sample, it is true, but the results are remarkably consistent. They indicate that prolonged periods of perceptual deprivation can produce a considerable degree of disorganization of brain activity, with effects still discernible a week later. In the light of these results one can only wonder about the possible physiological and psychological state of prisoners of war and others who, in the past, have been isolated for months or even years (9).

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References and Notes

1. J. P. Zubek *et al.*, *Can. J. Psychol.* **14**, 233 (1960); *ibid.* **15**, 83 (1961); *Perceptual and Motor Skills* **15**, 171 (1962).
2. P. E. Kubzansky, in *The Manipulation of Human Behavior,* A. D. Biderman and H. Zimmer, Eds. (Wiley, New York, 1961), p. 51.
3. W. Heron, *Sci. Am.* **196**, 1 (1957).
4. Unpublished results.
5. G. L. Engel *et al.*, *Arch. Neurol. Psychiat.* **51**, 134 (1944).
6. W. Heron *et al.*, *Can. J. Psychol.* **10**, 13 (1956).
7. G. E. Ruff and E. Z. Levy, *Am. J. Psychiat.* **115**, 793 (1959).
8. D. E. Cameron *et al.*, in *Psychophysiological Aspects of Space Flight,* B. E. Flaherty, Ed. (Columbia Univ. Press, New York, 1961), p. 225.
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Anoxia: Tolerance in Reptiles

Abstract. *Measurements of the lengths of time various reptiles can continue to breathe in atmospheres of nitrogen have shown that turtles are several times more tolerant of these conditions than are other reptiles. The major correlate of this tolerance is taxonomic, rather than ecological.*

Turtles (species not stated) breathing pure nitrogen are able to survive for 27 hours at 20°C (*1*). The loggerhead musk turtle, *Sternothaerus minor*, can tolerate complete anoxia for over 12 hours at 22°C; in order to do so it must use anaerobic glycolysis (*2*). If adult mammals of the several species which have been tested breathe pure nitrogen, they die after about 5 minutes; newborn altricial mammals survive up to 50 minutes of this treatment (*3*). Hibernating hedgehogs (*Erinaceus*) tolerate 1 to 2 hours of anoxia, while active hedgehogs are killed in 3 to 5 minutes (*4*). Similar resistance has been noted in other hibernating mammals, and is probably related to their relatively low metabolic rate. Data on the ability of other amniotes to survive anaerobically are not available. It would be interesting to know the systematic and ecological distribution of this neglected physiological parameter, as well as its biochemical basis. Accordingly, I have been systematically cataloging the lengths of time various reptiles can tolerate anoxia, and to date have made measurements on about 400 individuals representing 17 families, 45 genera, and 70 species.

Each animal is kept in the laboratory at 22 ± 3°C and starved for at least 7 days before being used in an experiment. The photoperiod is approximately 15 hours. Each measurement is made in the following manner. The animal is sealed in a gas-tight chamber made of glass; this is then completely filled with oxygen-free water. The water in the chamber is immediately displaced with nitrogen (containing less than 0.001 percent oxygen), which is then passed through the chamber and exhausted at the rate of $250\ \text{cm}^3/\text{min}$ for the remainder of the experiment. After an animal weighing more than 40 g has breathed nitrogen for about 2 minutes, the chamber is again flushed with water in order to expel exhaled oxygen. By means of a water bath, the temperature of the chamber and the animal contained therein is maintained at 22 ± 0.5°C. Under these conditions, all reptiles tested breathe the nitrogen freely, and in this manner all molecular oxygen is washed from their lungs, circulatory systems, and tissues. In control experiments in which air replaced nitrogen, none of the reptiles tested appeared to suffer any ill effects from the 90-second immersion in water. Each animal is observed visually during its exposure to nitrogen. When it has failed to breathe for a period more than five times the duration of the period between the preceding two breaths, it is removed from the chamber and can then usually be resuscitated by means of pulmonary inflation with oxygen. Tolerance time is defined as the period between the first and last breaths of nitrogen.

Table 1. Tolerance times of various families of reptiles.

