of being distracted by the ambiguities inherent in the detail of the slopes of short regions of the tracer activity curve.

Any biological system, into different points of which the tracer can be added, can be defined in different ways depending on the entry point and the entry flow. The occupancy-to-capacity ratios, of the same compartment in the different systems (defined in terms of different entry flows), can then be used for derivation of the relation between entry flows. Separate occupancy-to-capacity ratios can be obtained simultaneously by use of two or more isotopes.

In clinical studies, a small quantity of blood is commonly the most convenient part of the system for which the occupancy and the capacity can be readily obtained. Serial quantitative activity measurements of other parts of the body, with calibrated uptake counters, radioisoptope scanners, or high-resolution profile scanners, give the capacities of these other parts. If the material in the blood exists in two biochemically separable states, and if the occupancy-to-capacity ratio for the first can be measured, the occupancy for the second can be derived from the capacity, or the capacity from the occupancy.

Activity measurements cannot, of course, be carried on for infinite times. In many instances, however, an apparent final exponential decrease is reached and can be used for determination of the occupancy, provided due note is taken of implications of the assumption that the exponential decrease continues. When the capacity is very large and the entry flow is very small, chemical estimates of the entry flow and the capacity allow the occupancy to be determined even when part of it lies far beyond the time of the last measurement. From the knowledge of the total occupancy, an effective life can be derived, or the physiological consequences of a biphasic activity curve can be deduced. Such a biphasic curve commonly results from a recirculation; in some instances in which there is significant delay before the return of tracer from a part of the system, the system can be redefined to exclude the material that is in the part. The flow of material returning must then be considered a component of the entry flow to the new system.

Biological systems deviate from steady-state behavior over short times because of irregularities of food intake and because of response to external stress. An imposed deviation occurs when the normal entry flow is so small that a useful amount of tracer, when administered instantaneously, produces major irregularity in the entry flow. These problems can be overcome by slow administration of tracer over a period of time, thus averaging out the irregularities, and allowing the system to be regarded as steady state. However, major changes (resulting from therapeutic intervention, for example) cannot be studied before elapse of sufficient time for the system to reach a new steady state. Thus, the occupancy principle, embodying a remarkably simple but far-reaching property of steady state systems, has a wide range of biomedical applications.

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References and Notes

1. Let a steady-state system have an entry flow F, and consider a quantity of radioactive tracer that is administered instantaneously. A fraction $f(t)$ of the tracer is contained in a defined part t seconds after the tracer enters the system. Since the fates of the tracer and the material under study are identical, the same fraction $f(t)$, of the quantity $F\ \delta t$ of the material that entered the system during a time δt, is in the defined part t seconds after entry. In other words—there will be in the system at any time a fraction $f(t)$ of the material $F\ \delta t$ that entered the system t seconds earlier. The total amount of material in the part of the system is therefore the sum of the contributions from all the material that entered the system at all times between $t = 0$ and $t = \infty$ before the defined time. Therefore
$$C = \int_0^\infty f(t)\ F dt = F \int_0^\infty f(t)\ dt = F\Theta$$
$$\Theta / C = 1/F$$
Since no particular part was defined this relation holds for all parts; it is equivalent to the one established by P.-E. E. Bergner [*J. Theoret. Biol.* **6**, 137 (1964) (equation A2.7); *ibid.* **1**, 120, 359 (1961); *Acta Radiol.* **210**, Suppl., 1 (1962); *Science* **150**, 1048 (1965)].
2. P.-E. E. Bergner, in *Dynamic Clinical Studies with Radioisotopes*, R. M. Kniseley and W. N. Tauxe, Eds. (Atomic Energy Commission, Germantown, Md., 1964), pp. 13–15.
3. K. L. Zierler, in *ibid.*, p. 55.

5 August 1968

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Spectral Reflectance of Gull's Bill: Physiological and Evolutionary Implications for Animal Communication

Abstract. *The newly hatched laughing gull chick* (Larus atricilla) *begs food by pecking at the parent's dark red bill. The spectral reflectance of the bill over a range of 300 to 1200 nanometers reflects increasingly more with wavelength beginning about 575 nanometers. Because the chick shows a bimodal, true color preference in pecking, with modes at about 625 and 450 nanometers; the latter, blue peak in the spectral response curve is apparently not adapted to the natural stimulus of the parent's bill. The blue peak might thus be the result of limitations in the neural coding of color information in the chick's visual system.*

It is of interest in both physiological and evolutionary aspects of animal communication to discover how close a correspondence there is between the physical properties of the stimulus that serves as a social signal in nature and the differential responsiveness (stimulus preferences) of the receiver. Interactions between parent and young gulls exhibit one communication system simple enough for such analysis.

