

Sternberg and Scarborough (6) showed that, in arrays of size one, consecutively occurring numerals are processed at overlapping times, that is, that P3 is partly parallel and not purely serial. Taken together with our results, this means that all component operations of scanning overlap each other in time. Scanning may be concentrated on either a few locations or spread out over many; for a considerable range of conditions the overall scanning rate is approximately constant (13). For the two subjects, the maximum overall rate varies from about 75 to 125 letters per second (equivalent to the discrimination of 1 letter from a numeral every 8 to 14 msec).

What is the role of eye movements in visual search? In visual search, as in nearly all visual tasks, the eyes make quick saccadic movements at rates not exceeding about 4 or 5 movements per second, and thereby the eyes effectively transform the visual input into a sequence of stimuli with ISI's of 200 to 250 msec (14). Even these minimum times between eye movements (for example, 200 to 250 msec) are five times longer than the ISI's that produce the fastest scanning rates in the present experiment (40 to 50 msec). When arrays are presented at ISI's comparable to those between eye movements, scanning rates generally are much lower than the maximal rates—in fact, the data imply that most scanning occurs during the first half of the ISI (Fig. 2, c and d). Therefore, in the simple search for a numeral among letters, the rate of eye movements is a factor that significantly limits the rate of search, and a method like the sequential search paradigm is needed to estimate a scanning rate that is unconfounded by eye movements. Can replacing the sequence of stimuli generated by eye movements with a sequence of stimuli generated by a computer result in a comparable improvement in performance in complex visual tasks such as reading? That is, can eye movements gainfully be replaced by stimulus movements, even when the rate of processing rather than the rate of eye movements is the limiting factor? These are important practical questions, and the sequential presentation procedures offer the means to answer them.

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6. G. Sperling, in *Early Experience and Visual Information Processing in Perceptual and Reading Disorders*, F. A. Young and D. B. Lindsley, Eds. (National Academy of Sciences, Washington, D.C., 1970), p. 198. An alternative term is "simulated search," proposed by S. Sternberg and D. L. Scarborough, *Visual Information Processing and Control of Motor Activity* (Bulgarian Academy of Sciences, Sofia, in press).
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8. The viewing distance was 40 inches (1 inch = 2.54 cm); subjects maintained fixation at the center of the array. Letters were 0.4 inch high and spaced apart (center-to-center) 0.65 inch horizontally and vertically. The letters O, B, I, S, Z, and Q were not used. Letters were composed of 22 points (on the average) and illuminated briefly to a luminous directional energy of 1.1 candle-microseconds per point upon a uniform background of 1.6 footlambert (1 footlambert = 1.076 mlam) [see G. Sperling, *Behav. Res. Methods Instrum.* 3, 148 (1971)].
9. The difference in the estimated number of letters scanned ($\hat{p}L$) by assuming the most efficient or the most inefficient guessing strategy is $\hat{p}/(L-1)$, which is small for large arrays.
10. Within a daily session, array size was held constant and ISI was varied. Sessions and ISI's within sessions were conducted in a counterbalanced order; all of the sessions for detection of "2" occurred before any of the sessions for detection of "5." After every trial, subjects were given knowledge of results.
11. C. W. Erickson and T. Spencer [*J. Exp. Psychol. Monogr.* 79, 1 (1969)] in formally similar experiments obtained totally different results. In their experiments, a critical item remained detectable even at exceedingly high rates of presentation. In our experiments, such effects occur only when insufficient precautions have been taken to ensure that the characters that follow a critical item overlap every part of the critical item.
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15. We acknowledge an award of the John Simon Guggenheim Memorial Foundation to G. Sperling. Individual responsibility for the research was divided as follows. Most of the computer programming was done by Mrs. Judy Budiansky; Mrs. Martha C. Johnson tabulated the data and served as a subject; J. G. Spivak ran some preliminary experiments and served as a subject; G. Sperling did the rest.

