tecture of the membrane so that the polypeptide is released. In the second state, found only in cataractous lenses, it is presumed that the 43,000-dalton polypeptide has formed disulfide links with putative crystallin polypeptides. Other polypeptides such as the 9600-dalton species and the components larger than 43,000 daltons are also observed in the complex. In this state, the 43,000-dalton polypeptide may act as a nucleation site on the membrane for the formation of these large aggregates. The individual aggregates are probably composed of units that are stabilized by disulfide linkage and are associated with each other by strong noncovalent forces. Some noncovalently linked individual polypeptides may also be trapped in the matrix of the aggregate. An intermediate stage in which the aggregate is held primarily by noncovalent linkage is not shown. This intermediate condition reflects the situation observed in older normal lenses where aggregates with similar polypeptide composition are observed but are not disulfide linked.

The model does not attempt to be all-inclusive. No definition is presented of the heterogeneous streaky component of peak 1 (Fig. 1) and its association with 20,000-dalton components. It is not known whether such aggregates are associated with the membrane. Other membrane components may also be involved as interaction sites with soluble lens proteins. The model does not consider other insoluble components, some of which are probably not membrane bound.

This model would explain earlier reports of strong association of alpha-crystallin with the cell membrane (*24*). Further support also comes from measurements of Bragg diffraction of laser light caused by large fluctuation in the index of refraction (*25*). The evidence indicates that the amplitude of the change in the index of refraction increases with cataract formation. The scatter elements have the same periodicity as the lens fiber cell membranes.

ABRAHAM SPECTOR
MARGARET H. GARNER
WILLIAM H. GARNER
DEBDUTTA ROY
*Biochemistry and Molecular Biology
Laboratory, Department of
Ophthalmology, College of
Physicians and Surgeons,
Columbia University, New York 10032*
PATRICIA FARNSWORTH
SUSAN SHYNE
*Department of Physiology and
Ophthalmology, New Jersey College of
Medicine and Dentistry, Newark 07103*

References and Notes

1. A. Spector, T. Freund, L.-K. Li, R. C. Augusteyn, *Invest. Ophthalmol.* **10**, 677 (1971).
2. G. B. Benedek, *Appl. Opt.* **10**, 459 (1971).
3. A. Spector, *Is. J. Med. Sci.* **8**, 1577 (1972).
4. J. Jedziniak, J. H. Kinoshita, E. M. Yates, L. O. Hocken, G. B. Benedek, *Exp. Eye Res.* **15**, 185 (1973).
5. K. N. Liem-The and J. H. Hoenders, *ibid.* **18**, 143 (1974).
6. A. Spector, J. Stauffer, J. Sigelman, *Ciba Found. Symp.* **19**, 185 (1973); A. Spector, S. Li, J. Sigelman, *Invest. Ophthalmol.* **13**, 795 (1974); J. Jedziniak, J. H. Kinoshita, E. M. Yates, G. B. Benedek, *Exp. Eye Res.* **20**, 367 (1975); F. J. Giblin, B. Chakrapani, V. N. Reddy, *ibid.* **26**, 507 (1978).
7. R. Clark, S. Zigman, S. Lerman, *Exp. Eye Res.* **8**, 172 (1969).
8. D. Roy and A. Spector, *ibid.* **26**, 429 (1978) (discussion of soluble and insoluble lens proteins).
9. ———, *ibid.* **7**, 164 (1976).
10. A. Spector and D. Roy, *Proc. Natl. Acad. Sci. U.S.A.* **75**, 3244 (1978).
11. D. Roy and A. Spector, *Exp. Eye Res.* **26**, 445 (1978).
12. W. H. Garner, M. H. Garner, A. Spector, *ibid.*, in press.
13. H. Harboe and A. Ingild, *Quantitative Immunoelectrophoresis*, N. H. Axelson, J. Kroll, B. Week, Eds. (Universitetsforlaget, Oslo, 1975), pp. 161-164.
14. W. Becker, *Immunochemistry* **6**, 539 (1969).
15. W. H. Garner and A. Spector, *Doc. Ophthalmol.* **18**, 91 (1979).
16. Ö. Ouchterlony and L.-A. Nilsson, *Handbook of Experimental Immunology*, D. M. Weis, Ed. (Blackwell, Oxford, 1978), pp. 1917-1944.
17. M. Elzinga and R. C. Lu, *Contractile Systems in Normal Muscle Tissues*, S. V. Perry, A. Margreth, R. S. Adelstein, Eds. (Elsevier/North-Holland, Amsterdam, 1976), pp. 29-37.
18. P. R. Waggoner and H. Maisel, *Exp. Eye Res.* **27**, 151 (1978); P. R. Waggoner, N. Lieska, J. Alcala, H. Maisel, *Ophthalmol. Res.* **8**, 292 (1976).
19. L. T. Chylack, *Arch. Ophthalmol.* **96**, 888 (1978).
20. P. N. Farnsworth, S. C. J. Fu, P. A. Burke, I. Bahia, *Invest. Ophthalmol.* **13**, 274 (1974).
21. A. Ikeda and J. Zwaan, *ibid.* **5**, 404 (1966); *Dev. Biol.* **15**, 348 (1967); J. Zwaan, and A. Ikeda, *Exp. Eye Res.* **7**, 301 (1968).
22. M. K. Mostafapour and V. N. Reddy, *Doc. Ophthalmol.* **46**, 193 (1978).
23. W. H. Garner and A. Spector, *Proc. Natl. Acad. Sci. U.S.A.* **75**, 3618 (1978).
24. P. G. Bracchi, F. Carta, P. Fasella, G. Maraini, *Exp. Eye Res.* **12**, 151 (1971).
25. G. Benedek, J. Clark, E. W. Serrallach, C. Y. Young, L. Mengell, T. Sauke, A. Bragg, K. Benedek, *Philos. Trans. R. Soc. London*, in press.
26. H. B. F. Dixon and R. N. Perham, *Biochem. J.* **109**, 312 (1968).
27. K. Weber and M. Osborn, *J. Biol. Chem.* **244**, 4406 (1969).
28. O. U. Blumenfeld and B. Zvilichovsky, *Methods Enzymol.* **28**, 245 (1972).

