which was enclosed by wire mesh to permit observation from outside the room. The cats were weighed and then observed for a 2-hour period each day. Special attention was paid to affective interaction between the cats, play, aggression, levels of activity, and motivation for food.

The day following the operations both groups of lesioned animals were up, alert, moving about, and grooming. When presented with food they sniffed and licked and in general ate sparingly. By the second day, all the operated cats were more active and when allowed free access on the floor would chase each other and run about. There was always considerable neck and body biting, rolling over, and kicking with the rear legs. When food was presented all cats came to the front of the enclosure, vocalized, and pawed at the mesh. When the food was placed on the floor all gathered around and ate readily. After feeding, the kittens would lie down, lick, and groom. This general pattern was consistent throughout the observation period.

There was no growth deficit in any group. The groups with lesions in the amygdala and neocortex closely paralleled one another, and the slope of weight gain was the same as that for the slightly older normal group. Terminal body weight of the amygdalectomized group was 1172 ± 84 g, as compared with 1036 ± 151 for the neocortical group, and 1265 ± 135 for the normal group.

No hypopituitarism occurred. Adrenal weights for the amygdalectomized, neocortical, and normal groups were 0.203 ± 0.020, 0.212 ± 0.042, 0.189 ± 0.062 g, respectively. Pituitary weights were 0.024 ± 0.004, 0.023 ± 0.005, and 0.023 ± 0.002 g; testicular weights were 0.236, 0.216, and 0.340 g; thyroid weights were 0.131 ± 0.031, 0.172 ± 0.009, and 0.208 ± 0.009 g, respectively. Histological examination of the endocrine organs revealed no significant difference between groups. The testes of all males were immature, with no tubule formation or spermatogenesis.

The results indicate that the post-amygdalectomy syndrome of adult cats does not appear in kittens—at least not in kittens under 13 weeks old. There was very little difference in behavior between groups, either in the early postoperative period or after recovery. The only observable gross difference was that the amygdalectomized cats were possibly less competitive for food than the normals. However, since the normals were slightly older and larger they would be expected to be dominant.

No evidence of growth disturbance or endocrine deficiency was observed. The suggestion of precocious puberty in females is in agreement with the findings of Elwers and Critchlow (5), who observed precocious puberty in female rats after lesions were placed in the amygdala.

The behavioral effects of amygdalectomy in the cat may depend upon a certain level of neuroendocrine maturation.

ARTHUR KLING

Institute for Psychosomatic and
Psychiatric Research and Training,
Michael Reese Hospital,
Chicago, Illinois

References

1. L. Schreiner and A. Kling, *J. Neurophysiol.* **16**, 643 (1953).
2. A. Kling, J. Orbach, N. Schwartz, J. Towne, *Arch. Gen. Psychiat.* **3**, 391 (1960).
3. L. Schreiner and A. Kling, *A.M.A. Arch. Neurol. Psychiat.* **72**, 180 (1954).
4. H. Koikegami, S. Fuse, S. Hiroki, T. Kazami, Y. Koyeyama, *Folia Psychiat. Neurol. Japon.* **12**, 207 (1958).
5. M. Elwers and V. Critchlow, *Am. J. Physiol.* **198**, 381 (1960).

29 June 1962

Daily Rhythm in the Reaction of Fish to Light

Abstract. Bluegills in a 24-hour light-dark cycle were exposed briefly to light at a random time in the daily dark period. The duration of the accompanying "light-shock reaction" daily became longer at times early in the dark period and shorter at times in the later hours of darkness.

In the bluegill the light-shock reaction which immediately follows a sudden exposure to bright light after a time in darkness (or very dim light) is a sequence of peculiar movements and postures, beginning with a descent to the bottom of the aquarium. The fish may sink a short distance before halting and recovering, or it may continue to the bottom, staying there for varying periods. On the bottom it may remain immobile, fan its fins without locomotion, or move erratically backward or forward, sometimes butting into obstructions it would otherwise avoid. Eventually its movements become more organized and it rises. Fish kept in light beyond the time of recovery from the light-shock reaction and then placed in darkness fail to "react" to a second exposure during the first 5 or more minutes of darkness; the ability to react is lost with time in the light and regained with time in darkness. The duration of the light-shock reaction, or the "recovery time," is here defined as the interval that begins with the onset of bright light and ends when the fish returns to its normal attitude. The light-shock reaction, or similar reactions, in other fishes have been described elsewhere (*1, 2*). Apparently the light-shock reaction has not been extensively studied.

The light-shock reaction was of interest as a means of determining whether fish in a 24-hour light-dark cycle exhibit time-coordinated changes in behavior. The question was: Do recovery times following sudden exposure to light of a given brightness fluctuate predictably with time in the daily dark period, and does the timing of any such daily fluctuations indicate that they are regulated from within the fish by an internal rhythm which is in phase with the 24-hour light-dark cycle?