17 March 1971

Pineal Function in Sparrows:

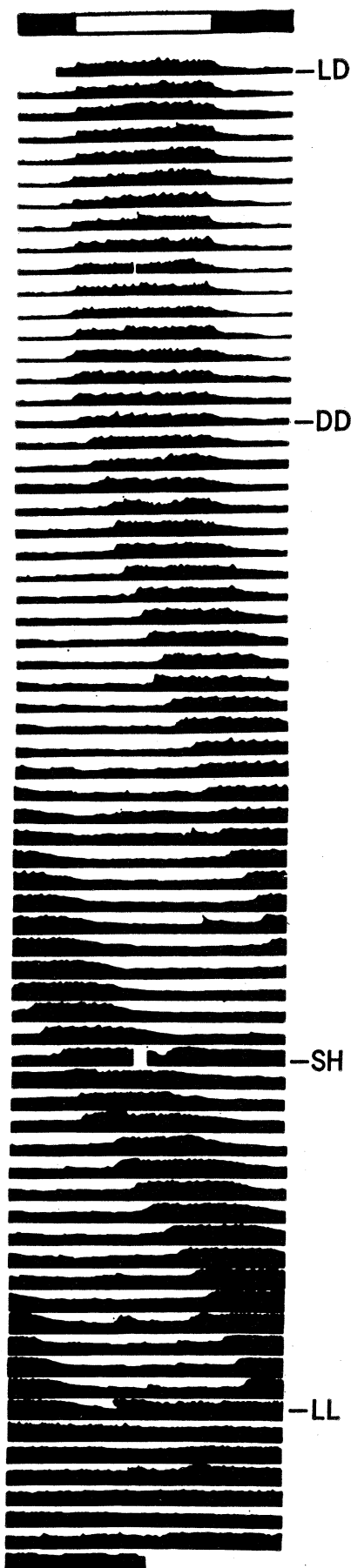
Circadian Rhythms and Body Temperature

Abstract. *Deep body temperature of the house sparrow, Passer domesticus, was monitored continuously by radio telemetry. Pinealectomy abolished the normal circadian rhythm of body temperature in constant darkness, and significantly altered the amplitude of body temperature rhythms entrained to light cycles. The body temperature minima of pinealectomized birds never fell as low as those of unoperated birds regardless of the light conditions; the temperature maxima of both normal and pinealectomized birds were higher in light than in darkness. In sparrows the pineal organ is essential to the normal function of the biological clock controlling both activity and body temperature rhythms and may be directly involved in thermoregulation.*

Only a few investigators have succeeded in interfering with the biological clock by surgical manipulation (1). The work of Gaston and Menaker showing that removal of the pineal organ results in the loss of the endogenous circadian rhythm of locomotor activity in the house sparrow is the only such study in vertebrates. The appearance of apparently aperiodic activity after pinealectomy of birds kept under constant conditions of darkness or dim light has been repeatedly confirmed in this laboratory and elsewhere (2). In order to determine the extent of the pineal's role in the

circadian system of birds, we have investigated the influence of pinealectomy on temperature. We have found that pinealectomy abolishes the endogenous temperature rhythm, and that it affects body temperature regulation in ways that may not result directly from its effects on rhythmicity.

As reported by Hudson and Kimzey (3), *Passer domesticus* has a circadian rhythm of body temperature change which we found to have an amplitude of 3.0° to 4.5°C (4). In our experiments this rhythm persisted with a circadian period in all unoperated birds for as long as they were main-



the bird was sham-operated (6) and replaced in DD. The free-running rhythm was unperturbed by this surgery. The bird was placed in constant light on the day marked LL. Body temperature rose and rhythmicity was lost.

tained in constant darkness (up to 42 cycles in one case). As was expected (5), the period of the rhythm changed as a function of time in DD. The rhythm was synchronized by (entrained to) light cycles (LD 12:12), and, under these conditions, its period was 24 hours and the onset of the daily temperature rise preceded lights on (Figs. 1 and 2).

Pinealectomy (6) abolished the body temperature rhythm in constant darkness in all eight birds on which it was successfully performed (Fig. 2). In no case did rhythmicity reappear. (The longest DD recording was 33 days.) Each of five birds served as its own control in that rhythmicity in DD was observed before surgery (as in Fig. 2); three other birds had been pinealectomized for some time before recording began. Sham operation had no effect on rhythmicity (Fig. 1).

Although arrhythmic in constant darkness, the body temperatures of pinealectomized birds were rhythmic in the presence of light cycles (LD 12:12) and were entrained by them. In pinealectomized birds on LD 12:12 the daily body temperature rise occurred earlier with respect to lights-on than in unoperated birds on LD 12:12—a difference not seen in the simultaneously recorded activity records. However Gaston (1) has reported a similar effect of pinealectomy on the phase of the activity rhythm in birds exposed to LD 6:18.