29. We thank C. Huang, G. Jenkins, and S. Lerman for technical assistance, and R. von Muchow for photographic assistance. Supported by grants from the National Eye Institute, National Institutes of Health. This investigation is part of the Cooperative Cataract Research Group effort.

22 November 1978; revised 15 March 1979

Rhythms in Human Performance:

$1^{1}/_{2}$- Hour Oscillations in Cognitive Style

Abstract. *Performance on verbal and spatial matching tasks was assessed every 15 minutes for 8 hours. Significant 90- to 100-minute oscillations were observed for each task. These oscillations were 180° out of phase, supporting the hypothesis that in humans the basic rest activity cycle involves alternating activation of processing systems residing in the two cerebral hemispheres.*

In the 1950's Kleitman and his colleagues (*1*) demonstrated that the sleep phase of the sleep-wakefulness cycle is not uniform, as had been thought, but rather is characterized by an ultradian (*2*) rhythm with striking variations in many behavioral and physiological functions. The two phases of this rhythm—which differ in electroencephalogram (EEG) pattern, heart and respiration rate, and muscle tone—are referred to as rapid-eye-movement (REM) sleep and non-rapid-eye-movement (NREM) sleep because transient eye movements occur during one phase but not during the other (*3*). In the human adult, a full cycle (period) of REM/NREM alternation lasts approximately 80 to 120 minutes. Kleitman (*4*) subsequently proposed that the alternation between REM and NREM sleep is one expression of a phylogenetically old basic rest activity cycle (BRAC), which continues throughout the day and on which the sleep-wakefulness cycle is superimposed. Many studies have since supported this proposal, although the choice of the terms "rest" and "activity" to describe the alternate phases has been questioned (*5*).

