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THE EFFECTS OF AMBIENT TEMPERATURE AND LIGHTING INTENSITY ON WHEEL-RUNNING BEHAVIOR IN A DIURNAL RODENT, THE NILE GRASS RAT (*ARVICANTHIS NILOTICUS*)

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Abbreviations: LD: light-dark; ZT: Zeitgeber time; SAD: Seasonal Affective Disorder; C: Celsius; MAD: Median Absolute Deviation; SEM: Standard Error of the Mean; DD: Constant Darkness; HDL: Heat Dissipation Limit

ABSTRACT

Environmental conditions, such as the light-dark cycle and temperature, affect the display of circadian rhythmicity and locomotor activity patterns in mammals. Here, we tested the hypothesis that manipulating these environmental conditions would affect wheel-running activity patterns in a diurnal rodent, the Nile grass rat (*Arvicanthis niloticus*). Whereas grass rats are diurnal in the field, a subset switch from a day-active to a night-active pattern of activity after the introduction of a running wheel. The mechanism of this chronotype switch remains largely unknown. In the present study, grass rats were presented with running wheels in 12:12 light-dark (LD) conditions. First, subjects were exposed to 25 degrees C during the day and 21 degrees C at night, which resulted in 100% of grass rats expressing diurnal behavior. Subjects were then exposed to manipulations of elevated ambient temperature, which resulted in a significant reduction in wheel-running activity. Reducing ambient temperature below 21 degrees C, however, did not disrupt the expression of diurnality or overall activity. Next, lighting intensity was reduced, which resulted in a switch from a diurnal to a nocturnal chronotype in a subset of animals and reduced overall wheel-running activity. Upon return to baseline lighting intensity, patterns of diurnal activity were restored. Altogether, increases in ambient temperature and decreases in lighting intensity significantly reduced overall wheel-running activity. Importantly, dim light resulted in a temporal niche switch in a subset of grass rats, suggesting a critical role for lighting intensity on the expression of wheel-running activity patterns.

INTRODUCTION

Environmental conditions influence physiology and behavior in mammals. In most regions on Earth, the cycle of a day brings about the rise and fall of the sun, generating predictable changes in lighting intensity and ambient temperature in nature. Importantly, environmental fluctuations, such as temperature and light, influence the display of circadian rhythms in physiology and behavior in organisms ranging from bacteria to mammals (Reilly, 1990; Pittendrigh, 1993). Light and temperature are important entraining stimuli (i.e., Zeitgebers) for diurnal animals, those that are active during the day (Vivanco, Rol, & Madrid, 2010), and also for nocturnal animals, those that are active at night (Refinetti, 2010).

The timing and intensity of light are powerful entraining stimuli, evoking behavioral and chronotype changes in mammals. Seasonal changes in behavior are significantly affected by changes in lighting intensity (Heldmaier, Steinlechner, Rafael, & Latteier, 1982). In humans, the lack of light in the winter months can induce seasonal affective disorder (SAD), which results in episodes of depression (Saeed & Bruce, 1998). In cases of SAD, light intensity treatments have been shown to reduce symptoms, suggesting that increased amounts of light can have a positive effect on behavior (Terman et al., 1989; Wakamura & Tokura, 2001). Likewise, light intensity affects the entrainment of biological rhythms, further emphasizing the role light intensity plays in behavior (Wever, Polasek, & Wildgruber, 1983). The effects of light intensity on behavior also extend to diurnal rodent models. Daytime dim light increases anxiety, evokes physiological changes, and results in depression-like behavior in the diurnal Nile grass rat (Ikeno, Deats, Soler, Lonstein, & Yan, 2016; Leach, Adidharma, & Yan, 2013). In addition, lighting intensity has been shown to affect temporal niche switching in some species (Chiesa, Aguzzi, Garcia, Sarda, & de la Iglesia, 2010; Kempinger, Dittman, Rieger, & Helfrich-Forster, 2009; Cohen, Smale, &

Kronfeld-Schor, 2010; Mrosovsky & Hattar, 2005; Doyle, Yoshikawa, Hillsosn, & Menaker, 2008), and may also affect the timing of the display of activity in grass rats, a hypothesis we tested here.