Family	No. of species tested	Mean and range of species means (min)
	Turtles	
Kinosternidae	5	876 (480–1140)
Chelydridae	1	1050
Testudinidae	14	945 (495–1980)
Cheloniidae	2	120 (114–126)
Trionychidae	1	546
Pelomedusidae	2	980 (738–1218)
Chelidae	2	465 (360–570)
	Lizards	
Iguanidae	6	57 (22–79)
Gekkonidae	1	31
Teiidae	1	22
Scincidae	4	25 (20–30)
Anguidae	1	29
	Snakes	
Boidae	3	59 (41–61)
Colubridae	22	42 (25–84)
Viperidae	3	95 (64–118)
Elapidae	1	33
	Crocodilians	
Crocodylidae	1	33

Results of these measurements are presented in Table 1. The most significant feature of these data is the presence of two distinct groups: one with a minimum tolerance time of more than 4.5 hours (usually about 12 hours), the other with a maximum tolerance time of less than 2.5 hours (usually about 45 minutes). The first group includes all the chelonians tested except the sea turtles, and the second group includes snakes, lizards, and crocodilians. The sea turtles (Cheloniidae) tested appear to be intermediate between these two groups. Thus, the major correlate of this trait is taxonomic, rather than ecological. Speculation concerning variation between the families within each of these two groups is unprofitable at this time because many families are as yet represented by only two or three individual measurements; intraspecific variation is great, so that some apparent differences may disappear when more data are collected. Two families, the Testudinidae and the Colubridae, are represented by samples containing a sufficient number of genera, species, and individuals to make an examination of the variation in and between the taxa within families worth while. Variation between genera appears to be no greater than variation between the species of a given genus. Intrafamilial variation between species shows no obvious correlation with habitat or ecology; tropical and boreal species show no consistent differences, nor do burrowing and diving species always appear to tolerate anoxia better than do terrestrial and arboreal ones. Within species, tolerance time exhibits a rough proportionality with the logarithm of body mass, seems unrelated to sex, and can be affected by the experimental animal's nutritive condition; animals starved for more than 2 months at 22°C tend to have smaller tolerance times than controls. Quiet individuals usually continue to breathe longer than excited ones. In contrast to newborn mammals, newborn or newly hatched reptiles appear to tolerate anoxia no better than adults. Current data suggest the possibility of significant seasonal differences in some species, but as yet there is insufficient information to confirm this.

The great intraspecific variation in tolerance of anoxia (coefficient of variation often greater than 20 percent) suggests that this trait is in itself of small adaptive significance, since characters maintained under strong selection pressure should show little random intraspecific variability. To determine the correlates of this variation, it is necessary to test statistically large numbers of individuals of each of a few selected species. A number of phylogenetically important groups, such as the Sphenodontidae, Dermochelyidae, Amphisbaenidae, and Typhlopidae also remain to be tested.

Knowledge of the distribution of tolerance of anoxia among reptiles is making possible a more effective study of the biochemical mechanisms responsible for the anaerobic survival of amniotes. I have previously suggested that the low metabolic rate of turtles (in contrast to mammals, who have much greater energy requirements) might allow them to survive anaerobically by utilizing the small energy yield of glycolysis alone (*5*). Since the energy requirements of other reptiles are about the same as those of turtles, the much shorter tolerance times for lizards, snakes, and crocodilians make it clear that the situation is more complex. Perhaps the explanation is related to the fact that turtles have much higher concentrations of bicarbonate ion in their body fluids than do other reptiles (*6*) and are thus better able to buffer anaerobically produced acid metabolites. The approximate ratio of plasma bicarbonate for turtles : sea turtles : other reptiles is 5 : 3 : 2. This ratio fits qualitatively with relative tolerance times but is quantitatively sufficient to explain less than half the difference. Measurements of total body buffer capacity and of lactic acid and carbon dioxide production during anoxia may clarify this problem and may indicate whether these reptiles have more exotic metabolic mechanisms. Carp exposed to long-term anoxia form fats, rather than lactic acid (*7*), and the possibility remains that turtles are also able to utilize anaerobic hydrogen acceptors other than pyruvate and produce substances less disturbing to tissue *p*H than lactic acid (*8*).