It has recently been hypothesized that the REM/NREM rhythm and its continuation during wakefulness (the BRAC) involves an alternation in the relative efficiency or activation of the two cerebral hemispheres (*6, 7*). Broughton (*7*) cites the following evidence in support of this hypothesis: (i) the subjective qualities of dreams reported on wakening from REM and NREM sleep differ radically with vividly visual dreams of an illogical nature reported following REM sleep awakenings and less vivid, more thoughtlike and rational dreams reported after NREM sleep awakenings (*8*); (ii) the right cerebral hemisphere shows greater EEG desynchronization than the left during REM sleep (*9*); (iii) 90- to 110-minute rhythms during wakefulness have been reported for a variety of measures, including oral behavior (*10*), the magnitude of the spiral aftereffect (*11*), heart rate (*12*), vigilance performance (*13*), and the fantasy content of day dreams (*14*); (iv) some of these rhythms may be in phase with the nighttime alternation between REM and NREM sleep (*15*); and (v) in most right-handed people, the two cerebral hemispheres have asymmetric cognitive abilities, with the right hemisphere specializing in visual-spatial, wholistic, nonlogical processes, and the left hemisphere specializing in verbal-linguistic, analytic, and logical processes (*16*). Taken together these findings suggest that the relative efficiency of the spatial-wholistic right hemisphere may be high during REM sleep and its corresponding waking phase, whereas that of the verbal-analytic left hemisphere may be high during NREM sleep and its corresponding waking phase. In this report we describe a study of daytime performance on verbal and spatial tasks that strongly supports this cyclic alternation hypothesis.

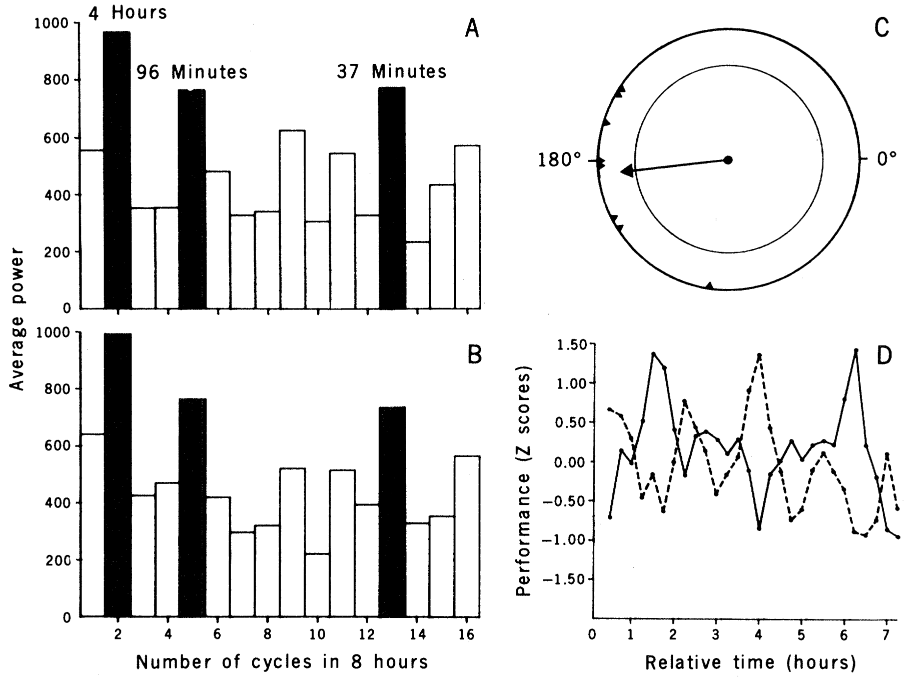

Fig. 1. Mean root power as a function of frequency shown separately for spatial (A) and verbal (B) performance. Power spectral peaks that are significantly larger than one would expect by chance [$P < .01$ on two tests (*21*)] are shaded and marked by the corresponding period. (C) Each mark on the outer circle represents the phase difference between the two tasks for each subject. The direction of the averaged resultant vector (arrow) indicates the average phase difference; its amplitude is significant at the .01 level (inner circle) (*22*). (D) Mean verbal (solid line) and spatial (dashed line) performance as a function of time. The performance oscillations were synchronized and averaged across the eight subjects (*23*). The average standard errors of the means were .24 and .31 Z units for the verbal and spatial tasks, respectively.

The basic strategy was to test a group of subjects frequently over an 8-hour period on two tasks, one predominantly verbal, the other predominantly spatial. If the hypothesis is correct, performance on each task ought to reveal rhythmic oscillations with a period of approximately 80 to 120 minutes, and equivalent phases of the two rhythms should be separated by one-half cycle (180°).