In addition to lighting intensity, the ambient temperature of an environment also affects behavior in mammals. Organisms use external temperature as an environmental cue, useful for entraining biological and behavioral rhythms (Pittendrigh, 1960; Pittendrigh, 1993). Behavioral responses to temperature changes are an adaptive feature exhibited by some organisms, reinforcing the plasticity of behavior in accordance to the environment (Kjaersgaard et al., 2015; Refinetti, 2010). Specifically, elevated ambient temperatures have been shown to decrease physical activity levels in many species (Clarkson & Ferguson, 1972; Pereboom, 1968; Stevenson & Rixon, 1957). Furthermore, rodents have been shown to exhibit a great deal of plasticity in their behavioral chronotype when presented with temperature fluctuations. Changes in ambient temperature switch the activity patterns of nocturnal mice to diurnal patterns (van der Vinne et al., 2014). A similar observation can be seen with diurnal Octodon degus exhibiting nocturnal patterns in altered temperature environments (Vivanco et al., 2010). Ambient temperature is therefore capable of affecting behavior in significant ways, including eliciting dramatic behavioral shifts such as changes in the expression of circadian rhythms.

The use of the diurnal rodent, the Nile grass rat (*Arvicanthis nilocticus*), provides a unique opportunity to observe a normally diurnal species that can become nocturnal under certain conditions. Grass rats are rodents indigenous to the continent of Africa where they display a diurnal activity pattern in the field (Blanchong & Smale, 2000). Under normal laboratory conditions, Nile grass rats continue to display a diurnal phenotype (Blanchong et al.,

1999). However, when a running wheel is introduced to the lab environment, some grass rats switch phenotypes and become nocturnal (Blanchong, McElhinny, Mahoney, & Smale, 1999; Schwartz & Smale, 2005).

The current study was performed to test the hypothesis that environmental conditions such as ambient temperature and light intensity would affect phase preference of Nile grass rats. To this end, we manipulated the ambient temperature and lighting intensity, while recording wheel-running activity patterns in Nile grass rats. Our results suggest that while ambient temperature contributes to overall activity levels, lighting intensity contributes to phase preference. Altogether, this study assesses the effects of environmental changes on behavior in a diurnal species.

MATERIALS AND METHODS

All experiments were carried out in accordance with the National Institutes of Health Guide for the Care and Use of Laboratory Animals (NIH Publication No. 80-23) and were approved by the Institutional Animal Care and Use Committee of Hope College. All efforts were made to minimize the number of animals used.

Subjects

A total of 18 adult Nile grass rats ($n = 9$ males; $n = 9$ females; *Arvicanthis niloticus*) were obtained from a breeding colony at Hope College. All animals were singly housed in Plexiglas cages (34 x 28 x 17 cm). Animals were provided with food (PMI Nutrition Prolab RMH 2000, Brentwood, MO) and water ad libitum.

Experimental Procedures

In order to measure activity patterns, running wheels (4.5" diameter, Vital View, STARR Life Sciences Company, Oakmont, PA) were placed in cages at the beginning of the experiment and remained in the cages for the duration of the study. The running wheels were connected to a computer located in an adjacent room. Total wheel revolutions were collected in 1-min bins using VitalView 1.2 software (Oakmont, PA) for 24 hours a day for the duration of the study. In all conditions of the experiment (with the exception of constant darkness), grass rats were exposed to 12 hours of light and 12 hours of darkness (LD), with lights on at 0700h, Zeitgeber time (ZT) 0, and lights off at 1900h (ZT12). Two sets of fluorescent lights (Lights of America, Model #7020 E, Walnut, CA) were placed 2 inches above each cage. The lighting intensity was 1,000 lux during the day, and <5 lux at night during LD. These fluorescent lights produced heat, so the baseline condition resulted in animals being housed at 25 degrees C during the lights-on period, and 21 degrees C during the lights-off period. Animals remained in this baseline condition for 3 weeks. Directly following baseline, subjects were exposed to a series of temperature manipulations. Animals remained in each of the following conditions for 7 days: constant 28 degrees C, constant 32 degrees C, constant 18 degrees C, and constant 15 degrees C. A quartz infrared heater (Life Pro 6, Model #PCHT1012US, Plano, TX) was placed in the room to raise the ambient temperature and an air conditioner (Soleus Air, Model #LX-140, City of Industry, CA) was placed in the room to lower the ambient temperature. Following this series, the ambient temperature was held constant at 25 degrees C and the lighting intensity was reduced (50 lux) during the subjective day. Animals remained in this condition for 7 days. Next, subjects

