the formation of associations. If the processes underlying delayed matching and discrimination learning were the same (for example, a single rehearsal process), then they should be susceptible to the same interfering treatments. That prediction was not confirmed here. To the contrary, more generally and in accord with other findings (*6, 7*), the present results suggest that those processes can operate independently of one another (*12*).

The implications are even more profound when considered in a broader historical and theoretical perspective. The present results imply that variations in the pigeon's immediate memory for reward and nonreward might be irrelevant to the effects of those events on preceding behavior. Thorndike anticipated this possibility by pronouncing that "The consequences of a connection seem to act on it directly at the time as well as, or instead of, acting on it indirectly by causing some repetition or rehearsal or reconsideration of it" (*13*). The present results seem compatible with such a view, once again raising the possibility that the relation between maintenance of STM and consolidation of LTM may be more correlational than causal.

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8. After acquisition of matching to sample with 0 second delays, delays were lengthened 1 second per day contingent on criteria (87.5 percent correct) performance. This procedure resulted in different delays sustaining performances in which criterion was reached by different birds. Delays ranged from 4 to 12 seconds after 31 to 40 days of training. See Maki *et al.* (*5*) for procedural details.
9. Different birds conformed to these requirements after different amounts of training, averaging 10.6 days (range, 5 to 22).
10. The data plotted in Fig. 1 from the last 3 days of uncorrelated training are presented separately for trials involving discriminative stimuli that were scheduled to be followed by light or dark delays during the next 8 days of discrimination learning. Illumination is thus a "dummy" variable in this plot and in the analyses of variance.
11. The center and side key colors were the same. However, the lack of a groups × illumination interaction suggests that the nominal similarity did not influence the present results. Also, pigeons show little generalization from center to side keys in related experiments [see D. E. Carter and D. A. Eckerman, *Science* **187**, 662 (1975); W. S. Maki, G. Gillund, G. Hauge, W. Siders, *J. Exp. Psychol. Anim. Behav. Processes* **3**, 285 (1977); T. R. Zentall, D. E. Hogan, M. M. Howard, B. S. Moore, *Learn. Motiv.* **9**, 202 (1978)].
12. The present results suggest that different memory processes may support discrimination learning and delayed matching performance. By themselves, however, the findings do not warrant speculation about the nature of those processes. The possibilities are numerous. For an alternative view of illumination effects on delayed matching, see M. R. D'Amato, in *The Psychology of Learning and Motivation: Advances in Research and Theory*, G. H. Bower, Ed. (Academic Press, New York, 1973), vol. 7, p. 227.
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The Psychophysical Function: Harmonizing Fechner and Stevens

Abstract. *The methods of Fechner and Stevens for assessing sensation quantity usually yield different psychophysical functions even when all other factors are controlled. In this experiment, corresponding differences occurred when different features of the same sensory receptor signals were analyzed. In the visual system, the receptor potential saturated if the peak but not the area was measured; these results match visual psychophysical functions obtained with the methods of Fechner and Stevens, respectively. This result suggests that both methods are equally valid but that each method yields the particular psychophysical function appropriate for a particular kind of information processing. A novel factor in determining sensation quantity, namely the time used by the observer to make a judgment, is implicated by the data.*

The psychophysical function (relating sensation quantity to stimulus intensity) has been estimated by two different methods. Fechner's method (*1*) has three parts—a psychophysical technique, a scaling assumption, and an empirical finding. The psychophysical technique is to ask observers to detect stimulus increments presented against different backgrounds. If the scaling assumption were valid and all just detectable increments were mediated by equal changes in sensation quantity, Fechner's method would yield a psychophysical function of any arbitrary form (*2*). But if the empirical outcome were that the just-detectable increment bears a constant ratio to the background intensity (Weber's law), Fechner's method would yield a particular psychophysical function, called Fechner's law (sensation quantity is proportional to the logarithm of stimulus intensity). Other empirical findings can (and do) lead to alternate psychophysical functions when Fechner's method is used. Stevens' method (*3*) asks observers to identify the sensation quantity produced by a stimulus of a given intensity and to report the magnitude of that sensory experience in numbers. Stevens' method produces data that have been generalized in Stevens' law (sensation quantity is a power function of stimulus intensity). Stevens' method has been supported by certain persuasive validations (*4*), but it is important to distinguish between Stevens' method and Stevens' law.

