Myers BL, and Drake CL.** Melatonin versus temperature as correlates of nighttime vigilance performance in humans. *Sleep* 21: 251, 1998.
53. **Wright KP Jr, Hughes RJ, Kronauer RE, Dijk DJ, and Czeisler CA.** Intrinsic near-24-hour pacemaker period determines limits of circadian entrainment to a weak synchronizer in humans. *Proc Natl Acad Sci USA* 98: 14027–14032, 2001.
54. **Wyatt JK, Ritz-De Cecco A, Czeisler CA, and Dijk DJ.** Circadian temperature and melatonin rhythms, sleep, and neurobehavioral function in humans living on a 20-h day. *Am J Physiol Regul Integr Comp Physiol* 277: R1152–R1163, 1999.