were exposed to baseline lighting conditions (1,000 lux) during the subjective day of 12:12 LD for 7 days to re-entrain them, followed by constant darkness (DD) for 14 days. Finally, lighting intensity in 12:12 LD was increased back to baseline levels for 14 days.

A summary of environmental conditions used in the experiment is presented in Table 1. The temperature of the room was monitored every 15 minutes using a USB temperature data logger recorder with external sensor (RC-4, Elitech, London, U.K.). The temperature in the room remained within two degrees of the target temperature conditions when a heater or air conditioner was placed in the room.

Analyses

The mean total number of wheel revolutions per subject per hour for each condition (baseline, 28 degrees C, 32 degrees C, 18 degrees C, 15 degrees C, dim light, and return to baseline) was calculated using Microsoft Excel and imported into IBM SPSS Desktop 23.0. For each condition, we calculated the percentage of activity during the light phase by dividing activity during the light phase by total activity and multiplying by 100 (hereafter referred to as diurnal/total activity percentage). This percentage was compared for each condition to the baseline condition. Animals were considered diurnal if the diurnal/total activity percentage was >50%. A repeated measures one-way ANOVA was first used to test for within-subjects differences between conditions. For all data that were normally distributed, a series of paired samples t-tests were performed to compare each condition to the baseline condition within subjects. Normally distributed data are presented as means +/- the standard error of the mean (SEM), and effect size is reported by calculating Cohen's *d*. A Bonferroni correction was used

to adjust to multiple comparisons. We had 6 pre-planned comparisons (e.g., baseline as compared to 28 degrees C, 32 degrees C, 18 degrees C, 15 degrees C, dim light, and return to baseline). For these comparisons, alpha was considered significant if $p < .0083$ (.05 / 6 = .0083). Since some conditions, most notably the dim light condition, resulted in a bimodal distribution that was not normal according to the Shapiro-Wilk test of normality, medians +/- median absolute deviation (MADs) along with effect size r are reported. The Wilcoxon signed-rank test was used to test for differences between conditions that resulted in activity that was not normally distributed. Finally, alpha and period were analyzed in constant darkness. Alpha was calculated by analyzing the onset of the early morning bout to the offset of the evening bout of activity. Onset and offset, along with period, were determined using ActogramJ (Schmid, Helfrich-Forster, & Yoshii, 2011) along with visual inspection of actograms.

RESULTS

The mean wheel revolutions per 24-hour period per subject for each experimental condition were analyzed in comparison to the baseline condition using a paired samples t-test (Fig. 1). A repeated measures one-way ANOVA revealed a significant effect on mean wheel revolutions between conditions ($F(5,85) = 11.358, p < .001$). As shown in Fig. 1a, the condition of constant 28 degrees C heat resulted in a non-significant difference in mean wheel revolutions compared to baseline ($t(17) = 2.277, p = .036, d = 0.611$). Constant heat of 32 degrees C resulted in a statistically significant decrease in mean wheel revolutions ($t(17) = 6.263, p < .001, d = 1.493$) compared to baseline. The comparisons between the 18 C degrees ($t(17) = 1.419, p = .174, d = 0.350$) and 15 C degrees ($t(17) = 1.175, p = .256, d = 0.277$) mean wheel revolutions

and baseline means were not statistically significant. Importantly, as shown in Fig. 1b, the dim light condition resulted in a statistically significant decrease in wheel revolutions (z = -3.201, p = .001, r = -.76). Finally, also as shown in Fig. 1b, the return to baseline conditions did not result a significant difference from baseline ($t(17)$ = 1.571, p =.135, d = 0.37).

