

arbitrary tracer system). An equation similar to Eq. 1 has been applied in the study of iodine metabolism (11), but ζ_{sc} is replaced by the influx into the specific compartment (organ), and θ^0 is interpreted as "the biological half-life for iodine in the thyroid gland"; essentially, the equation is used to define that entity.

The practical example I have chosen is perhaps not very appropriate: the short half-life of ^{42}K may introduce serious difficulties regarding observations during the later part of the tracer process, which are necessary for estimation of the integrals; the possible use of other potassium isotopes (such as ^{40}K) should be investigated. Moreover, if excretion is mainly in feces, the lag may distort the whole-body curve $b_s(t)$, especially if the considered element has a high relative turnover—that is, if ζ_{sc}/b_s is large. This distortion could be a problem in the determination of the exchangeable mass of sodium, but whole-body counter data on retention of $^{22}\text{Na}^+$ look promising (12). The exchangeable mass of certain elements may prove impossible to determine.

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4. Especially if the considered substance is excreted mainly by way of the kidneys, the blood compartment is "peripheral" in the sense that it is the one closest to the environment—that is, it is the last internal compartment from which the particles irreversibly leave the organism. From section 4 in the first reference of (2) it follows that one would then expect the observed specific activity in blood to be lower than anywhere else in the system; the results reported in the second reference in (2) confirm this.
5. W. H. Blahd, B. Cassen, M. Lederer, in *Proc. Symp. Whole-Body Counting* (International Atomic Energy Agency, Vienna, 1962), p. 427. These authors determined the whole-body content of $^{40}\text{K}^+$ and used $^{42}\text{K}^+$ for isotopic dilution. The result was that the exchangeable mass sometimes exceeded the total mass of potassium; the authors explain this by referring to changes in the clinical states.
6. J. Anderson, S. B. Osborn, R. W. S. Tomlinson, D. Newton, J. Rundo, L. Salmon, J. W. Smith, *Lancet* **1964-II**, 1201 (1964). Neutron-activation analysis seems to have yielded confident estimates of total body sodium in two subjects. The dilution method, simultaneously employed, gave exchangeable masses that almost equaled (in one subject were slightly greater than) the total masses. This completely opposes the common belief that about 25 percent of the total sodium is in the skeleton and slowly exchangeable [see G. C. H. Bauer, A. Carlsson, B. Lindquist, in *Mineral Metabolism*, C. L. Comar and F.

7. P.-E. E. Bergner, *J. Theoret. Biol.* **6**, 137, (1964).
8. The mean time of sojourn in *C* is the total time a particle (here, a potassium ion) is expected to have spent in *C* before leaving the system for good. In tracer context this concept was originally introduced in (2b), appendix II; in a similar context the same term has been used, but with a different meaning, by G. Marsaglia, *Boeing Sci. Res. Lab. D1-82-0280* (1963).
9. The tracer supply is said to be equivalent [see (7)] when the tracer particles arrive at the system in the same way as the particles of mother substance; that is, the two kinds of particles, represented by the same stochastic process, have equal initial conditions. Thus intravenous injection, intramuscular injection, and oral administration of ^{42}KCl theoretically should all give different results; whether the differences have practical significance can only be decided experimentally.
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13. Work performed under contract with the AEC.

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Frog Retina: Detection of Movement

Abstract. *The response of class 2 ganglion cells in the frog retina is dependent on the angular velocity of a black visual stimulus whose size (1.2°) and contrast against a background are held constant. The relation between neuronal discharge rate and the angular velocity of the stimulus may be expressed as a power function.*

Microelectrode recordings from retinal ganglion cells indicate that the retina of the frog performs several distinct types of operations on the visual world (1). One class of ganglion cells, called convex-edge detectors or class 2 neurons, is especially sensitive to the movement of objects which are smaller than

the excitatory receptive field (ERF) (1, 2). Previous studies have shown that the neuronal discharge rate elicited by the traverse of a stimulus through the ERF increases with increasing angular velocity of the stimulus; however, this relation was not examined quantitatively. In our investigation we studied quantitative characteristics of the neural integrative process which determines the class 2 operation. We found that the relation of the angular velocity of the stimulus to ganglion-cell activation could be expressed as a simple mathematical function.