Arrhythmic body temperatures, similar to those of pinealectomized birds in DD, were recorded from normal sparrows in constant light (Figs. 1 and 3). Birds in LL raised their temperatures immediately (Fig. 1) and main-

tained them at high level indefinitely. However, the recovery of rhythmicity in subsequent LD cycles was different from a like process in pinealectomized birds. The transfer of a normal bird from LL to LD produced an immediate recovery of body temperature rhythmicity (Fig. 3 top), whereas the transfer of a pinealectomized bird from DD to LD initiated rhythmicity

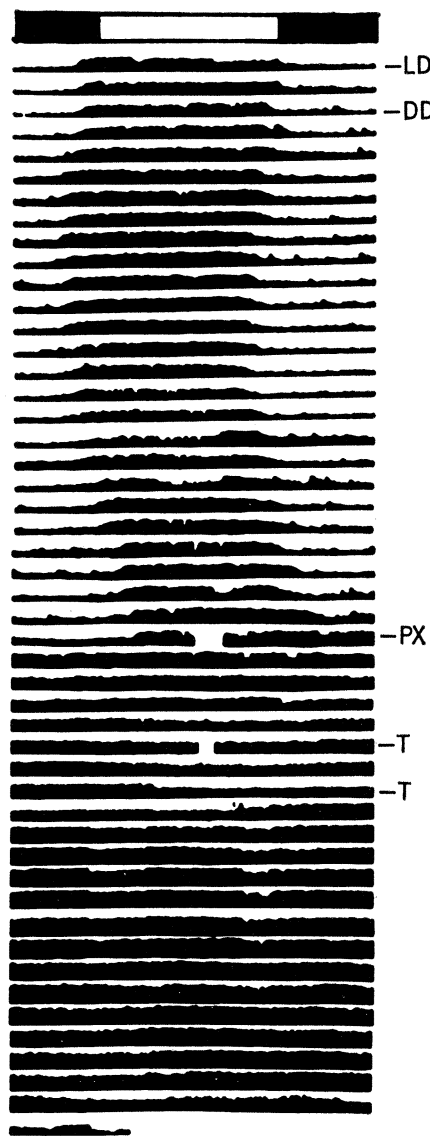


Fig. 2. The effect of pinealectomy on body temperature. The telemeter was implanted in the bird whose record is shown 103 days before body temperature recording began. During that period the bird was maintained on the light cycle, as is indicated by the bar at the top of the record. On the day marked DD, the bird was placed in constant darkness. At PX the bird was pinealectomized and returned to DD. T indicates technical problems with the monitoring system. The faint rhythm discernible for several days during the second week after pinealectomy is believed to have been due to a light leak. The data were handled as in Fig. 1.

only gradually (Fig. 3 bottom and Fig. 4).

Analysis of variance in daily temperature maximums, minimums, and temperature maximums, whether or not ment indicates that (i) light raised the temperature maximums, whether or not the birds were pinealectomized; (ii) pinealectomy raised the temperature minimums regardless of whether the birds were in LD or DD; (iii) pinealectomy had a greater effect on the amplitude of daily temperature changes than did light; and (iv) the effects of pinealectomy and light on the temperature maximums, minimums, and amplitudes were independent (Fig. 5). Examination of the records obtained from individual birds in the different conditions fully supports the results obtained for the

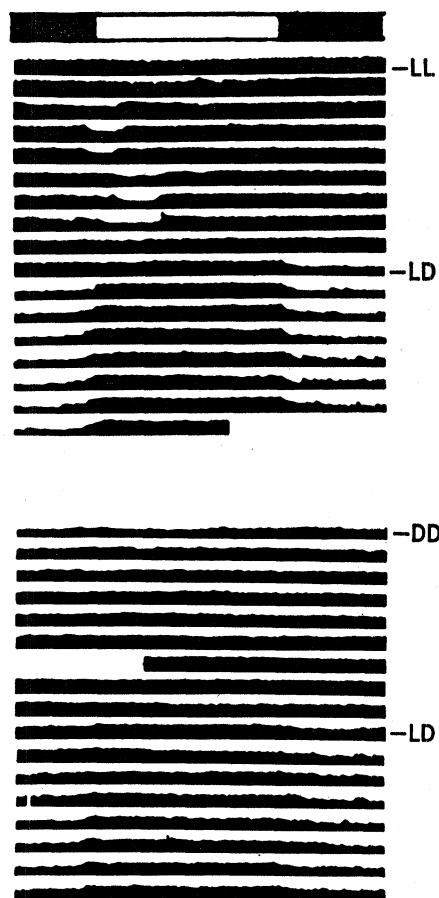


Fig. 3. Comparison of arrhythmicity produced by constant light with that produced by pinealectomy. The two types of arrhythmicity and the subsequent responses of the bird to LD can be compared in two records taken from the same bird before (top) and after (bottom) pinealectomy. The change from LL to LD initiates rhythmicity immediately in the normal bird, whereas after pinealectomy the change from DD to LD produces rhythmicity more gradually and the resulting rhythm is of lower amplitude.

data grouped by treatment. As is suggested by Fig. 5, pinealectomy lowers the temperature maximum in DD significantly ($P < .01$ in a two-tailed t -test).