Fig. 2a presents the distribution of wheel revolutions per hour in the baseline and 28 degrees C condition, which did not result in a significant change in activity as compared to baseline. Fig. 2b presents the distribution of wheel revolutions per hour in the baseline and 32 degrees C condition, which shows a further significant suppression of activity in 32 degrees C condition compared to baseline. The significant drop in wheel revolutions in dim light can be seen in Fig. 2c. Importantly, the return to baseline lighting conditions restored wheel revolutions, to result in a non-significant difference as compared to the original baseline lighting conditions.

Diurnal activity patterns were analyzed using the calculated diurnal/total activity percentage (Fig. 3). A repeated measures one-way ANOVA revealed a significant effect on diurnal/total activity percentage between conditions ($F(5,85)$ = 17.023, p < .001). Using a paired samples t-test, each experimental condition of temperature manipulation was compared to the baseline condition (Fig. 3a). The constant heat of 32 degrees C resulted in a significant decrease in percentage of activity during the light phase from baseline ($t(17)$ = 3.548, p = .002, d = 1.011). In comparison to baseline, the 28 degrees C ($t(17)$ = .650, p = .524, d = .153), 18 degrees C ($t(17)$ = -1.116, p =.280, d = -.268), and 15 degrees C ($t(17)$ = -.697, p = .495, d = -.168) conditions did not result in a statistically significant difference in percentage of activity during the light phase. Importantly, the dim light condition resulted in a statistically significant decrease in percentage of activity during the light phase from baseline (Fig. 3b; z = -3.245, p = .001, r = .76). Finally,

the return to baseline conditions did not result in significant difference from baseline (Fig. 3b; z = -1.807, p = .071, r = .32).

Analysis of the actograms of individual subjects showed variance in activity patterns, specifically in the dim light condition. Most subjects (n = 11) showed a reduction in wheel-running activity in the dim light condition but remained diurnal. However, seven individuals (n = 7) displayed a clear nocturnal pattern of activity in the dim light condition in addition to reducing their overall wheel-running activity. Fig. 4a shows the actogram of a diurnal subject that remained diurnal in all conditions of the experiment, while Fig. 4b presents the actogram of a subject that switched from a diurnal to nocturnal chronotype in dim light conditions. In contrast, in 32 degrees C, all animals remained diurnal, as defined by >50% of their wheel-running activity occurring during lights-on. The reduction in wheel-running activity expressed during lights-on in animals in 32 degrees C was much smaller than the reduction seen in dim light, with no animals completely switching chronotypes. Importantly, although animals were more likely to become night-active in dim light, when the animals were placed in constant darkness (DD), period (mean: 23.76 +/- 0.05) and alpha (mean: 13.27 +/- 0.61) were very similar to what has been reported previously for grass rats (Gall, Smale, Yan, & Nunez, 2013). Altogether, a fundamental difference in wheel-running activity was observed in dim light as compared to baseline conditions.

DISCUSSION

The present study was performed to evaluate the impact of environmental factors on wheel-running behavior in a diurnal rodent model. We found that experimental manipulations to

both ambient temperature and lighting intensity resulted in behavioral changes in wheel-running activity in grass rats. Specifically, increasing ambient temperature resulted in a significant decrease in the total amount of wheel-running activity, while reducing the intensity of the lights resulted in a significant decrease in the total amount of wheel-running activity, but also induced temporal niche switching in a subset of grass rats. These findings provide evidence that ambient temperature and lighting intensity affect the plasticity of wheel-running behavior in the Nile grass rat in different and important ways.

In Nile grass rats, the elevation of ambient temperature resulted in a reduction in wheel-running activity levels. The warmer 32 degrees C condition had a greater inhibitory effect on wheel-running activity than the 28 degrees C condition. This effect of high ambient temperatures lowering wheel-running activity levels has previously been observed in nocturnal and diurnal rodents (Clarkson & Ferguson, 1972; Pereboom, 1968; Finger, 1976; Stevenson & Rixon, 1957). According to the heat dissipation limit (HDL) hypothesis, endotherms are predicted to reduce energy expenditure when ambient temperatures are high (Speakman & Krol, 2010). Therefore, this hypothesis predicts that endotherms will avoid hyperthermia by significantly reducing activity and energy expenditure in increased ambient temperatures. Our results provide evidence in support of the HDL hypothesis, suggesting that reduced wheel-running activity is a result of a decreased need for thermoregulation due to elevated ambient temperature.

