cular hemerythrocytes in sipunculids arise originally from the same mesodermal cell, and since there is no trace of coelomic hemerythrin in vascular hemerythrocytes, and vice versa, there must also be separate "control genes" regulating the activation of the different hemerythrin cistrons. One is tempted to draw analogies between such "control genes" and those that have been found in microorganisms (*23*) and in maize (*24*), and those found to be regulators of the differentiation of human (*25*) and vertebrate (*4*) ontogenetic hemoglobin sequences.

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10. These results give a gene frequency of 0.34 for the "fast" hemerythrin gene and 0.66 for the "slow" hemerythrin gene. Assuming a Hardy-Weinberg equilibrium, one would expect, out of a total of 181 individuals, 78.2 "slow's," 81.5 "heterozygotes," and 21.3 "fast's." Thus, the data given here do not show a significant deviation from genetic equilibrium ($\chi^2 = 2.98$; degrees of freedom, 2. For significance at the 5-percent level, the χ^2 must be greater than 5.99). Selection pressure must be quite strong to show a significant deviation from Hardy-Weinberg equilibrium; in spite of vigorous selection pressures for various economically advantageous traits, no significant departure from the Hardy-Weinberg equilibrium is seen for various genetically based polymorphisms of ovalbumins and ovoglobulins in nine populations of the domestic fowl [C. M. A. Baker and C. Manwell, *Brit. Poultry Sci.* **3**, 161 (1962)].
11. Irving Klotz (personal communication) and I have found independently that urea dissociates the hemerythrin molecule into 14 to 15 $\times 10^3$ molecular-weight subunits, eight such subunits making up the native hemerythrin molecule. I. M. Klotz and S. Keresztes-Nagy [Nature **195**, 900 (1962)] have reported similar results in studies in which they used succinylation to eliminate the quaternary structure of this molecule.
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7 January 1963

Signal Detection in the Rat

Abstract. *An auditory detection experiment was performed with rats as subjects, and the data were analyzed with a signal detection model. Rats were run at fixed sound pressure levels, and their responses were partitioned so that operating characteristics could be constructed. Measures of detectability, $(d_e)^{1/2}$, were calculated from the operating characteristics, and show that $(d_e)^{1/2}$ is a function of sound pressure levels, rising as these levels rise.*

The theory of signal detectability (*1*) has been used over the past several years as a model for the decision-making processes inherent in psychophysical studies with man. This model allows an observer's responses to be partitioned into two parts, the probability of a *yes* response when a signal is present, $p(y/\mathrm{SN})$, and the probability of a *yes* response when a signal is absent, $p(y/\mathrm{N})$. These two probabilities are determined by the parameters of the testing situation. By sampling from a variety of testing conditions and recording the $p(y/\mathrm{SN})$ as a function of the $p(y/\mathrm{N})$, a set of points emerge which define a response-conditional operating characteristic, from which $(d_e)^{1/2}$, a detectability index, can be calculated. This model provides a theoretical basis of assessing this index, which is largely independent of specific testing parameters that are associated with a correct detection.

In order to determine this model's applicability in the field of infrahuman psychophysics, where the interaction of reward and sensitivity has been generally neglected, the following experiment was performed.

Four male albino rats weighing approximately 350 g were allowed access to water for 1 hour per day for 2 weeks before experimentation was begun. The rat worked in a small cage constructed of stainless-steel rods, mounted in a 1¼-inch plywood enclosure lined with 3 inches of fiber glass. Two levers entered the cage through its floor, one on the left of a rat facing the cage front, lever L, and one on its right, lever R. The auditory signals were presented by an electrostatic speaker facing the front of the cage, by means of an oscillator, electronic switch, attenuator, and amplifier chain.