A typical experiment consisted of exposing fish for a number of minutes to a bright light (giving them a "light-shock") at a randomly determined time in the daily dark period. The light-shock was given randomly so that the influence (if any) of exposure in the dark period on one day on responses in the dark period of the next day would be randomized; thus, any regularity in the observed daily changes in recovery time would not be attributable to the timing of the light-shock. At the chosen time each day the observer illuminated the fish and actuated a stopwatch. If a fish hovered or continued to swim above the bottom, a reaction of zero duration was recorded. If a fish descended but halted before touching the bottom, a 5-second reaction was recorded. Longer reactions were measured to the nearest 5-second interval in which the fish rose from the bottom. After a number of days the daily measurements of recovery time were combined to obtain independent estimates of mean recovery time at the randomly selected points in the daily dark period (*2*).

In one experiment nine bluegills [*Lepomis m. macrochirus* (Rafin.)] were confined, in groups of three, to separate, light-tight chambers in a darkened room. A fluorescent tube

(400 lux at the water surface) in each chamber was regulated automatically to provide alternating daily periods of 12 hours 10 minutes of light and 11 hours 50 minutes of darkness. Light-shocks in the daily dark period were given by means of an incandescent lamp (1000 lux at the water surface), which was connected to a toggle switch near an observation window in the chamber. The chambers were opened daily for 20 to 30 minutes, beginning several minutes after the onset of the daily light period, to measure the water temperature, feed the fish (with earthworms), and clean the tanks and replenish them with tempered water. Water temperatures increased 2°C or less during the light period and decreased a corresponding amount during the dark period. But during the 63-day test period temperatures varied irregularly from 22° to 26° (average, 23.8°); therefore it may be assumed that, over a number of days, the temperature changes during the dark period were irregular.

For the first 20 days each group of three fish was given a 5-minute light-shock (1000 lux) at a random time in the dark period. The estimates of mean recovery time obtained by combining these daily measurements are shown in Fig. 1 (dashed curve). The daily rhythm in the light-shock reaction was manifest in a regular oscillation of mean recovery time with time in the daily dark period. The light-shock reaction increased from zero duration a few minutes after the onset of the dark period to a maximum in the early-middle hours of darkness and then decreased somewhat in the later hours of the dark period. Pooling of the daily measurements obscured day-to-day changes in the rhythm of the light-shock reaction. On the first day, mean recovery time remained constant (or decreased only a small amount) with time in the later hours of the dark period. In the succeeding 15 to 18 days, mean recovery time in the later hours of the dark period became shorter and was shortest in the last hour of darkness. In later studies with other fish, under similar conditions, this alteration in the rhythm of the light-shock reaction occurred during the first 10 to 20 days.