In *P. domesticus* the persistence in constant darkness of two overt rhythms (locomotor activity and body temperature) has now been shown to depend on the presence of the pineal. Although persistence in constant darkness is abolished by pinealectomy, the presence in pinealectomized birds of residual time-keeping machinery is indicated by the fact that, when entrained (LD 12:12), their daily body temperature rise occurs in anticipation of lights on. The question now arises as

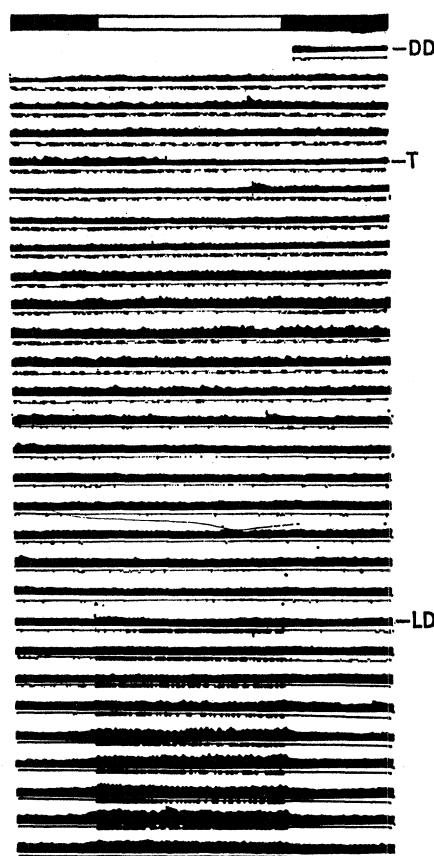


Fig. 4. Simultaneously recorded body temperature and perch-hopping activity records from a pinealectomized bird. The bird had been pinealectomized for 28 days and had been in DD for 16 days when the telemeter was implanted (just prior to the initiation of body temperature recording). Each day's activity record has been placed below the corresponding temperature record. Both activity and body temperature appear to be aperiodic in DD. At LD the bird was placed in the LD 12:12 cycle indicated by the bar at the top of the record. Rhythmicity in the activity record appears rapidly, while the response of the body temperature cycle is slower. T indicates a 30-hour period of technical difficulty.

to how closely coupled are these two overt rhythms. Is the circadian rhythm of body temperature simply a direct reflection of that of activity (or vice versa) or are the two rhythms causally independent?

In humans entrained to short-period cycles or in constant conditions, temperature and activity rhythms may dissociate, exhibiting different periods (7). This is direct evidence that the two rhythms may not be causally related. No such evidence exists for birds, and the data in our study do not bear directly on the question of possible dissociability. However, many of the details of the body temperature records did not directly correspond to the perch-hopping records made simultaneously (for example, the beginning of the daily temperature rise almost always preceded the onset of perch hopping). While this observation suggests that the two rhythms may not be causally related, its force is weakened by the fact that only perch-hopping behavior (not total activity) was monitored. Another kind of observation however, makes clear that if a causal relationship does exist between these two rhythms, it is not complete. The data shown in the bottom of Fig. 4 are simultaneously collected activity and body temperature records from a pinealectomized sparrow ex-

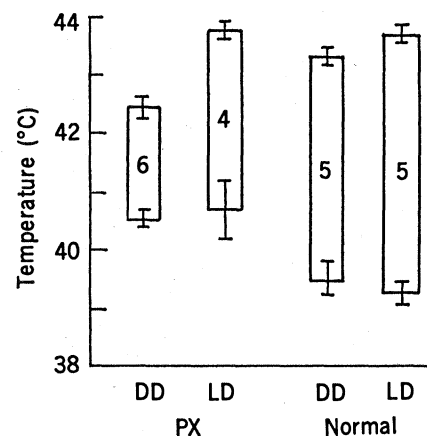


Fig. 5. Daily body temperature maximums and minimums of birds grouped by treatment. The bars of the graph are defined by the mean daily body temperature maximums and minimums. One standard error is indicated in each direction for each mean. The number on the bar indicates the number of birds from which data were used to calculate the means (measurements on 3 days were averaged for each bird). Temperature measurements were taken manually from the continuous records and were based on telemeter calibrations preceding and following a record.

posed to a light cycle after many days of arrhythmicity in DD. The activity rhythm is evident from day 1 of the light cycle, whereas it is at least 4 days until a clear body temperature rhythm can be discerned.

