that similar conductance changes underlie both potentials.

The evidence shows clearly that the local interneuron inhibits the flexor motoneuron by the graded release of transmitter and that such interactions between neurons are of behavioral significance. The possibility must be considered that there is widespread use of this method of information transfer among other neurons.

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11. The tibia of a locust hind leg is moved by two antagonistic muscles, the flexor and the extensor. The flexor muscle is innervated by at least seven excitatory motoneurons and by two inhibitory neurons [M. Burrows and G. A. Horridge, *Philos. Trans. R. Soc. London Ser. B* **269**, 49 (1974)]. The extensor muscle receives, by contrast, only one slow and one fast (not used in walking) excitatory motoneuron, one inhibitory neuron, and one modulatory neuron. There are many local interneurons characterized physiologically (*7, 8*) and anatomically [M. V. S. Siegler and M. Burrows, *J. Comp. Neurol.*, **183**, 121 (1979)] that affect these motoneurons. The interneuron discussed here has similar physiological and morphological characteristics in each locust. It is either the same neuron in each locust or a member of a limited class.
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Discrimination Learning Without Short-Term Memory: Dissociation of Memory Processes in Pigeons

Abstract. *Pigeons were trained to perform delayed matching to samples of food and no food when each sample concurrently served as the outcome of a discrimination learning trial which immediately preceded each matching trial. Ambient light presented during the delays after the samples of food or no food severely disrupted matching but had no effect on the rate of discrimination learning.*

A popular view of animal learning holds that things are learned about to the extent that their representations persist in a labile, short-term memory (STM) for some time after a learning episode. Learning is thus viewed as the transfer of associative information from STM to a long-term memory (LTM). The transfer processes have been variously referred to as "backward scanning" (*1*), "consolidation" (*2*), or "rehearsal" (*3*). The general idea is that rehearsal of information in STM promotes the eventual representation of that information in LTM. The rehearsal construct has also been used to interpret performances in tasks that appear to measure only maintenance of STM (*4, 5*). However, rats (*6*) and humans (*7*) have been reported to show signs of LTM while showing little signs of STM, implying that maintenance of STM need not be prerequisite to formation of LTM. The findings reported here support such a dissociation between STM and LTM; discrimination learning was found to occur in the absence of measurable STM for outcomes of learning trials.

In the experiment described herein, STM was tested throughout associative learning. Pigeons were first trained to perform a version of delayed matching to sample in which reward for a choice between two comparison stimuli was conditional upon the prior occurrence of one of two sample stimuli (a presentation of food or no food). Then, discrimination learning trials were introduced in which the food and no-food samples were preceded by different stimuli. Thus, in the resulting procedure, shortly after each discrimination learning trial, a bird's memory for the outcome of that trial was tested. The measure of STM was the accuracy with which the birds could report occurrences (match to samples) of food and no food after a delay. The measure of association formation was the rapidity with which differential responding was established to the different signaling stimuli (discrimination learning). The question was whether a treatment, ambient light (*5*), that is known to reduce delayed matching performance (interfere with STM) would also reduce the rate of discrimination learning (interfere with the establishment of a new association).

Ten experimentally naive White King pigeons were maintained at about 80 percent of their free-feeding weights. The birds worked in a normally darkened operant conditioning chamber (*5*). The front panel of the chamber contained three pecking keys, a grain hopper mounted below the center key, and a houselight mounted above the center key. Stimuli were presented by in-line projectors mounted behind each key. The chamber was situated in a larger lightproof enclosure with ventilation and sound attenuation provided by an exhaust fan. Scheduling of experimental events and recording of data were accomplished with the aid of an Automated Data Systems 1800E computer located in an adjacent room.

