smoke (Fig. 2) show that the vertical component is frequently more significant close to the ground where large temperature differences and low wind speeds predominate. At higher levels the horizontal component accounts for most of the air movement as entrainment, increased wind speeds, and a shift to thermal stability interact to reduce the vertical flow.

If relatively small vertical temperature gradients impart directionality to air movement, then a behavioral response which does not occur under vertically isothermal conditions (that is, subthreshold pheromone concentrations) ought to be elicited in males downwind in a temperature gradient. In isothermal (neutral) conditions the *Periplaneta americana* sex pheromone did not elicit searching in males (*11*); no courtship responses were observed. However, when temperature was made to decrease with height, and the pheromone was introduced below the males, their locomotion increased significantly (*t*-test, $P < .01$), and the complete courtship sequence was elicited (*12*). Clearly, the thermal gradient imparts a new directionality to the airflow. The 360° emission angle of Fickian diffusion decreases to a narrow vertical plume in the direction of the males. Hence, more molecules per unit volume of air impinge on the male antennae, and threshold concentrations are more likely to be reached (*13*).

Silverman and Bell (*14*) found that *P. americana* males tethered on a vertical surface showed gravitational responses to sex pheromone delivered perpendicularly to the vertical surface. Air without pheromone caused the males to run up, whereas air currents with sex pheromones caused them to run down. These data are consistent with my convective model for volatile pheromones.

In conclusion, the vertical distribution data, predictable nocturnal micrometeorological profiles, pheromone dispersion models, male orientation behavior, and laboratory experiments suggest that intraspecific height stratification in these species of cockroaches is a mechanism that enhances the efficiency of the mate-finding process.

COBY SCHAL
Department of Entomology,
University of Kansas, Lawrence 66045

References and Notes

1. Stable conditions: temperature inversion, where temperature increases with height above the ground. Unstable conditions: buoyant or temperature lapse profile, where temperature decreases with height above the ground. Free convection: thermals move vertically because of temperature and density gradients; near the ground, this process may occur at low wind speeds. Forced convection: vertical wind shear against surfaces generates turbulent eddies which mix vertically.
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6. F. Enders, *Ecology* **55**, 317 (1974); L. Partridge, in *Behavioural Ecology*, J. R. Krebs and N. B. Davies, Eds. (Blackwell, Oxford, 1978).
7. I have observed "calling" or pheromone emission behavior in three of the eight species listed in Fig. 1 and in several others which are not mentioned. Behavioral tests in the laboratory indicate that males are attracted to calling females. Copulations in the field are most common at the heights where females occur. Attraction of females to males (which may operate over short distances and usually in the context of courtship) has not been observed in any of the eight species. E. R. Willis [*Biotropica* **2**, 120 (1970)] reports this behavior in three *Latiblattella* species from Honduras.
8. Data on temperature profiles are somewhat confusing as researchers have generalized open terrain and temperate deciduous forest patterns to dense tropical rain-forest habitats [for example, P. W. Richards, *The Tropical Rain Forest: An Ecological Study* (Cambridge Univ. Press, Cambridge, 1952)]. Detailed temperature recordings in a South Carolina coastal swamp forest similar in structure to a tropical rain forest confirm my results for nighttime thermal instability in the lower strata [Melpar, Inc., *Diffusion Under a Jungle Canopy* (Publication No. AD-835261L, U.S. Army Dugway Proving Ground, Dugway, Utah, 1969), vol. 1].
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11. A 1 centigrade degree vertical gradient was installed over a vertical distance of 60 cm with resistance wire and two temperature regulators (Yellow Springs Instruments models 71 and 73). A continuous output of the temperatures was provided by a two-channel strip-chart recorder (Esterline-Angus Speed Servo 2). I used 5×10^{-6} µg of synthetic (±)-Periplanone B [M. A. Adams, K. Nakanishi, W. C. Still, E. V. Arnold, J. Clardy, C. J. Persons, *J. Am. Chem. Soc.* **101**, 2495 (1979)] adsorbed onto 1-cm^2 Whatman No. 1 filter paper to elicit sexual responses in *P. americana* males in a screen cage above the pheromone source. The test recorded the number of times in 30-second intervals that the males crossed a line bisecting the floor of the cage. Each test was 4 minutes. I performed ten tests in isothermal and ten in temperature lapse conditions.
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15. I thank R. C. Sapp for technical assistance with the temperature gradient, W. J. Bell and R. Shaw for critical reading of the manuscript, and F. W. Fisk for identifying the voucher specimens. Supported by NSF grants BNS 80-06284 and BNS 77-24898 to W. J. Bell and DEB 80-07556 to C.S.