We chose two simultaneous matching tasks which, on the basis of the literature on hemispheric specialization, ought to be performed asymmetrically by the two hemispheres (*17*). In the verbal task, the subject had to decide whether pairs of letters (one uppercase, one lowercase) had the same name. In the spatial task the subject had to decide whether pairs of seven-dot random patterns were exactly identical. We developed paper-and-pencil versions of the two tasks (*18*) in which the subject recorded same/different choices by crossing out S's and D's located between the two members of each pair. We tested eight young adult volunteers (18 to 24 years; five female, three male) who were right-handed and had no left-handed parents or siblings.

All eight subjects were tested on the same day in a group testing room. On the desk before each subject were two booklets, one for each task. They were told to make their same/different choices as quickly as possible without making errors and were given practice at each task. Starting at 9:00 a.m. performance on each task was tested for 3 minutes every 15 minutes over the 8-hour period. Lunch was from 12:30 to 1:00 p.m.; subjects were not permitted to talk to one another, but were allowed to read, doodle, walk around, and so forth between test trials (*19*).

The dependent variable used was the number of pairs correctly matched on each task in each 3-minute test period. Since the error rate was low (1.6 percent), the scores reflect the rate at which subjects could accurately perform the matching tasks. Average performance was 182 correct verbal pairs and 115 correct spatial pairs in a 3-minute test period. For each subject the 32 scores for each task were normalized (converted to Z scores) and subjected to Fourier analysis (*20*). Power spectral peaks centered at 4 hours, 96 minutes, and 37 minutes (Fig. 1, A and B) were significantly larger than one would expect by chance ($P < .01$ for each of two analyses) (*21*). Although this analysis suggests that performance may be affected by multiply nested rhythms, in this short report our emphasis is confined to the approximately 96-minute oscillation that is in the frequency range of the BRAC. Verbal and spatial performance maintained a consistent phase relationship across subjects [Rayleigh test (*22*), $P < .01$], and the two oscillations were, as predicted, approximately 180° out of phase (Fig. 1C).

For purposes of graphic illustration, each subject's data were smoothed and then shifted so that the approximately 96-minute cyclic alternations would be in phase across subjects (*23*). The average performance oscillations and their reciprocal relationship can be seen clearly in Fig. 1D. To appreciate the magnitude of the performance fluctuations, consider, for example, that the first upswing in verbal performance represents an improvement from roughly 165 to 215 correct matches in 3 minutes, while the simultaneous downswing in spatial performance is from about 125 to 108 correct matches.

In summary, we have found that daytime performance on verbal and spatial matching tasks fluctuates cyclically with a 90- to 100-minute period and that increases in performance on one task are accompanied by decreases on the other. This finding is consistent with the hypothesis that in humans the BRAC is characterized by oscillations in the relative activation or efficiency of the two cerebral hemispheres, which are specialized for the performance of verbal and spatial tasks (*24*). The scientist or diagnostician should be alert to the possibility that rhythmic changes in cognitive style may contaminate measures of performance on tasks that are processed asymmetrically by the two cerebral hemispheres.

RAYMOND KLEIN
ROSEANNE ARMITAGE
Department of Psychology,
Dalhousie University, Halifax,
Nova Scotia, Canada B3H 4J1