Temperature also had an effect on the expression of wheel-running activity during the lights-on phase, but only when placing animals in the warmest condition. The escalation of ambient temperature to 32 degrees C yielded a significant reduction in the percentage of wheel-running revolutions during the day compared to baseline. Importantly, the percentage of activity

during the lights on phase only reduced by about 5% in the warm conditions, and no animals became night-active. Therefore, heat affected the expression of activity during lights-on, but only modestly. In contrast, a slight elevation of ambient temperature (28 degrees C) and a reduction in ambient temperatures (18 and 15 degrees C) did not affect the expression of wheel-running activity during the lights-on phase. Temperature has been shown to have an effect on the expression of circadian rhythms in other rodent models (Vivanco et al., 2010; van der Vinne et al., 2014). Our data suggest that temperature can slightly modify the distribution of wheel-running activity patterns in a diurnal species, the Nile grass rat.

In the present study, the reduction of lighting intensity during the light phase (50 lux) significantly decreased the percentage of diurnal activity. The shift to dim light during the light phase also reduced overall wheel-running activity. A similar result is observed when Nile grass rats are placed in constant darkness conditions (Gall, Shuboni, Yan, Nunez, & Smale, 2016). These observations suggest that behavior is significantly affected by lighting intensity. Critically, here we found that not only were diurnal activity patterns disrupted in dim light, but a subset of grass rats switched chronotypes completely from diurnal to nocturnal. Importantly, changes in environmental conditions have been shown to result in chronotype switches in other rodent species that are also diurnal in the field, such as tuco-tucos (Tachinardi et al, Tøien, Valentinuzzi, Buck, & Oda, 2015). Taken together, this evidence suggests that the intensity of light has a significant impact on the chronotype an organism adopts.

Importantly, when grass rats were placed back in bright light conditions at the end of the experiment, diurnality was restored, and overall activity levels approached the original baseline conditions. Although we did not obtain a significant difference between the original baseline

condition and the final return to baseline conditions, the overall activity levels did not reach as high as they did initially. We hypothesize that this is due to the repeated-measures design. This type of design has several advantages; we are able to examine how activity patterns within each individual changed over time, and it is more powerful to see how individual animals switch in response to manipulations of environmental conditions. However, the temperature changes that occurred before placing the animals in the final lighting conditions likely affected the behavior of the animals. Even so, the animals returned back to baseline activity levels and diurnal patterns in bright light, suggesting that lighting intensity plays an important role in the expression of wheel-running activity patterns and levels.

Running wheel activity in rodents gives insight to more aspects of behavior than just general activity alone. The practice of running on a wheel activates reward pathways and can be addicting for many species of rats and mice (Novak, Burghardt, & Levine, 2012), including the Nile grass rat (Castillo-Ruiz, Nixon, Smale, & Nunez, 2010). Wheel-running behavior can be used as a measure of reward-seeking behavior, in addition to physical activity (Brené et al., 2007; Morris, Na, & Johnson, 2012). The presentation of dim light has been shown to decrease reward-seeking behavior in Nile grass rats (Ikeno et al., 2016; Leach et al., 2013). Dim light in the present study resulted in an overall decrease in wheel running activity and an alteration of wheel running patterns. The effect of dim light on wheel-running patterns suggests a possible relationship between lighting intensity, reward-seeking behavior, and chronotype.

We have shown that environmental variables involved in entraining circadian rhythms (ambient temperature, light intensity) were shown to have effects on wheel-running activity in the Nile grass rat. Elevation of ambient temperature resulted in decreased wheel-running activity

and weaker diurnal chronotypes. The introduction of cold temperatures did not affect the expression of diurnal behavior or promote nocturnal activity. Additionally, dim light during the lights-on phase significantly reduced wheel-running activity and promoted nocturnal activity patterns in a subset of grass rats. These changes observed in wheel-running behavior suggest that environmental variables significantly affect the expression of activity patterns in a diurnal animal model.