The naive rat was placed in the cage with only the lever L present, with a 2-kcy tone at a sound pressure level of 65 db (relative to 2×10^{-4} dyne/cm^2) continuously present. The rat was trained to press this lever, for which it received one drop of water per lever press. Gradually the on-time of the tone was reduced to about 5 seconds, and alternated with a 10-second tone-off period. At this time the rat was rewarded only for presses occurring in the presence of the tone. When this behavior became stable, lever R was placed in the cage, and the rat was trained to press this lever on a fixed-interval 7-second schedule (FI 7). Under this schedule the first press after a 7-second interval had elapsed turned on a 2-second tone. During this time a single reward was available if the rat then pressed lever L. A small photoelectric system was mounted over lever R. When its beam was broken by the rat the FI timing circuits were operative. This arrangement tended to stabilize the rat's

working position, since nonstandard positions did not break the beam and were therefore ineffective.

In order to test for a measure of detectability the above-described procedure was modified so that a fixed-interval experiment could be performed. Presses on lever R under FI 7 now turned on a small signal lamp for 1 second, after which the 2-second tone appeared with an a priori probability determined by the experimenter. In this way the lamp signaled a 2-second interval during which a tone was or was not present. During this interval the rat either pressed lever L if the tone was detected, or did not. If the tone had appeared, and the rat had pressed lever L, it was rewarded. In either event a new sequence was initiated by the rebreaking of the photo beam over lever R.

Since one of the parameters affecting the partitioning of responses into $p(y/SN)$ and $p(y/N)$ is the a priori probability of a tone's appearance, this parameter was varied in all animals from .75 to .14, in an attempt to determine an operating characteristic from which $(d_e)^{1/2}$ could be calculated. The rat's responses were monitored and stimuli were presented automatically by means of relay programming. Rewarded responses were totaled on one counter, and the number of tone presentations on another, so that $p(y/SN)$ could be computed. Similarly, unrewarded responses were totaled on one counter and no-tone presentations on another, so that $p(y/N)$ could also be computed. All rats were run at three sound pressure levels, and each level at which the rat was run enabled the experimenter to plot an operating characteristic and thus compute a detectability index for that level.

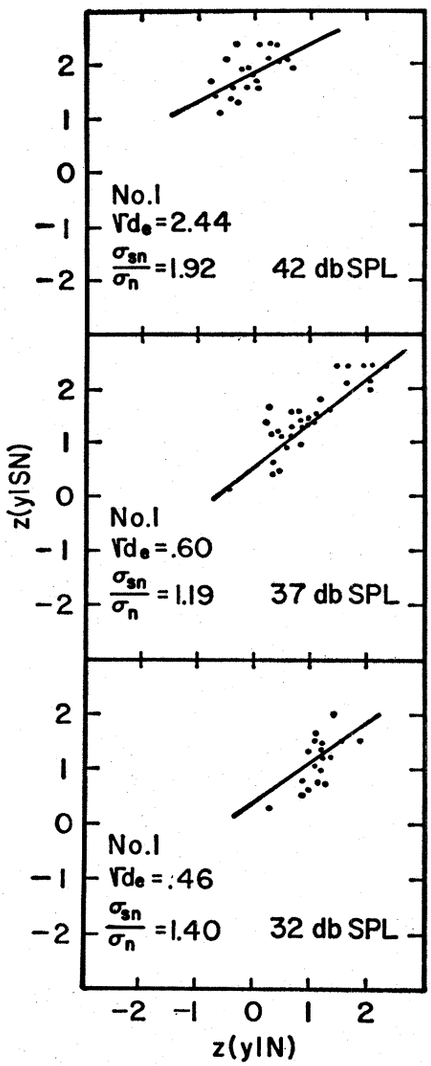

Fig. 1. Normalized response-conditional operating characteristics for rat 1 at three sound pressure levels.

According to the theory, the operating characteristic will be linear when plotted on normal-normal coordinates. The value of $(d_e)^{1/2}$ is determined by the intersection of the operating characteristic and the negative diagonal, and is defined as the ordinate minus the abscissa of this point of intersection. This index, plus the slope of the operating characteristic, completely define the rat's behavior at a given stimulus level. As shown in Fig. 1, the data provide a reasonable approximation of a linear array. The operating characteristics for rats 2 and 3 are similar to those shown for rat 1. The straight lines drawn through all the data points in this experiment were fitted by the method of least squares. In the case of the fourth rat no detectability index could be calculated from the data, since this rat's response probabilities remained essentially the same (100 percent) for any a priori probability. In one sense this behavior might be considered optimal, since the rat was rewarded maximally. At the same time, however, it was penalized maximally, and its behavior was not as efficient in terms of false alarms per reward as it was for the other rats.