This communication system has already been partially analyzed. When ready to feed its young, the adult laughing gull (*Larus atricilla*) lowers its dark red bill in front of the chick. A hungry chick pecks at the tip of the bill, a form of begging that elicits regurgitation of partially digested food from the parent (*1*). The spectral response curve of the chick shows a maximum at about 625 nm in the orange-red and a secondary maximum at about 450 nm in the blue part of the spectrum (*1, 2*). This is a true color preference, not merely a brightness function (*1*). Furthermore, the preference curve for background is unimodal in the green, and apparently the spectral mirror-image of the curve for the stimulus-object (*3*).

Because the vegetation surrounding the gull's nest reflects green, and the parent's bill appears red to the human eye, the question arises as to why blue should also be an effective color for eliciting pecking. One possibility is that the parent's red bill actually contains a secondary blue peak of reflectance detected by the chick, even though the bill appears pure red to the human observer (as do some blue-containing red dyes).

The bills of three adult male laughing gulls—birds collected for histological studies of the reproductive organs—were removed from the specimens in the field and were immediately frozen in the dark on 21 June 1967. These were then taken to the laboratory on

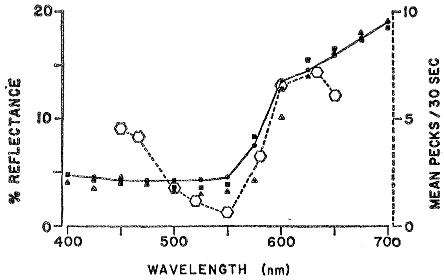

Fig. 1. Comparison between the reflectance of the parent's bill (filled symbols and unbroken line, left ordinate) and the response of the chick (unfilled symbols and broken line, right ordinate). The reflectance has no secondary blue maximum matching that of the chick's response. Filled symbols connected by unbroken lines indicate the composite sample; other filled symbols indicate masked samples.

24 June for reflectance measurements in a DU spectrophotometer with a diffuse reflection attachment. For the first of two methods, which measured the reflectance of single mandible pieces, it was necessary to mask the large aperture of the apparatus and to correct for the effects of masking. In the second method the full apparatus opening and a composite of several mandible pieces were used. The three lower mandible specimens were bisected in the midsagittal plane to form six halves; five of these six were placed in the full sample holder (2.5 cm in diameter) to cover about 96 percent of the viewing area.

The results (Fig. 1) rule out the hypothesis that the blue-preference of the begging chick corresponds to a blue peak of reflectance in the parent's bill. Measurements on one mandible were taken from 300 nm in the ultraviolet to 1200 nm in the infrared. The ultraviolet curve remains at its blue level in Fig. 1, and the infrared curve continues to rise with about the same slope as shown between 600 and 700 nm. Similarities in absorption spectra suggest that the pigment responsible for reflectance might be a form of melanin (*4*).

Why does the chick respond to red and blue, when the parent's bill is just red and there are no really blue objects in the chick's environment? Two of many possible interpretations of this mismatch are worth considering (*5*).

The first is that the chick's pecking preference may be primarily adapted to avoid green grass surrounding the nest, and only secondarily adapted to the red bill of the parent (*6*). A "green-avoidance" in pecking leaves a remaining high responsiveness to the spectral extremes, red and blue. In this case, the parent's bill would not even have to be colored (although a neutral color would reflect some green); or the bill could be either red or blue, or both. For example, the related skuas and jaegers (Family Sterocorariidae) feed their young in a like manner as gulls, but the bills of the adults have no bright coloration; the color preferences of skua chicks are unknown. Thus, the color of the parent gull's bill could have arisen under other selection pressures, such as for courtship displays. In fact, the laughing gull's bill appears much brighter red during earlier courtship than later during the chick-rearing phase.