COMPLIANCE WITH ETHICAL STANDARDS

All experiments were carried out in accordance with the National Institutes of Health Guide for the Care and Use of Laboratory Animals (NIH Publication No. 80-23) and were approved by the Institutional Animal Care and Use Committee of Hope College.

DECLARATION OF INTEREST

The authors report no conflicts of interest.

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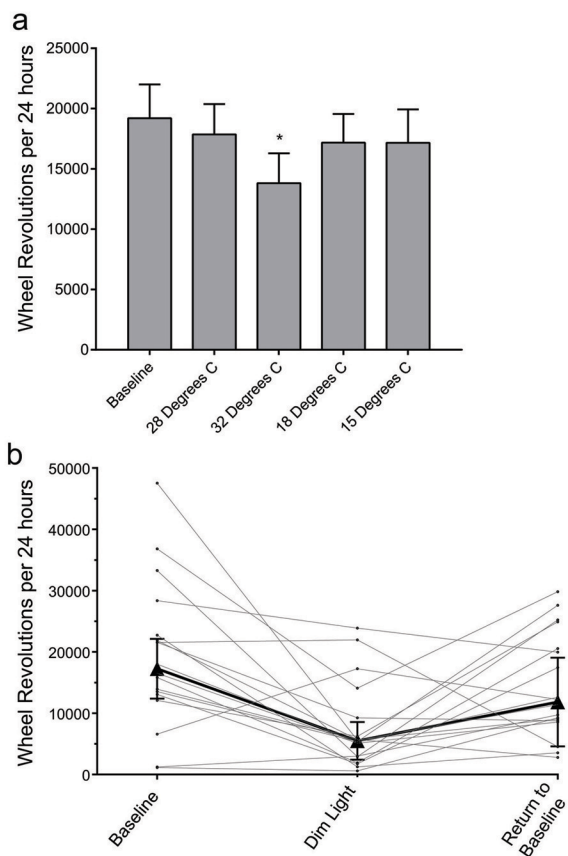
Fig. 1 Wheel revolutions for temperature and lighting conditions compared to baseline. (a) Mean wheel revolutions per subject per 24-hour period for baseline conditions, 28, 32, 18, and 15 degrees C are presented. Means are presented with SEMs. Significant results compared to baseline are represented by * ($p < .01$). (b) Mean wheel revolution counts per 24 hours for each subject are presented for the baseline, dim light, and return to baseline conditions. Due to a non-normal distribution of the means, bold triangles represent the medians $\pm$ MADs of all subjects.
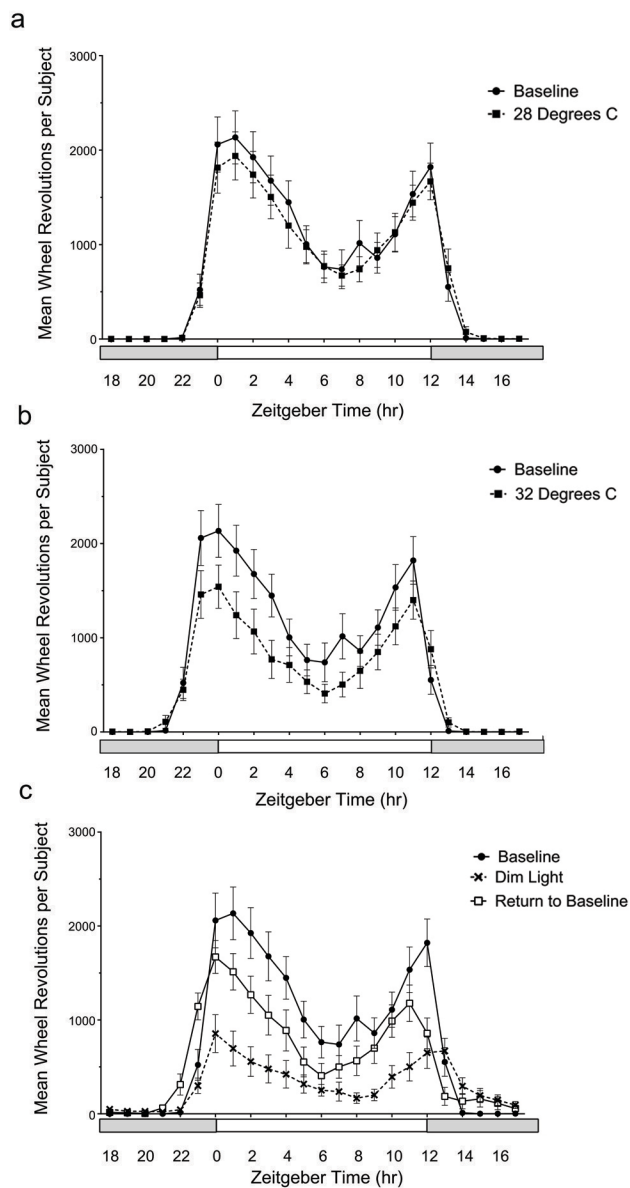