In a few cases the two approaches have been thought to yield similar results. For example, Fechner's method suggested that brightness increases as the logarithm of light intensity while Stevens' method suggested that brightness increases as the cube root of intensity; but these two functions are virtually indistinguishable. In other cases, the two methods give quite different psychophysical functions, most strikingly when Stevens' method suggests power functions with exponents greater than 1.0 (*4*). These discrepancies have lead to a discussion that has often been couched in terms of accepting one method and downgrading the other (*5*) because of the assumption that only one underlying law can be correct, even though it has long been known that the data acquired from the two methods are equally reliable (*2*). We report here (*6*) data which support the hypothesis that neither method is invalid. Instead, the assumption that there can be only one universally valid psychophysical function is probably incorrect. Abandoning this assumption harmonizes Fechner's and Stevens' methods with each seen as a valid measure in its own domain and with more than one psychophysical "law" (*7*).

Our investigation was stimulated by research by others on a discrepancy between a particular property of both Fechner's and Stevens' results and recent data obtained from sensory physiology: psychophysical functions usually do not saturate; increases in stimulus intensity usually continue to produce increases in sensation quantity. Early

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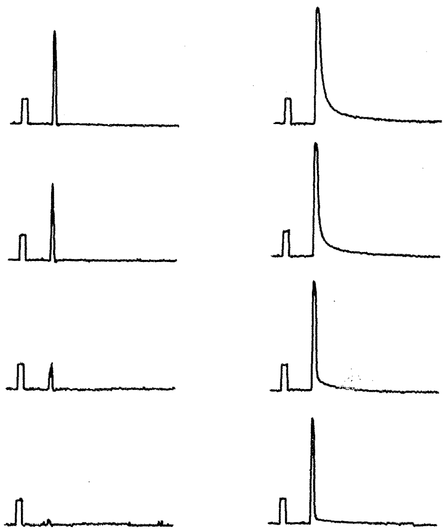

Fig. 1. Receptor potentials evoked by light flashes of different intensities. Each trace represents the response at a particular intensity. The lowest intensity is at the lower left and higher intensities are shown successively with the highest intensity (320 W/m^2) at the upper right. Neighboring traces represent responses to stimuli whose intensities differed by a factor of 4. Each trace is 20 seconds long and consists of a calibration marker (500 msec and 10 mV) followed by the response to a 250-msec flash applied 5 seconds after the beginning of the trace.

physiological investigations (8) had seemed consistent with this property of psychophysical investigations, and it is still not uncommon to find references in physiological papers to Fechner's logarithmic law. But more recent studies, particularly of cells in the visual system (9), have shown that response saturation can be prominent. The question of psychophysical saturation was therefore reinvestigated by Hood *et al.* (10). Using visual stimuli, they found that even though a logarithmic relation held at low intensities, Fechner's method did yield a saturating psychophysical function (under the right conditions). Stevens' method produced quite different results even with the identical stimulus conditions: saturation was clearly absent, the data approximated a power function, and there was a notch in the power function at those intensities that produced saturation with Fechner's method. This difference in results is striking in a modality (brightness) wherein it had been previously thought that both methods would yield approximately the same function, even if one were described by the logarithm of intensity and the other by the cube root. Neither traditional law is obeyed here and yet the two methods still give different results (11).

The methods do not assess the same behaviors, however. Fechner's method assesses detection while Stevens' method assesses identification. The differences between detection and identification have been a subject of substantial recent interest (12). Psychobiological investigations of temporal summation have also shown that detection and identification differ considerably; detection is mediated by the peak of a sensory signal, and identification is mediated by its integral (13). This work removed the response integral from the status of a candidate code to that of a true sensory code (14). If this interpretation of temporal summation is correct, one would expect that estimates of sensation quantity based on the peak of a sensory signal would saturate, because the peak of a sensory signal itself saturates (9). Estimates of sensation quantity based on the integral of a visual signal, on the other hand, might follow a different pattern. What is the relation between intensity and the integral of a sensory signal whose peak is known to saturate? Would this relation, in particular, be an approximately nonsaturating power function of stimulus intensity with a notch at intensities that cause the peak to saturate? We investigated this question by recording intracellularly from the photoreceptor cells of the lateral eye of *Limulus*, the horseshoe crab. Microelectrodes were inserted into single photoreceptors; stimulation and recording used conventional techniques (15).