There are two effects of pinealectomy on the body temperature regulation of *P. domesticus*. The circadian rhythm is abolished, and the amplitude of the temperature fluctuations is reduced. These two effects may be but are not necessarily related. One could imagine that it would be possible to produce arrhythmicity without affecting amplitude or conversely to affect amplitude without abolishing rhythmicity. Thus it may be that independent of its role in the circadian system, the pineal is involved in the fine tuning of the hypothalamic thermostat (8).

The pineal organ and its metabolites have both been linked to circadian rhythmicity and to the control of body temperature. In two independent studies (9), pinealectomized rats shifted the phase of their activity rhythms more rapidly than did normals in response to a change in the phase of the light cycle. Daily rhythms in pineal level of serotonin, melatonin, and norepinephrine have been described, as have rhythms in the activity of two enzymes (hydroxindole-*O*-methyl transferase and *N*-acetyltransferase) involved in the conversion of serotonin to melatonin (10, 11). Melatonin injected subcutaneously in mice lowers the body temperature by 2° to 3°C (12). Pinealectomy lowers cloacal temperature in lizards (13)—an effect that may be due either to a change in thermoregulatory behavior or to direct interference with physiological mechanisms of temperature control.

In most previous studies the circadian system has been treated as a "black box"; the organism has been subjected to environmental "input" (usually light or temperature signals), and the resulting changes in its rhythmic behavior have been measured and analyzed as "output." Our own results and those of others indicate that further analysis of pineal function may provide a lever with which to pry the lid off the "black box" of circadian organization.

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4. Birds were obtained from local populations in the vicinity of Austin, Texas, and were maintained in outdoor aviaries (natural lighting) and indoor aviaries (LD 12 : 12) until used in the experiment. Body temperatures were monitored with telemeters (S-TELE, 22322 Shady-croft, Torrance, California 90505) which were embedded in paraffin (m.p. 61°C). The telemeter receiving and recording equipment was designed and built by Edward Kluth and George Wyche. The telemeters weighed 1 to 1.5 g and were about 9 by 18 by 4 mm. Telemeters were calibrated and then implanted in the abdominal cavities of the birds under aseptic conditions and Equi-Thesis (Jensen-Salsbery Labs.) anesthesia. Polyotic (soluble tetracycline, American Cyanamid Co.) was administered in the drinking water for 3 days after surgery. The birds were placed in individual recording cages, isolated in temperature-controlled incubators, and insulated from sound disturbance by continuous white noise. Each bird had free access to food and water and to two activity-recording perches. The temperatures in the isolation incubators were between 19.5° and 25.0°C. The largest daily fluctuations (which occurred during the LD 12 : 12 light cycles due to heat from the 4-watt Ken Rad Cool White fluorescent bulb) did not exceed 3.5°C and had no discernible influence on the birds' body temperatures. Light intensities in the chambers during constant light or light cycles ranged from less than 100 lux in the corners to 500 lux in the brightest portions of the cages.
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Color- and Edge-Sensitive Channels in the Human Visual System: Tuning for Orientation

Abstract. After subjects scanned red stripes tilted clockwise off vertical and green stripes tilted equally but counterclockwise, vertical test stripes appeared tilted counterclockwise when red but clockwise when green. As the angle between scanned and test stripes was increased from 0° to 75°, the magnitude of the tilt aftereffect rapidly increased to a peak between 10° and 15° and then dropped close to zero at about 40°, a result consistent with narrowly tuned edge-sensitive channels.

The existence of channels in the human visual system which are both selectively sensitive to color and tuned to a limited range of edge orientations was suggested by early observations and has been further supported by recent psychophysical experiments (1). In 1965 McCollough (2) reported that following a period of alternately scanning an orange-black vertical grating and a blue-black horizontal grating, a vertical

black-white test grating appeared faintly blue-green, while its horizontal counterpart appeared faintly orange. When ordinary chromatic afterimages are excluded as an explanation (3), McCollough's demonstration implies desensitization of color and edge-orientation specific channels, although the breadth of tuning for orientation remains unspecified (4). We have found confirming evidence for such channels by show-