Fig. 2 Quantitative analyses of wheel running behavior. Mean wheel revolutions per subject per hour are presented comparing the baseline condition to constant 28 degrees C (a), constant 32 degrees C (b), dim light and return to baseline lighting conditions (c). Means are presented with SEMs. Gray bars indicate lights off; white bar indicates lights on.
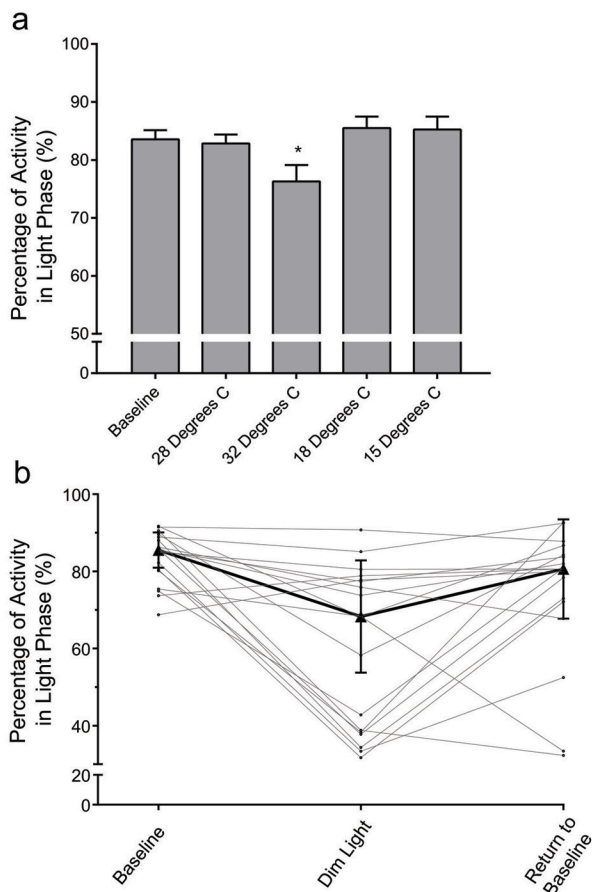
Fig. 3 Percentage of wheel running activity in light phase for temperature and lighting conditions compared to baseline. (a) Mean percentages of wheel revolutions in the light phase of a 12:12 LD period for baseline conditions, 28, 32, 18, and 15 degrees C are presented. Means are presented along with SEMs. Significant results compared to baseline are represented by * ($p <$ .01). (b) Mean percentages of light phase activity for each subject are presented for baseline and dim light conditions. Due to a non-normal distribution of the means in the dim light condition, bold triangles represent the medians ± MADs of all subjects.
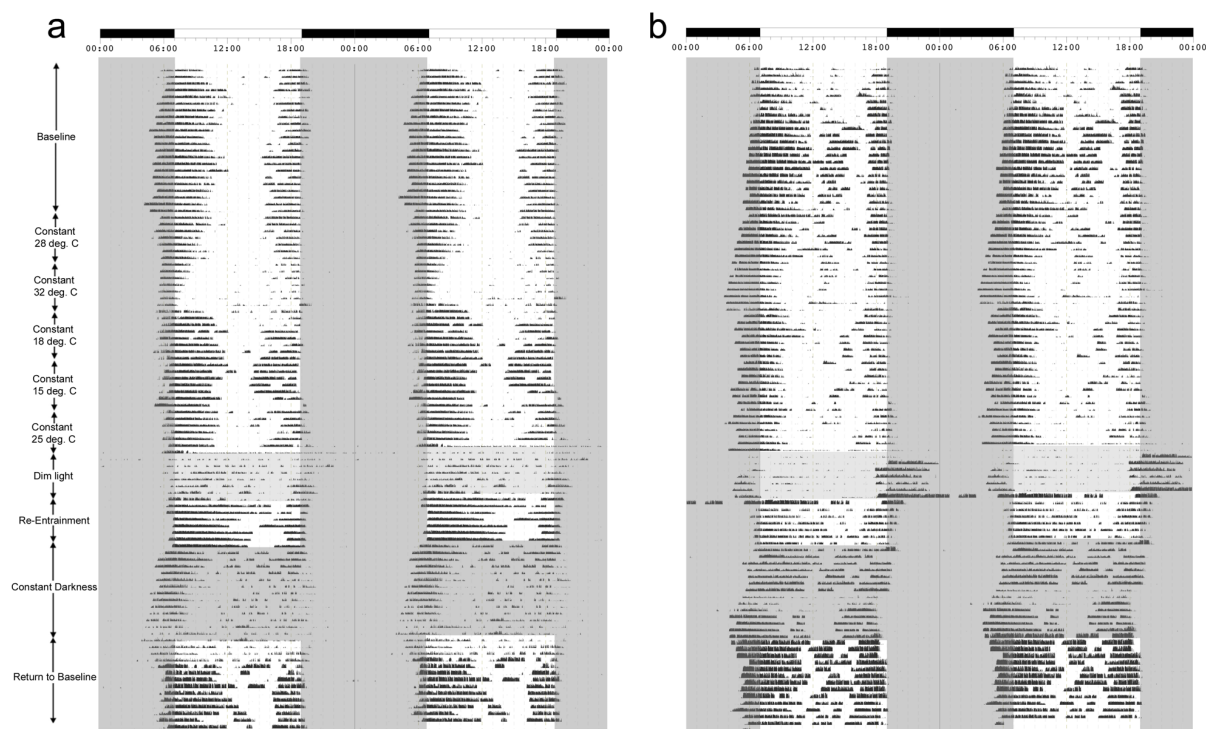