The second possible interpretation is that there are certain receptor-neural constraints in the coding of color information in the chick's visual system, and that a "red-preference, green-avoidance" cannot be coded without a secondary "blue-preference." Despite the fact that there are no blue objects in this species' natural breeding habitat, secondary blue peaks have also been found in the adult's spectral response curves both to retrieving eggs and to removing eggshell fragments (*7*). If the color-coding system is under certain constraints, the neural-receptor processing may be rather simple (*1–3*) —more simple than, for example, that which underlies hue perception in man —and thus may be amenable to physiological analysis.

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References and Notes

1. J. P. Hailman, *Behaviour Supplement 15*, (Brill, Leiden, 1967).
2. ———, *Nature* **204**, 710 (1964).
3. ———, *Experientia* **22**, 257 (1966).
4. J. M. Bowness, R. A. Morton, M. H. Shakir, A. L. Stubbs, *Biochem. J.* **51**, 521 (1952); M. S. Mason, D. J. E. Ingram, B. Allen, *Arch. Biochem. Biophys.* **86**, 225 (1960); B. Schmidli, *Helvet. Chim. Acta* **38**, 1078 (1955); L. E. Arnow, *Biochem. J.* **32**, 1281 (1938); R. H. Hackman, *ibid.* **54**, 371 (1953).
5. Ethology has uncovered many examples of behavior patterns that can be elicited more readily by an artifically constructed stimulus than by the usual stimulus-object in nature; such artificial stimuli are termed "supernorma"; see N. Tinbergen, *The Study of Instinct* (Oxford Univ. Press, London, 1951).
6. This possibility was raised by D. A. Quine and J. M. Cullen [*Ibis* **106**, 164 (1964)] with respect to pecking in young arctic terns *Sterna macrura.*
7. J. P. Hailman, *Amer. Zool.* **6**, 568 (1966).
8. Supported in part by PHS-NINBM grant 07075 and a biomedical sciences support grant from the University of Maryland. I thank Drs. M. Impekoven, W. M. Schleidt, and C. G. Beer for comments on the manuscript and A. Segre and S. Hoyt for the specimens, taken at the Brigantine Field Station of the Institute of Animal Behavior at Brigantine, N.J. Details of masking procedure available from author upon request. Contribution No. 7 from the Brigantine Field Station of the Rutgers University Institute of Animal Behavior.

5 June 1968

Evolutionary Effects of Cosmic Radiation

One of the earliest discoveries of paleontology and stratigraphy was that there have been episodes of marked biotic change in the history of the earth. The most radical, or at least most apparent, of these have been taken as major dividing lines in geochronology: times of apparent great organic diversification (such as Precambrian-Cambrian), of apparent great extinction (such as Pleistocene-Recent), or both (Permian-Triassic and Cretaceous-Tertiary, for example). Since the discovery that various kinds of radiation have strong effects on organisms, not only somatic damage but also increased mutation rates, it has been suggested repeatedly that major biohistorical episodes of extinction or proliferation, or both, have been related to episodes of heightened radiation. Some relatively crude and easily refuted hypotheses have supposed the relevant radiation to be telluric (*1*). At least as early as 1950, however, a hypothesis implicating cosmic radiation, of one sort or another, was clearly expressed (*2*). In view of later proposals of the same idea, it is interesting that Schindewolf had then already explicitly suggested that the relevant radiation might come from supernovae. Russian scientists, who have shown special interest in this subject, had also advanced the supernova hypothesis (*3*).

To make the causation of biohistorical episodes by cosmic radiation plausible, it must be supposed that impact of such radiation on the earth was exceptionally intense at a few widely spaced times in the past. After apparent reversal of the geomagnetic field was deduced from remanent rock magnetism, it was suggested that during reversal there could be a relatively brief time of near zero field intensity and that during that time impacts of cosmic rays on the earth would be greater than usual. That was then advanced as a possible mechanism behind the biohistorical episodes in question (*4*). It was, however, soon argued that increased radiation due to that cause alone would be so slight that appreciable effects on the evolution of any organisms would be inconceivable (*5*). Shortly thereafter, and quite recently, the already old idea of increased radiation from explosion of a supernova was again advanced (*6*). Serious doubts as to the efficacy of that mechanism were also soon raised (*7*).

It seems that recent discussion and