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References and Notes

1. J. M. Johlin and F. B. Morland, *J. Biol. Chem.* **103**, 107 (1933).
2. D. A. Belkin, *Physiologist* **5**, 105 (1962).
3. H. E. Himwich, *Brain Metabolism and Cerebral Disorders* (Williams and Wilkins, Baltimore, 1951), p. 127.
4. G. Biörck, B. Johansson, H. Schmid, *Acta Physiol. Scand.* **37**, 71 (1956).
5. D. A. Belkin, dissertation. Univ. of Florida; *Dissertation Abstr.* **22**, 3300 (1961).
6. H. W. Smith, *J. Biol. Chem.* **82**, 651 (1929); F. C. Southworth, Jr., and A. C. Redfield, *J. Gen. Physiol.* **9**, 387 (1926).
7. P. Blazka, *Physiol. Zool.* **31**, 117 (1958).
8. Supported by grants from the National Science Foundation (G 9817) and the National Institutes of Health (2 G 251).

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Scotopic Spectral Sensitivity in the Monkey

Abstract. *Three rhesus monkeys learned to adjust a small illuminated spot to threshold intensity. Then, while dark adapted, they "tracked" their thresholds to stimuli spaced across the visible wavelength spectrum. Spectral sensitivity functions were determined for each animal from these threshold records. The functions agreed well with results obtained from a human subject in the same apparatus, and with the standard human scotopic function defined by the International Commission on Illumination. However, the monkeys' relative sensitivity was slightly higher in the long-wavelength portion of the spectrum.*

A great deal of behavioral and physiological work is being done with monkeys, yet there is a lack of detailed information on the sensory capacities of these animals. Recently, new behavioral techniques for obtaining such psychophysical data have become available. The research reported here (*1*) uses one such technique to determine the dark-adapted absolute threshold of rhesus monkeys as a function of stimulus wavelength.

The method was devised by one of us to determine absolute thresholds in the pigeon (*2*). The procedure is often called "tracking" and is based on a method of human audiometry invented by Békésy (*3*). The subject keeps the stimulus intensity varying up and down across its absolute threshold by alternately pressing on two levers, and a continuous record of the intensity "tracks" the threshold through time.

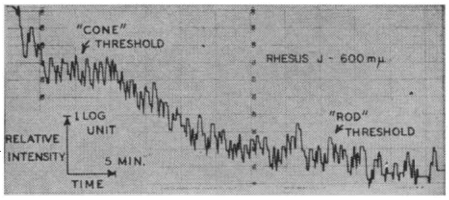

Fig. 1. Dark adaptation curve of a monkey after previous exposure to a white screen illuminated by photoflood lights. Note the two segments, first "cone," then "rod."

The subjects were three young rhesus monkeys, two male and one female. During an experimental session, the monkey sat in a restraining chair in a small light-tight room facing a stimulus panel. The collar of the monkey's chair held its head with the eyes about 25 cm from the panel. On the panel was a circular stimulus patch 18 mm in diameter. Two response levers protruded below the patch. The monkey's task was to press the left lever repeatedly when the patch was visible, and the right lever when the patch appeared dark. This behavior was maintained by a chain of events that led to food reinforcement. Two or three times a minute, presses on the left lever closed a shutter in the stimulus beam path. When the stimulus had been turned off in this way, presses on the right lever caused a banana flavored pellet (*4*) to fall into a cup between the levers. However, the shutter and the pellet dispenser were activated by the levers only at randomly spaced intervals. At other times, presses caused the rotation of an optical wedge located in the stimulus beam. Presses on the left lever moved the wedge in such a way as to reduce the stimulus intensity, and presses on the right lever acted to increase the intensity. As a result, the stimulus kept oscillating about the monkey's threshold. When the stimulus disappeared below threshold, the monkey pressed the right lever, causing the stimulus to get brighter; when the patch became visible, the monkey pressed the left lever, causing the stimulus to dim and disappear. The monkey had no way of knowing when this tracking procedure, rather than the shutter-food pellet sequence, was in effect, so it gave a steady stream of responses. This procedure has complexities not mentioned here; further details are described elsewhere (*5*).

After a few weeks of practice the monkeys became proficient at the tracking task. Changes in the stimulus lumi-