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Suprachiasmatic Stimulation Phase Shifts Rodent Circadian Rhythms

Abstract. *The integrity of the suprachiasmatic nuclei (SCN) of the hypothalamus is essential to the expression of normal circadian rhythms in rodents. Electrical stimulation of the SCN caused phase shifts and period changes in the freerunning feeding rhythms of rats and activity rhythms of hamsters. The phase response curve for SCN stimulation appears to parallel that for light pulses. These findings strengthen the hypothesis derived from lesion studies that the SCN are the dominant light-entrained oscillators in the rodent circadian system.*

Circadian rhythms synchronized to the solar day are a pervasive feature of mammalian physiology and behavior (*1*). Until recently little was known about the mechanisms responsible for either endogenous generation or environmental synchronization (entrainment) of these rhythms.

A significant advance was the identification of the hypothalamic suprachiasmatic nuclei (SCN) as structures critical to the generation and entrainment of mammalian circadian rhythms (*2*). Ablation of the SCN results in the disruption of a variety of behavioral, physiological, and endocrine rhythms in rodents (*3*). These observations generated the hypothesis that the SCN act as a pacemaker in the mammalian circadian system. The observation of circadian rhythms in spontaneous electrical and metabolic activity in SCN neurons (*4*) is consistent with this hypothesis.

A pacemaker in a circadian system should regulate both phase and period of circadian oscillations; the available data do not establish that the SCN serve this function. The strongest support for this hypothesis would be provided by evidence that manipulation of spontaneous SCN neural activity modifies these features of circadian rhythms. The first evidence for such a mechanism was the finding that infusion of carbachol near