References and Notes

1. E. Aserinsky and N. Kleitman, *Science* **118**, 273 (1953); W. Dement and N. Kleitman, *Electroencephalogr. Clin. Neurophysiol.* **9**, 673 (1957).
2. The term ultradian is used to refer to oscillations with frequencies greater than one per day (periods shorter than 24 hours) [F. Halberg, *Int. J. Chronobiol.* **1**, 31 (1973)].
3. A. Rechtschaffen and A. Kales, Eds., *A Manual of Standardized Terminology, Techniques and Scoring System for Sleep Stages of Human Subjects* (Public Health Service, Government Printing Office, Washington, D.C., 1968).
4. N. Kleitman, *Sleep and Wakefulness* (Univ. of Chicago Press, Chicago, 1963); in *Sleep: Physiology and Pathology*, A. Kales, Ed. (Lippincott, Philadelphia, 1967).
5. D. Kripke, in *Advances in Sleep Research*, E. Weitzman, Ed. (Spectrum, New York, 1974); M. Sterman and T. Hoppenbrouwers, in *Brain Development and Behavior*, M. Sterman, D. McGinty, A. Adimolfi, Eds. (Academic Press, New York, 1971).
6. M. Jouvet, *Arch. Ital. Biol.* **111**, 564 (1973); L. Van Valen, *Biol. Psychol.* **15**, 19 (1973).
7. R. Broughton, *Can. Psychol. Rev.* **16**, 217 (1975).
8. A. Rechtschaffen, in *The Psychophysiology of Thinking*, F. McGuigan and R. Schoonover, Eds. (Academic Press, New York, 1973).
9. L. Goldstein, N. Stoltzfun, J. Gardocki, *Physiol. Behav.* **8**, 811 (1972).
10. S. Friedman, *Am. Psychoanal. Q.* **15**, 317 (1967); D. Kripke, *Psychosom. Med.* **34**, 221 (1972); I. Oswald, J. Merrington, H. Lewis, *Nature (London)* **225**, 959 (1970).
11. P. Lavie, C. Levy, F. Collidge, *Physiol. Psychol.* **3**, 144 (1975).
12. W. Orr and H. Hoffman, *IEEE Trans. Biomed. Eng.* **BME-21**, 130 (1974).
13. W. Orr, H. Hoffman, F. Hegge, *Aerosp. Med.* **45**, 995 (1974).
14. D. Kripke and D. Sonnenschein, in *The Stream of Consciousness*, K. Pope and J. Singer, Eds. (Plenum, New York, 1978).
15. K. Destrooper and R. Broughton, *Psychophysiology* **6**, 231 (1969); G. G. Globus, in *The Sleeping Brain*, M. Chase, Ed. (Brain Information Service/Brain Research Institute, University of California, Los Angeles, 1972), pp. 211–213; P. Lavie, *Physiol. Psychol.* **2**, 107 (1974).
16. J. Bogen, *Bull. Los Angeles Neurol. Soc.* **34**, 135 (1969); S. Dimond and J. Beaumont, Eds. *Hemisphere Function in the Human Brain* (Wiley, New York, 1974).
17. G. Cohen, *Percept. Psychophys.* **11**, 139 (1972); M. Gross, *ibid.* **12**, 357 (1972); G. Geffen, J. Bradshaw, N. Nettleton, *J. Exp. Psychol.* **95**, 25 (1972).
18. In our initial test of this hypothesis (presented at the Annual Meeting of the Canadian Psychological Association, Vancouver, B.C., 8 to 10 June 1977) latencies to discrete presentation of the letter and pattern pairs were collected under computer control. The results from a single subject who was tested in four 8-hour sessions were consistent with those reported here.
19. Subjects recorded any thoughts they had at the end of each 15-minute period.
20. All analyses were performed on a PDP-11 computer with software provided by DEC (Sparta) or written by R.K.
21. In one method (rank test) the power spectra values (root power) for each subject were ranked in order of increasing values from 1 to 16. For each period, a mean rank across the eight subjects was computed. Mean ranks above 12.3 are larger than one would expect by chance at the .01 level (one-tailed test). In the second method (randomization test) 500 random orderings of each subject's scores for each task were subjected to Fourier analysis. For each subject, task, and period, the mean root power and standard deviation of root power of the random sequences were used to determine the probability of obtaining, by chance, a root power as large or larger than that actually observed. The probabilities for each task and period were combined across subjects according to a method developed by R. A. Fisher [see W. Wallis, *Econometrika* **10**, 229 (1942) for a discussion] to determine for the group as a whole which periods had consistently larger peaks than would be expected by chance at the .01 level.
22. For each subject, the phase difference between the approximately 96-minute oscillations in spatial and verbal performance is represented on the circumference of the unit circle. Each of these points was treated as the end of a vector from the center, and their averaged vector sum (arrow in Fig. 1C) was computed. In this case, the length exceeds that required for significance at the .01 level (inner circle of Fig. 1C) [J. Greenwood and D. Durand, *Ann. Math. Stat.* **26**, 233 (1955)].
23. For each subject, the phase of the oscillations in the difference scores (verbal minus spatial performance) was used to determine the amount and direction of shift, which was then applied to both tasks. A three-point smooth, $0.25(i - 1) + 0.5(i) + 0.25(i + 1)$, was used to eliminate high-frequency oscillations and noise. Overhanging points (those contributed by fewer than eight subjects) have been dropped from Fig. 1D.
24. Complete verification of the proposal outlined by Broughton (*7*) requires the demonstration that these daytime oscillations in performance reflect changes in hemispheric functioning and that they bear an appropriate phase relation to the alternation between REM and NREM stages of sleep.
25. We thank B. Rusak for his comments and encouragement, R. Rodger for his advice, and the National Research Council of Canada for its financial support of this research.