Receptor potentials obtained from a representative cell are shown in Fig. 1. These receptor potentials are complex and have different features, which change in different ways with changing stimulus intensity. The peak of the response increases with increasing intensity, but it eventually saturates at high intensities. The integral or area under the response behaves quite differently, however. For weak flashes, the receptor potential hardly outlasts the 250-msec stimulus. At high intensities, however, when the peak has begun to saturate, a prolonged tail starts to appear, and the increasing prolongation of the tail causes the integral of the response to continue to grow at intensities above peak saturation. Such prolonged tails are a universal feature of visual receptor responses (16), although the time scale varies with temperature and species differences. Since there is no a priori upper limit on the length of the tail, one would not expect the integral to saturate (17).

The effects (Fig. 1) were quantitated in six cells (Fig. 2). The area was computed by integrating for 15 seconds after stimulus onset, although the major contribution of the tail to the integral is made within 1 to 2 seconds after the 250-msec flash terminates. Except for the highest intensity, all responses had completely returned to baseline within 15 seconds. The peak data saturate, as has been shown before (9). Of interest here is the function yielded by the areal data. That intensity-response function almost follows a straight line in these log-log coordinates and, therefore, could be reasonably approximated by a power function. Saturation is absent. In addition, the areal function has a notch at precisely those intensities wherein the peak saturates. (Error bars are not shown, but, in the vicinity of the notch, the standard errors would be about the size of the data points; the hypothesis that the notch represents a random variate can be rejected.) The cause of the notch is an uneven trade-off between the two factors that determine the area—the height and length of the response. At low intensities, the area grows mainly because the peak is getting higher, whereas at high intensities, the area grows because the tail is getting longer. The only way a notch could fail to appear would be if peak saturation and tail prolongation compensated exactly.

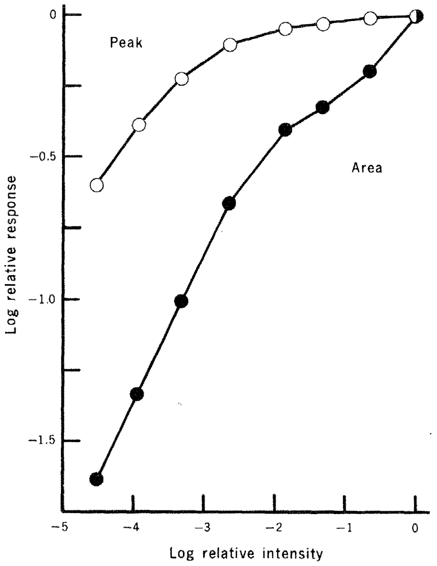

Fig. 2. The logarithm of the response evoked by a light flash as a function of the logarithm of the light flash intensity. All data have been normalized to the highest intensity (320 W/m^2). Open circles represent the peak of the receptor potential; closed circles represent the area under the receptor potential integrated for 15 seconds after stimulus onset, although the bulk of the integral comes from the first 1 or 2 seconds of the response.

This experiment provides a simple basis for the individual differences (18) frequently reported in psychophysical experiments, because a family of functions could have been obtained from the receptor by simply varying the integration period. This family would have varied continuously from a saturating function to a power function with a notch. Our interpretation is therefore subject to test because it emphasizes a novel factor, the amount of time used by an observer to evaluate a stimulus. If an observer offered rapid brightness judgments, then that observer should produce a more saturating psychophysical function. On the other hand, if an observer were more deliberate, one would expect a power function with a notch. One can even hypothesize an observer who emphasized the later portions of the sensory signal; then one would expect a positively accelerating psychophysical function. These predictions could be tested by (i) varying the instructions to the observer; (ii) measuring the reaction times of brightness judgments, partitioning those judgments into fast and slow groups, and erecting separate psychophysical functions from the partitioned judgments; and (iii) imposing response deadlines of different durations.