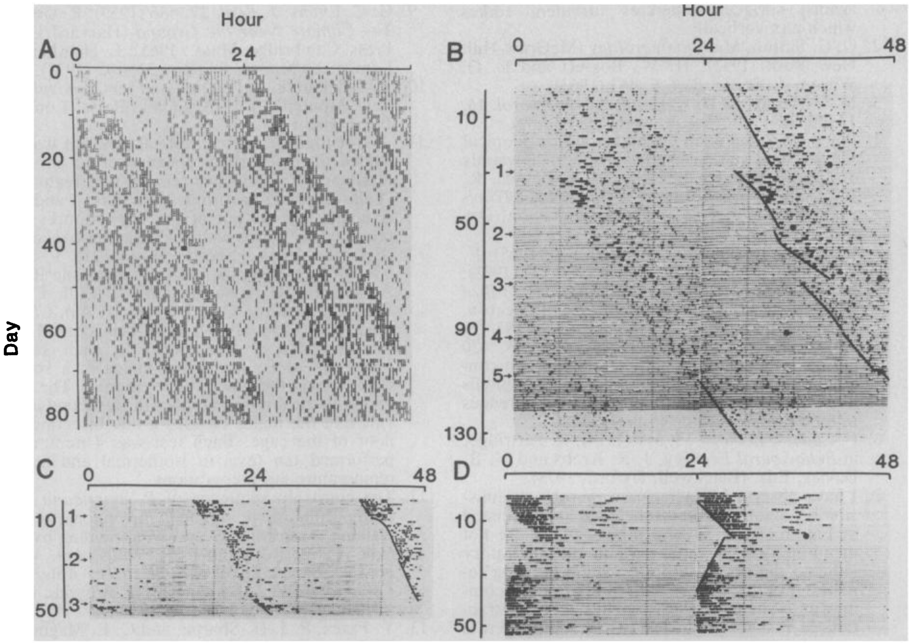

Fig. 1. (A) Record of feeding activity in a blinded rat that received electrical stimulation in the suprachiasmatic nuclei at the time indicated by the black rectangle on day 41. The density of the record reflects the intensity of feeding. Stimulation late in the subjective night (active phase) produced a phase advance of the rhythm. The 24-hour record is double-plotted to permit visualization of the freerunning rhythm. (B to D) Wheel-running activity records of blinded hamsters that received electrical stimulation in the suprachiasmatic area on the days indicated by arrows and at the times shown by filled circles. Stimulation produced phase delays or advances or failed to shift the rhythm depending on the circadian phase of stimulation.

the SCN causes a phase shift in the circadian rhythm of pineal serotonin-*N*-acetyltransferase activity (*5*). We report that electrical stimulation of the SCN systematically alters phase and period of circadian behavioral rhythms in rats and hamsters. This evidence provides direct support for a pacemaking function for the mammalian SCN.

We recorded the freerunning feeding rhythms of bilaterally enucleated rats for a minimum baseline period of 4 weeks (*6*). We then anesthetized each rat and implanted into its brain a stainless steel monopolar electrode in or near the SCN, and, with the rat under anesthesia, applied current for 20 to 60 seconds at two to four closely placed sites (*7*).

Stimulation in or near the SCN generally disrupted feeding for several days, whereas anesthesia alone or accompanied by sham stimulation did not significantly affect any aspect of feeding rhythms. Of nine rats receiving SCN stimulation, two showed a slight shortening of the subsequent freerunning rhythm.

During the subjective day (inactive phase) SCN stimulation in two rats did not shift the feeding rhythm; similar stimulation delivered to five rats during the late subjective night (active phase) caused significant phase advances of the rhythms (Figs. 1a and 2) (*8*). Stimulation applied to two rats during the early subjective night caused only small phase delays (Fig. 2). Stimulation of the regions caudal or lateral to the SCN changed neither period nor phase in spite of the fact that stimulation was applied during the late subjective night.

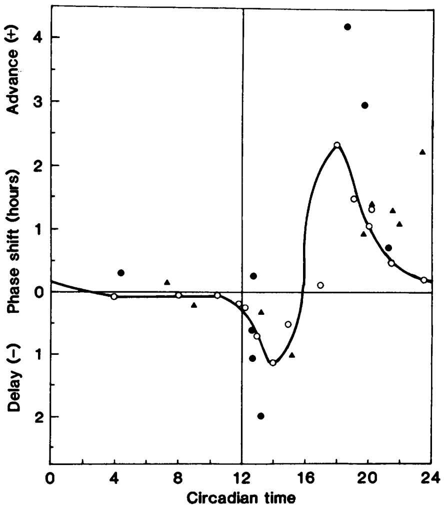

Fig. 2. The amplitude and direction of phase shifts of circadian rhythms produced by electrical stimulation of the suprachiasmatic area in hamsters (●) and rats (▲) plotted against the circadian phase of stimulation. Similar plots of the shifts produced by 10-minute light pulses given to hamsters in constant darkness (○) are shown for comparison. The light-pulse data and the fitted phase response curve are replotted from DeCoursey (*13*).

In another study (*9*), bipolar stainless steel electrodes aimed at the SCN (*10*) were permanently implanted into the brain. Each hamster was housed in a Plexiglas cage equipped to record wheel-running activity while the hamster was tethered by a lead attached to the electrode and to an overhead commutator. When an individual's activity rhythm had stabilized, we delivered electrical stimulation for 10 minutes without handling or disturbing the animal (*11*). The hamster's behavior was usually observed and recorded both during stimulation and for 5 minutes before and after stimulation. Changes in period or phase of the activity rhythm were assessed by eye-fitting lines to activity onsets for 10-day periods before and after the treatment day.