27 November 1978; revised 12 March 1979

Trace Chemicals: The Essence of Sexual Communication Systems in *Heliothis* Species

Abstract. *Analysis of heptane-soluble compounds from ovipositors of* Heliothis zea *and* Heliothis virescens *shows that both species produce relatively large amounts of (Z)-11-hexadecenal, with traces of (Z)-9-hexadecenal, (Z)-7-hexadecenal, and hexadecanal.* Heliothis virescens *females differ from* Heliothis zea *in that they also produce trace amounts of tetradecanal, (Z)-9-tetradecenal, and (Z)-11-hexadecen-1-ol. In both species, trace compounds are essential to pheromonal activity and specificity of chemical signals.*

The moths of *Heliothis zea* (Boddie) and *H. virescens* (F.) are among the most devastating pest insects of American agriculture. The species infest a wide range of crops, including cotton, corn, soybeans, sorghum, peanuts, tobacco, tomatoes, cabbage, and lettuce. We report the identification of trace chemicals that heretofore have gone undetected in females of these pests and show that the newly discovered compounds are essential elements in the chemical signaling systems of these species.

The sex pheromones of *H. zea* and *H. virescens* have been studied by others (*1–4*). Females of *H. zea* have been

Table 1. Percentage composition of heptane washes from seven *Heliothis zea* and six *H. virescens* female ovipositors determined by capillary chromatographic analysis. Mean values and the range (in parentheses) of analytical values are shown.

Component	$\bar{X}$ percentage (range)	
	H. zea	*H. virescens*
(Z)-7-Hexadecenal	1.1 (0.4 to 1.9)	1.0 (0.1 to 1.56)
(Z)-9-Hexadecenal	1.7 (1.1 to 2.4)	1.3 (0.3 to 2.34)
(Z)-11-Hexadecenal	92.4 (89.8 to 95.7)	81.4 (76.8 to 91.1)
Hexadecanal	4.4 (1.8 to 7.1)	9.5 (3.0 to 19.0)
(Z)-9-Tetradecenal		2.0 (0.7 to 3.1)
Tetradecanal		1.6 (0.7 to 2.7)
(Z)-11-Hexadecen-1-ol		3.2 (0.9 to 4.5)

Table 2. Responses of male *Heliothis zea* and *H. virescens* to synthetic compounds and to virgin females of the respective species (*8*). Means followed by the same letter are not statistically different from each other according to Duncan's multiple range test ($P = .05$).

Stimulus in trap	Males per trap per night	
	H. zea	*H. virescens*
Test 1		
115.5 μg of (Z)-11-hexadecenal	0.3 b	0
133.6 μg of mixture A*	11.7 a	0
Heliothis zea (four females)	12.0 a	0
Test 2		
115.5 μg of (Z)-11-hexadecenal + 6.9 μg of (Z)-9-tetradecenal	0	7.8 c
151.8 μg of mixture B*	0	38.1 a
Heliothis virescens (four females)	0	21.7 b

*Mixture A consisted of 2.6 μg of (Z)-7-hexadecenal, 4.5 μg of (Z)-9-hexadecenal, 11.0 μg of hexadecanal, and 115.5 μg of (Z)-11-hexadecenal. Mixture B contained the same chemicals plus 6.9 μg of (Z)-9-tetradecenal, 2.3 μg of tetradecanal, and 9.0 μg of (Z)-11-hexadecen-1-ol.