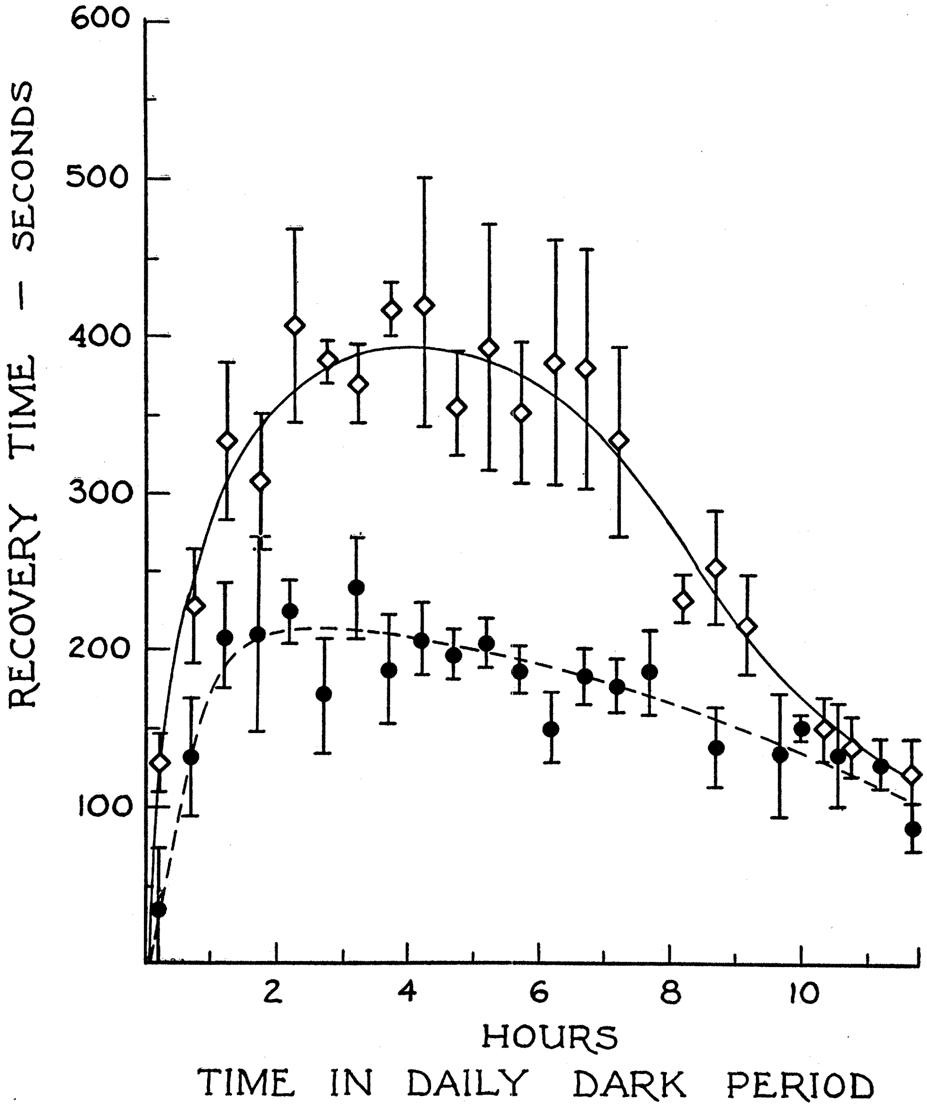

Fig. 1. Plot of combined daily measurements of recovery time. (Dashed curve) Mean recovery time of nine bluegills during the first 20 days of the 63-day test period; (solid curve) mean recovery time during the last 17 days of the test period. The fish were given alternating daily periods of light (12 hours, 10 minutes) and darkness (11 hours, 50 minutes); a period of feeding at the start of the daily light period; and a brief light-shock at a random time in the daily dark period. Each mean and standard deviation is an independent estimate of recovery time based on the reactions of three, six, or nine fish to the random light-shock (see text).

After the first 20 days recovery time in the middle hours of the dark period became longer. The prolongation of recovery time began between days 24 and 36 for different fish, but, owing to the method of measurement, it was difficult to tell whether the prolongation was continuous from day to day. To measure the longer reactions, the random light-shock was lengthened from 5 to 10 minutes from day 24 onward. The estimates of mean recovery time at random times in the dark period on the last 17 days are shown in Fig. 1 (solid curve). In subsequent work with other fish a similar lengthening of recovery time was observed after 20 to 40 days.

The dependence of the 24-hour rhythm of the light-shock reaction on the corresponding periodicities of illumination and feeding is not settled (*2*). The decrease in recovery time with time in the later hours of the daily dark period suggests that the fish "anticipated" either the start of the daily light period or the time of feeding, or both. There was no detectable change in the physical environment paralleling the decrease in recovery time. Accordingly, the reduction in recovery time in the later hours of the dark period during the first 10 to 20 days reflects an internal regulation of the rhythm of light-shock reaction.

Bluegills (and other fishes) trained to use the sun as a directional reference are able to compensate for changes in solar time by remaining oriented in the "trained" direction throughout the day (*3*). It has been proposed that the sun-orientation rhythm is regulated by an internal rhythm, or inner time sense. The rhythmic fluctuations in the light-shock reaction in phase with the daily light-dark cycle could be a manifestation of this capacity. Such clear-cut behavior rhythms of fishes could be used in further investigations of the so-called time sense (*4*).

ROGER E. DAVIS

Department of Fisheries,
School of Natural Resources,
University of Michigan, Ann Arbor

References and Notes

1. C. M. Breder, Jr., *Bull. Am. Museum Nat. Hist.* **117**, 393 (1959).
2. R. E. Davis, *Dissertation Abstr.* **21** (Dec. 1961).
3. A. D. Hasler and H. O. Schwassmann. *Cold Spring Harbor Symp. Quant. Biol.* **25**, 429 (1960).
4. I conducted this work in the department of zoology at the University of Wisconsin, Madison. I wish to thank Dr. John C. Neess, who supervised this project and obtained support for it through the National Science Foundation.

7 March 1962

Gravity Factor for Auxin Transport

Abstract. The elongating internodes of the axis of a vigorous dicotyledonous plant develop strong curvatures if the tropistic effect of gravity is eliminated on a clinostat. Similar curvatures are produced by unbalancing either the supply of auxin or its transport paths, but only in the absence of unidirectional gravity as a distributive force.