Stimulation delivered through electrodes in the suprachiasmatic region produced both delays and advances of the activity rhythm, depending on the circadian phase of stimulation (Fig. 1, b–d). Changes in period often accompanied phase shifts (Fig. 1d; stimulation 3, Fig. 1b). Stimulation at sites remote from the SCN failed to produce phase shifts (*12*).

Stimulation during the early subjective night produced phase delays while stimulation during the late subjective night elicited phase advances. In one hamster (Fig. 1b) stimulation in the late subjective night produced large phase advances (stimulations 1 and 3), stimulation in the early subjective night produced only period lengthening (stimulation 2) or a small phase delay (stimulation 5), and stimulation during the subjective day had little or no effect (stimulation 4).

Brief light exposure of intact animals housed in darkness produces systematic phase shifts of circadian oscillators (*13*, *14*). The direction and amplitude of shift plotted against the time of light exposure, as determined for hamsters by DeCoursey (*13*) is shown in Fig. 2, along with the results of our studies. While it would be premature to plot such a phase-response curve for electrical stimulation, the timing of delays and advances is consistent with the light-pulse phase-response curve. More data are needed to establish whether this curve reflects the convergence of light information on the suprachiasmatic region.

The transients observed during some phase shifts (Fig. 1, b and c), may reflect either a failure to stimulate all oscillators in the SCN or the gradual resynchronization of remote oscillators to those that were shifted by the stimulation. The relative difficulty in producing phase delays in both species is unexplained. No correlation was observed in hamsters between the effectiveness of stimulation in producing phase shifts and behavioral changes during stimulation.

The large stimulation field presumably generated by the electrodes used in the hamster study do not permit localization of the effects of stimulation to the SCN. However, the similar effects produced by stimulation within the SCN of rats strengthens the conclusion that changes in neural activity within the SCN mediate the observed effects of stimulation in both species.

These findings are consistent with the hypothesis that neural activity in the SCN regulates phase and period of rodent circadian rhythms. There is, however, substantial evidence for the existence of circadian oscillators outside the SCN (*15*). Therefore, the SCN may function as a pacemaker by generating a circadian rhythm of neural activity that is entrained by photic input and which regulates the activity of other oscillators in the circadian system.

BENJAMIN RUSAK
Department of Psychology,
Dalhousie University,
Halifax, Nova Scotia, Canada B3H 4J1
GERARD GROOS
Laboratorium voor Fysiologie,
Rijksuniversiteit te Leiden,
3300 RC Leiden, Netherlands

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6. Adult male albino rats (Wistar) were housed in an open vivarium under a light-dark cycle, but their rhythms did not entrain after they were blinded by bilateral enucleation. Surgery was performed under Hypnorm anesthesia (Philips-Duphar; 1 ml/kg). Blinding was necessary to ensure that stimulation did not affect visual afferents to the SCN. Feeding was recorded as described [W. J. Rietveld, F. Ten Hoor, M. Kooij, W. Flory, *Physiol. Behav.* **21**, 615 (1978)].
7. Nine rats were stimulated in the SCN, two were stimulated lateral or caudal to the SCN, two were sham-stimulated (no current), and two were anesthetized controls. Stimulation consisted of 0.5-msec constant current pulses (300 μA) at 25 pulses per second; electrode tip diameters were 10 to 30 μm. Small lesions were placed near the last stimulation site to permit histological localization of the stimulated area. No visible necrosis was detected at the stimulation sites in the SCN.
8. The first daily burst of eating at the beginning of the subjective night was determined by visual inspection of the records. Linear regressions through these points before and after stimulation were used to assess changes in phase and period.
9. Adult male hamsters (Charles River–Lakeview; LVG:lak) were enucleated several weeks before the electrodes were implanted; all surgery was performed under Nembutal anesthesia (Abbott; 80 mg/kg). At the time of enucleation, hamsters were implanted subcutaneously with two 50-mm lengths of melatonin-filled (Sigma) Silastic tubing (Dow-Corning) to prevent testicular regression [F. W. Turek, C. Desjardins, M. Menaker, *Science* **190**, 280 (1975)] which can disrupt hamster activity rhythms [G. A. Eskes and I. Zucker, *Proc. Natl. Acad. Sci. U.S.A.* **75**, 1934 (1978); G. B. Ellis and F. W. Turek, *J. Comp. Physiol.* **132**, 277 (1979)].
10. The electrodes (MS 303/3; Plastic Products) were oriented with the tips in the anterior-posterior plane separated by 0.1 to 0.4 mm. They were implanted in the midline, 0.0 to 0.3 mm anterior to bregma and 8.0 mm below the top surface of the skull, with the upper incisor bar at 2 mm below the interaural line.
11. Bipolar stimulation was delivered as either 0.2-msec square wave pulses, 200 pulses per second at 150 V or 10 msec pulses, 20 pulses per second at 50 V with the use of a Grass S44 stimulator. A 0.5-megohm resistor in series with the stimulator provided essentially constant current stimulation of 100 to 300 μA.
12. Of three hamsters (Fig. 1) two had electrode tips at the dorsal anterior border of the SCN; necrosis around the tips in one hamster did not permit electrode localization. Rhythms of hamsters with electrode placements anterior or lateral to the SCN were not phase-shifted by stimulation.
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Accommodative Defocus Does Not Limit Development of Acuity in Infant *Macaca nemestrina* Monkeys