Metal-filled micropipettes were used to record the discharges of single, afferent, optic-nerve fibers in the superficial layer of the optic tectum of the European water frog, *Rana esculenta*. The frog was curarized and fixed before a specially constructed hemispherical perimeter with a radius of 25 cm. The stimulation apparatus has been described in detail (3). The stimulus, a black round spot on a white background, was carried by a motor-driven stage behind a window cut in the back of the hemisphere. The motor was geared to permit movement of the stimulus at nine specific angular velocities, between 0.05° per second and 24° per second; higher angular velocities were possible by manual movement of the stage. The traverse of the stimulus was along a straight line, tangential to the hemisphere. The luminance of the white stimulus background was 64 millilamberts, and that of the black spot was 1.9 millilamberts.

Twenty-five class 2 neurons were tested with at least five of the nine possible angular velocities; the sequence of the velocities was varied during the course of the experiments. Each stimulus traverse was followed by a 75-second "rest period" (15 seconds

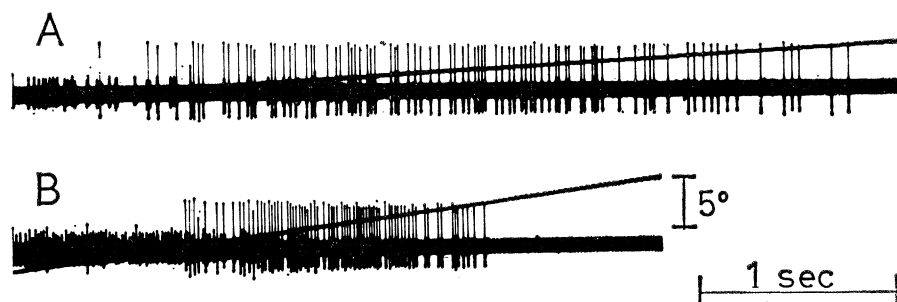


Fig. 1. Record of responses of a class 2 neuron to a 1.2° -black spot on a white background moved at two different angular velocities. The diagonal trace represents the stimulus movement. (A) Stimulus angular velocity is 0.95° per second; total discharge number per stimulus traverse of the ERF is 86; average discharge rate per traverse is 24 per second. (B) Stimulus angular velocity is 2.4° per second; total discharge number is 71; average discharge rate is 48 per second.

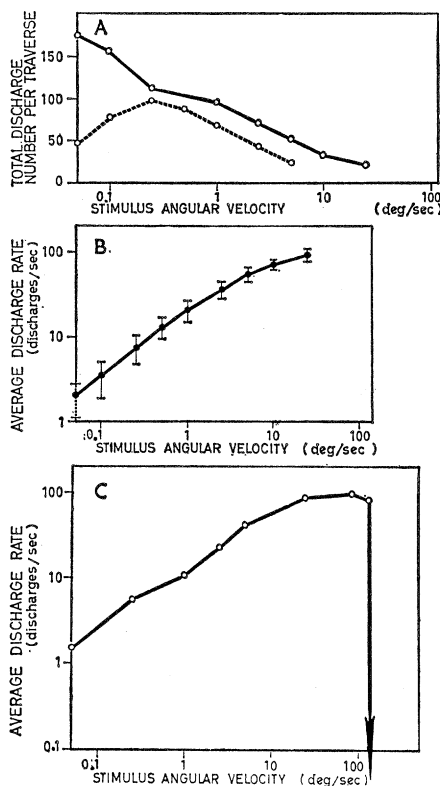


Fig. 2. (A) Total discharges per traverse for two units tested with a 1.2° -stimulus. The variability in response patterns demonstrated by these two neurons was found in many of the neurons tested. (B) Dependence of the means of the average discharge rates of 25 units on the velocity of a 1.2° -stimulus. Bars represent standard deviation of the collective values. (C) Dependence of average discharge rate of a single neuron on the velocity of a 0.7° -stimulus.

of dark followed by 60 seconds of light) in order to eliminate the effects of neural and photochemical adaptation (4). The neural responses were displayed on a cathode-ray oscilloscope and photographed together with a synchronized display of the stimulus movement which was monitored by a potentiometer.