The corrective growth response in the axis of a plant after its placement in a nonvertical position is known to be mediated by an imbalance of auxin induced by gravity (*1*), yet no experimental evidence has been offered to support the possibility that the vertical position of the axis is maintained by a similar effect of gravity on transport of its growth regulators. In 1952 Söding (*2*) made the broad statement that such transport is not influenced by gravity, but Snow (*3*) noted that "phenomena of polarity make it probable that gravity does affect longitudinal transport of auxin."

When such 19th-century workers as Sachs and Pfeffer were using horizontal clinostats in their studies of plant form and movements, they had no knowledge of auxins. Asymmetric growth of the primary axis was never reported. Authors of current textbooks appear to be guided by Sachs's observation (*4*, p. 256) that the axis of the plant continued to grow "in the direction in which it was placed."

From a continuous series of tests started in 1958, using over 20 species of dicotyledonous plants on horizontal clinostats turning at rates from 1/240 to 1 revolution per minute, about 96 percent of plants with active apical meristems have been found to show pronounced growth curvatures in the elongating internodes of their major axes, in the region of expanding leaves and regardless of their phyllotaxy. Strong curvatures develop within a day or two, depending on the growth rate rather than on age or size of the plant. They exhibit minor fluctuations and vary from approximately 45° to 180°, as illustrated in Fig. 1. The rate and degree of curvature are independent of the intensity or period of illumination and of the speed of rotation.The tests were made with vigorous plants rooted mostly in plastic pots of loam soil, watered normally and tested in a temperature range from 17° to about 25°C.

The direction of the curvature of an undisturbed axis is unpredictable unless the stalk of the plant leans perceptibly to one side; in these cases the growth curvatures of the tip will be in that direction. Adjoining internodes commonly develop their curvatures in the same plane, but exceptions occur in a few species, with resultant twisting effects. A predictable curvature can be produced by removing the leaves from one side of a growth zone, as illustrated with the stock plant in Fig. 2. The growing tip bends toward the defoliated side but only when the plant is rotated on the clinostat. The force of gravity seems to equalize some material supplied by the leaves, even to the extent of straightening the curvature in less than 24 hours if the plant is returned to the vertical position before the axial tissues have matured. Possible differences in the nutrition, auxin supplies, and water relations within leafy plants are thus regularly equalized unless the effects of gravity are eliminated on a clinostat.

A predictable curvature that appears only if the plant is turning on a clinostat can be produced if a film of lanolin containing 1 percent triiodobenzoic acid (TIBA) is applied to one side of the growth zone of an intact plant such as tomato or sunflower. The growth curvature is always toward the triiodobenzoic acid, which is known to interrupt the transport of auxin in tissues affected by it (*5*). Return of the plant to the vertical position results in straightening the curvature if a minimal amount of triiodobenzoic acid has been applied. This curvature is clearly due to more endogenous auxin moving down the

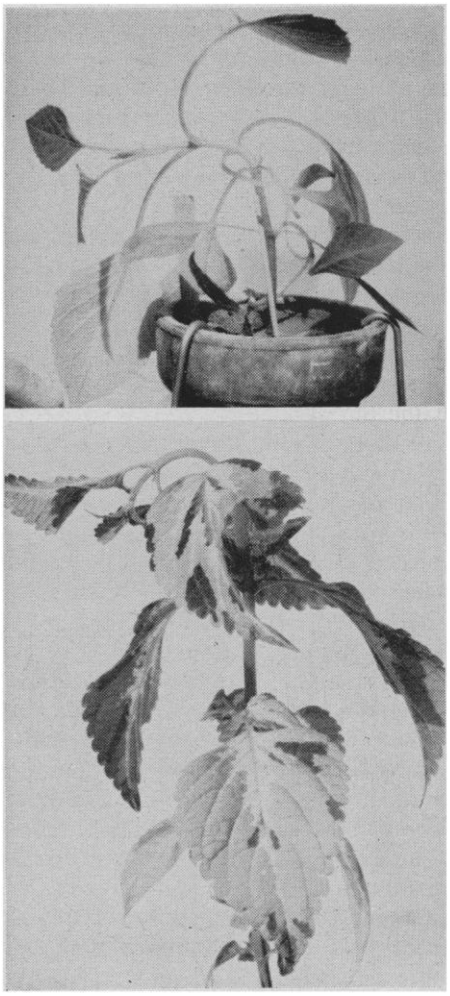

Fig. 1. (Top) *Dahlia pinnata* with 90° bend in axis after 3 days on clinostat. (Bottom) Strong curvature in tip of *Coleus blumei* after 24 hours on clinostat.

Fig. 2. Growth zone of *Matthiola incana* bent to defoliated side after 24 hours on clinostat.