Fig. 4 Wheel-running actograms for two individual grass rats in all conditions. (a) A representative actogram is presented for a subject that presented diurnal activity in all conditions. (b) A representative actogram is presented for a subject that switched chronotypes in the dim light condition. Black tick marks indicate wheel revolutions. The white area indicates lights on, the dark gray area indicates lights off, and the light gray area indicates dim light. Times are presented as clock time.

TABLES

Environmental conditions during the various phases of the experiment

	Light Phase Temp. (℃) (+/- 2 ℃)	Dark Phase Temp. (℃) (+/- 2 ℃)	Lighting Intensity (lux)	Light/Dark Cycle
Baseline	25	21	1000	12:12 LD
28 Degrees C	28	28	1000	12:12 LD
32 Degrees C	32	32	1000	12:12 LD
18 Degrees C	18	18	1000	12:12 LD
15 Degrees C	15	15	1000	12:12 LD
Dim Light	25	25	50	12:12 LD
Re-Entrainment	25	21	1000	12:12 LD
Constant Darkness	21	21	<5	DD
Return to Baseline	25	21	1000	12:12 LD

Table 1: Ambient temperatures, lighting intensities, and light/dark cycles are shown in the order animals were subjected to each condition of the experiment. Temperatures were measured every 5 minutes and did not deviate more than ± 2℃ from the target temperature. Lighting intensity was kept at <5 lux during the dark phase.