Abstract. *In an experiment with ten macaque monkeys (*Macaca nemestrina*), a combination of photorefraction and corneal reflex photography was used to measure simultaneously the plane of focus and direction of gaze while they were presented with fixation targets. The monkeys ranged in age from 2 days to 10 weeks. Some of the infants that were less than 1 month old failed to change accommodation to targets at any distance, whereas others showed limited accommodative abilities. The magnitude of the accommodative response of infants older than 4 weeks appeared to be adultlike. Infant monkey's visual acuity improves dramatically after 4 weeks. These results, which show that the improvement in spatial resolution cannot be accounted for by increased accommodative accuracy, parallel those obtained from human infants where accommodative competence is attained by about 4 months of age.*

Visual resolution, or acuity, is poorer in infants than in adults (*1*), but it is not known to what extent the improvements in acuity with age are due to changes in the optics or in neural processing. Experiments to determine this issue are often potentially invasive and not feasible with humans. Infant macaque monkeys (*Macaca nemestrina*) are useful for studying mechanisms of human visual development (*2*), and we now present results obtained from this animal model.

Previous work has shown that the optical quality of the infant monkey eye, as assessed by the line spread function for well-focused images, is not responsible for its poor resolution (*3*). However, if infants are unable to accommodate properly to bring targets into sharp focus at the retina, the poor resolution might be due to optical defocus. We have measured accommodative defocus and our results demonstrate that infants over 4 weeks of age accommodate similarly to adults. Therefore, the improvements in spatial resolution after 4 weeks of age cannot be accounted for on the basis of improvements in accommodative accu-

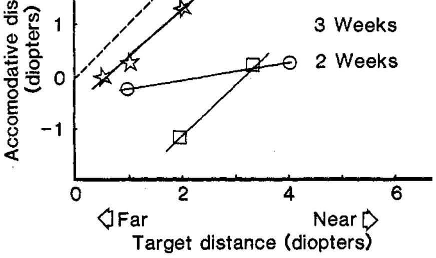

Fig. 1. Accommodation in infant monkeys. The abscissa shows the fixation target plane specified in diopters (1/target distance in meters). The ordinate is the fixation plane of the monkey, also specified in diopters. Zero on the ordinate indicates that the animal is fixated at optical infinity. Positive values indicate that fixation is closer than optical infinity; negative values indicate fixation beyond optical infinity. The dotted line indicates the performance we would expect from an animal with perfect accommodation. Data points falling above this line indicate that the animal is fixating in front of the target, whereas data points below this line indicate fixation beyond the target. Data are shown for three separate animals aged 6 months (stars), 3 weeks (squares), and 2 weeks (circles). Solid lines through the symbols are least-squares linear regression lines.

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