In general, false alarm rate seems to increase with a priori probability, though there are exceptions, since the independent a priori probability is confounded with other variables not under strict experimental control, such as motivational factors and amount of deprivation.

Table 1 describes $(d_e)^{1/2}$ as a function of the level at which each rat was run, and shows that for all animals detectability increases as the sound pressure level increases. Table 1 also shows the value $\sigma SN/\sigma N$, the reciprocal of the slope of the operating characteristic. These values indicate that under the threshold conditions of this experiment more variability was attached to a signal-present hypothesis than to a signal-absent hypothesis.

Table 1. Values of $(d_e)^{1/2}$ and $\sigma SN/\sigma N$ as a function of sound pressure level (SPL).

SPL	Rat 1	Rat 2	Rat 3
		$(d_e)^{1/2}$	
42	2.44	2.50	1.96
37	.60		
32	.46	1.50	.95
27		.46	.73
		$\sigma SN/\sigma N$	
42	1.92	3.23	1.75
37	1.19		
32	1.40	2.22	1.72
27		.96	1.69

This experiment differs from those usually performed, in that no specification can be made of the noise present during the tone and no-tone presentations. However, it is still possible to construct response-conditional operating characteristics without this information.

The method of signal detection offers some advantages over other methods of psychophysical testing in animals, especially in those situations where a lack of adequate control exists over the factors involving decision-making. Since reinforcement of one type or another is used in all operant studies with animals, it becomes important to have a measure of sensitivity that is independent of the reinforcement pattern, or of the methodology.

This method provides more usable data than the typical threshold study, where much data is rejected because it does not reach an arbitrary criterion. Much of the rejected data may represent criterion changes within the animal, and as such are as relevant as any other data. This method may be of use in drug or other studies where uncontrolled changes in the animal's criterion may invalidate changes in sensitivity apparently under experimental control.

The results of this experiment show that a signal detection model can be applied to animal psychophysics, and that in some cases it might represent a closer approximation to sensitivity than do other methods, which do not treat the interaction of reward patterns and sensitivity (*2*).

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Behavior in Hydra: Contraction Responses of Hydra pirardi to Mechanical and Light Stimuli

Abstract. Hydra pirardi *contracts in response to light and mechanical agitation. The animals show a reduction in the number of contractions in response to mechanical agitation on repeated testing but continue to contract in response to a light stimulus. Excision of all the tentacles of the animal completely inhibits contraction in response to mechanical agitation but does not affect contraction in response to light. The results of these experiments suggest that* H. pirardi *has different receptors for light and for mechanical agitation and that the control mechanisms for the contraction responses to these two stimuli are independent.*

Trembley (*1*) described the normal movements of hydra in detail, observing that the animals contract and expand spontaneously. More recently, Reiss (*2*) studied rhythmic spatial patterns in the spontaneous contractions of hydra. The experiments described in this report are concerned with the contraction rates for *Hydra pirardi* (*3*) in response to two external stimuli: light and mechanical agitation. The rates of stimulated contraction are much greater than the rate of spontaneous contraction.

Trembley reported that the movements of *Hydra viridis* show a definite relation to a light source (heliotropism). Wilson (*4*) extended this early work and observed that the animals collect on the side of the aquarium having the greatest illumination and appear to be most sensitive to blue light. We observed that when strong sunlight fell on a culture of *H. pirardi*, the animals contracted within 15 to 30 seconds. Artificial lights of various sorts had a similar effect, but stimulation for longer periods (1 to 2 minutes) was required. Doubtless this phenomenon has been observed before, but we have found no reference to it in the literature.