Figure 1 shows the recordings of a single neuron responding to two of the nine angular velocities. We examined two qualities of the neural response: (i) the total discharge number per stimulus traverse and (ii) the average discharge rate per stimulus traverse.

The total discharge number per traverse showed no simple relation to the angular velocity of the stimulus. The angular velocity which elicited the maximum number of discharges per traverse varied for different class 2 neurons. Sixteen of the 25 units gave a maximal discharge number at the two slowest angular velocities possible with our perimeter (0.05° and 0.1° per sec-

ond). The responses of two of the 25 units are illustrated in Fig. 2A.

The discharge rate (a measure of neural activation probably of more physiological significance than the total discharge number) was not constant as the stimulus moved through the ERF (see Fig. 1). The average discharge rate per stimulus traverse showed a strict dependence on the angular velocity of the stimulus in all 25 neurons that were tested (Fig. 2B). The relation may be expressed by the power function

$$R = k_0 \cdot v^{0.7}$$

where R is the average discharge rate per second, k_0 is a constant, and v is the angular velocity of the stimulus in degrees per second. With a 1.2° -black spot and a black-white luminance ratio of 1:34, the value of k_0 is 20 discharges per degree. This power function is valid for values of v from at least 0.05° to 10° per second. In examining the relation of the discharge rates in the peripheral thirds of the ERF or in the central third of the ERF to the angular velocity of the stimulus, similar power functions were found, differing only in the value of k_0 . It appears, therefore, that the class 2 neurons perform the same operation at different degrees of excitability in different parts of the ERF.

The stage that carried the stimulus was moved by hand in order to observe the neural response to angular velocities higher than 24° per second. Figure 2C illustrates that the class 2 operation breaks down rapidly at angular velocities above 100° per second, and, at 140° per second, this neuron responded with only one discharge per traverse.

Class 2 ganglion cells code a number of characteristics of a visual stimulus, such as size, shape, contrast, and angular velocity. We used a motor-driven perimeter, varied the angular velocity of the stimulus over a series of fixed values, and kept the other visual parameters constant. The relation of the average discharge rate of ganglion cells to the angular velocity of the stimulus suggests the possibility of further quantitative studies in order to analyze the functional properties of the neural network which determines the class 2 operation.

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Growth Hormone: Important Role in Muscular Exercise in Adults

Abstract. Measurement by radio-immunoassay of growth hormone in the plasma of adults showed consistently low concentrations in subjects in bed in the morning. Exercise caused marked increases except when the subjects ingested carbohydrate during the exercise.

Pituitary growth hormone is secreted in the adult in response to muscular exercise. Small increases in its concentration in plasma were found in two subjects after they had walked 8 km (1), and concentrations were high in three subjects after they had played squash for 2 to 3 hours (2). Injection of growth hormone raises the concentration of nonesterified fatty acids in the plasma (3), and these constitute the principal fuel during exercise (4). This report, based on measurement of growth hormone in plasma by radio-immunoassay (5, 6), suggests an important role for the hormone in mobilizing fuel for muscular exercise. As a corollary it shows that studies of growth hormone in plasma are of little value unless the subject's rate of expenditure of energy is known.

After an overnight fast, plasma samples from normal adults sometimes show high values for growth hormone, although most have values below the sensitivity of present assays [1 to 2 ng(μ mg)/ml] (6, 7). In our laboratory ten adult males sampled in bed before rising all had concentrations below 1 ng/ml, whereas 9 of 23 subjects, who traveled to the laboratory and rested for 1 hour before sampling, yielded 17 elevated values (range, 2 to 53 ng/ml) from a total of 44 samples from the 23. Eight of the nine individuals showing high concentrations were later sam-