We conclude that there may not be any single psychophysical function, and the quest for one may have been in vain. Instead both Stevens' and Fechner's methods may represent equally valid ways of assessing the particular psychophysical functions associated with particular tasks; there may well be many task-specific psychophysical functions. Seen in this way, the psychophysical function is a conjoint property of both the sensory signal itself and the task-dependent analysis of this signal. If this interpretation is correct, we should seek harmony in this field by honoring both Fechner's and Stevens' methods and by using both methods to gain further insight into perception (*19*).

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11. Hood and his collaborators also found that very intense increments were somewhat more detectable than would be predicted by a Naka-Rushton saturating rectangular hyperbola. This deviation may occur because a very intense increment produces a complex response; although the stimulus is a pure increment, the response consists of an increment followed by a decrement, which is larger the closer to saturation. Examples of such complex receptor responses are in G. Felsten and G. S. Wasserman [*J. Comp. Physiol. Psychol.* **92**, 778 (1978)].
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17. In behavior, of course, there is an upper limit imposed by the latency of the behavioral response (*13*). So the integral might in principle saturate within this limit. But the intensities necessary would substantially exceed the threshold for tissue damage. At normal intensities, there is no reason to expect the integral to saturate. With very long stimuli (on the order of 10 seconds or more), saturation of the receptor potential integral seems to occur [R. B. Barlow and E. Kaplan, *J. Gen. Physiol.* **69**, 203 (1977)].
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A Source of Nonshivering Thermogenesis in Fur Seal Skeletal Muscle

Abstract. *The mitochondria from the subscapular muscle of naturally cold-stressed 10- to 15-year-old northern fur seals (*Callorhinus ursinus*) were loosely coupled upon isolation, whereas the mitochondria from the same muscle of warm-acclimated pups of the same age were tightly coupled. Thus, loose-coupled muscle mitochondria might provide an important vehicle for nonshivering thermogenesis in this species.*

The presence of nonshivering thermogenesis (NST) in skeletal muscles was reported by Jansky and Hart (*1*) as far back as 1963, but the cellular mechanisms inherent in this intriguing mode of heat production have hitherto not been found (*2, 3*). This might well be because most studies have been conducted with laboratory rats. In this report we present strong evidence for a loose coupling of mitochondrial respiration as an important source of nonshivering thermogenesis in northern fur seal (*Callorhinus ursinus*) pups.

Northern fur seal pups (cover picture) are subjected to frequent or constant cold stress as soon as they are born on the Pribilof Islands in the Bering Sea (*4*), where strong winds often play in concert with rain and temperatures of 6° to 8°C. We used a total of 18 animals. Some were obtained directly from the rookery at St. Paul Island, where a field laboratory was made operational in 1977; others were brought to the University of Alaska at Fairbanks in 1978. The animals were kept for a maximum of 5 days under constant cold stress, unless otherwise stated.

Cytochrome c oxidase activity is a useful index of the aerobic oxidative capacity of a tissue (*2*). Since NST is primarily aerobic in nature, muscle groups engaged in its maintenance might be expected to have a high capacity for oxidative metabolism. A survey of specific cytochrome c oxidase activity (*5, 6*) of different muscle groups in the newborn fur seal revealed considerable variation (17 to 25 microgram-atoms of oxygen per minute per gram of muscle), the highest activity being found in the substantial subscapular muscle. Enzyme activities were generally higher in 10-day-olds than in the newborns, indicating some development in oxidative capacity. We therefore used for this study the subscapular muscle (with a specific enzyme activity of about 35 μg-atom oxygen $\mathrm{min^{-1}g^{-1}}$) of pups aged 10 to 15 days (*7, 8*).

Immediately after the pups were killed, the subscapular muscles were excised and placed in ice-cold 0.15*M* KCl. The muscles were dissected free of connective tissue and visible fat and were finely minced with scissors. Homogenization of the tissue was performed according to Bullock *et al.* (*9*) by means of Nagarse digestion (*10*). Digestion at a concentration of 1 g of tissue per 5 ml of medium (*11*) containing 20 μg of Nagarse per milliliter was conducted at 0°C by the mixture being stirred magnetically for 30 minutes. Mitochondria were then obtained by differential centrifugation (*12*) with application of a field of 9200*g*