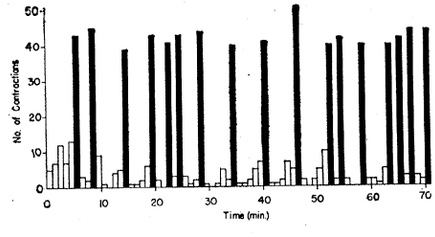

Fig. 1. Number of contractions induced in 50 *Hydra pirardi* by light. (Solid columns) Number of hydra that contracted during 1-minute periods of exposure to strong light; (open columns) number of hydra that contracted during 1-minute periods in which the animals were not exposed to strong light.

Experiments were carried out to measure the contraction rates for *H. pirardi* in response to various light sources. The contraction rate is defined as the proportion of animals that contract during a specified time. The *H. pirardi* were cultured by the methods of Loomis and Lenhoff (*5*). In one series of studies the light source was a Mercury vapor arc lamp (*6*) with an emission spectrum that corresponds approximately to that of mercury vapor superimposed upon a low-level continuous spectrum. Unfiltered light from this source was reflected by means of a mirror onto a dish of *H. pirardi* that had been starved for 24 hours at 21°C. The total distance traveled by the light was 40 cm. Four groups of either 12 or 13 hydra were exposed to the light for 1-minute periods at intervals ranging from 1 to 5 minutes. The sequence of these intervals was chosen by a random process for the first group; the same sequence was used for the three groups subsequently tested. During the intervals the animals were exposed to the diffuse light of the laboratory (*7*). Figure 1 shows the number of hydra that contracted during each 1-minute period of exposure. The solid columns of the histogram correspond to the 1-minute periods during which the animals were exposed to the strong light. The open columns indicate spontaneous contractions of the animals in 1-minute periods during which they were not exposed to strong light. As Fig. 1 shows, *H. pirardi* contracts in response to a light stimulus.

In a second series of experiments the effect of mechanical agitation on contraction was investigated. Wagner (*8*) showed that specimens of *Hydra viridis* contract when the outsides of their culture dishes are tapped. He noted that if the animals are stimulated in this way at 1-second intervals, they

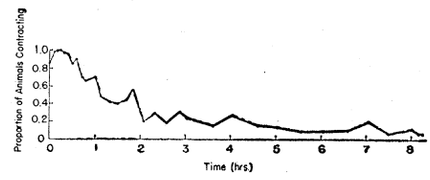

Fig. 2. Curve for the contraction response of *Hydra pirardi* to mechanical agitation. Each point represents the average proportion of animals that contracted within the 2-second period that followed a 2-second shaking period and is based on observations for five animals during ten successive periods.

contract completely. Soon afterward they begin to expand, and they remain extended. Thus it appears that *H. viridis* becomes accustomed to a slight, recurrent, nonlocalized mechanical stimulus and no longer responds to it. Wagner found, however, that if the interval between the stimuli is increased, to allow the animals to expand fully after each contraction, no habituation occurs and the animal always contracts. In contrast to this result we have repeatedly demonstrated that *H. pirardi* becomes accustomed to nonlocalized mechanical stimulation even when the interval between the stimuli is long enough to allow the animal to expand completely. This was demonstrated in more than 98 percent of more than 1000 *H. pirardi* tested. In a typical experiment, five animals which had not been fed for 24 hours were placed in 50 ml of water in a Stender preparation dish. After the animals had attached themselves to the

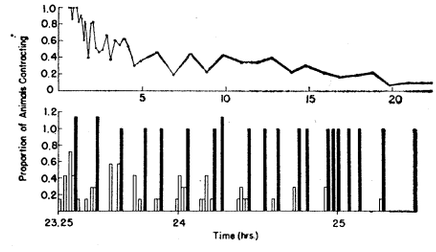

Fig. 3. The effectiveness of light in inducing contraction in *Hydra pirardi* previously habituated to shaking. (Top) Curve for the contraction response of the animals to shaking. Each point represents the average proportion of animals that contracted within the 2-second period that followed a 2-second shaking period and is based on observations for five animals during ten successive periods. (Bottom, solid columns) Proportion of animals that contracted during subsequent 1-minute periods of exposure to strong light; (open columns) proportion of animals that contracted spontaneously or in response to shaking alone.