Initially, the birds were trained to keypeck and then to perform delayed matching to samples of food and no food. After about 40 days of such training, each bird was performing the following task with accuracies in excess of 87.5 percent correct. After an intertrial interval of 20 seconds, each trial commenced with a white disk displayed on the center key. A single peck darkened the key and produced one of two samples: 2 seconds of access to grain from the illuminated food

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hopper, or 2 seconds of darkness during which no food was presented and the hopper remained dark. After a delay interval averaging 6.7 seconds (*8*), the two side keys were lit with red and green disks. A peck on either key darkened both keys and initiated a 2-second interval during which the grain hopper was activated if (i) the red side key was pecked and the trial had begun with a sample of food or (ii) the green side key was pecked and the trial had begun with a sample of no food. Each daily session consisted of 64 such trials with each of the four types of trials, defined by sample (food or no food) and position of correct side key (red on the left or green on the left), occurring equally frequently in a random sequence.

In the next two stages, one of four discriminative stimuli preceded the presentation of food or no food during each trial. These stimuli were first uncorrelated with the presentation of the sample stimulus (food or no food) so as to equalize response tendencies toward the various stimuli. A peck at the white center key beginning each trial produced one of the discriminative stimuli on that key (a red or green disk or a vertical or horizontal white line). During one-half of the presentations of each stimulus, the first peck on the center key after 10 seconds (fixed interval, or FI 10 seconds) terminated the stimulus and produced a sample of food and the remainder of the matching trial (delay, side keys, and reward for a correct choice). During the other half of the presentations, the stimulus on the center key remained lit for 10 seconds and ended, independently of pecking, in a sample of no food (extinction, or EXT 10 seconds) and the remainder of the trial. Training continued for each bird until matching accuracy was at or above the 87.5 percent criterion, the frequencies of pecking the two colors on the center key were about the same, and the frequencies of pecking the two lines were about the same (*9*).

The final discrimination learning stage involved two further changes in procedure. First, the discriminative stimuli were correlated with the presentation of food and no food so that two simple discriminations could be learned; the learning of these discriminations provided the indices of the development of new associations. When the center key was illuminated with either S+ (the red disk or vertical line), key-pecking inevitably produced a sample of food (FI 10 seconds). When the center key was illuminated with either S− (the green disk or horizontal line), a sample of no food inevitably followed (EXT 10 seconds). In both cases, the sample was followed by the remaining trial events. Second, the houselight was turned on during the delay intervals of half of the trials in order to disrupt the STM process responsible for the delayed matching performance. This illumination occurred in those trials in which colors served as the discriminative stimuli for five of the birds. For the other five birds, delay-interval illumination occurred during trials in which lines served as discriminative stimuli. Training continued under these conditions for eight daily experimental sessions.

The data from these last eight sessions (and those from the immediately preceding three sessions) are summarized in Fig. 1. The mean percentages of correct matching as a function of training days are shown in Fig. 1, A and B. The data are presented separately for trials containing light and darkness during the delay. Analyses of variance performed on these data included days, illumination (light versus dark), and groups (light after colors versus light after lines) as factors. During the last 3 days of uncorrelated training before the houselight was introduced (*10*), matching was extremely accurate; no main effects or interactions were significant, all probabilities were > .10. During the next 8 days of discrimination learning, matching accuracy was significantly reduced after illuminated delays [F (*1*, *8*) = 2045.43, $P < .001$]. There was a slight tendency for the size of the illumination effect to vary across groups [F (1, 8) = 5.43, $P < .05$] but the interaction was a small one; group matching scores following dark and light delays, respectively, averaged 88 and 52 percent (light after color stimuli) and 91 and 51 percent (light after line stimuli). No other main effects or interactions were reliable, and all probabilities were > .10. Thus, as assessed by delayed matching, the houselight had a complete and persistent amnesic effect on STM throughout the course of discrimination learning.

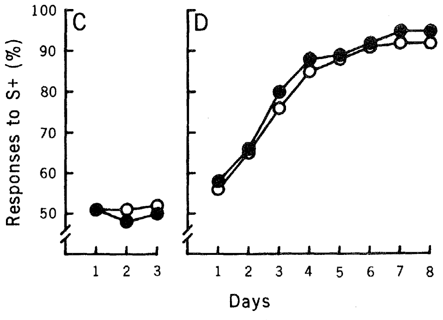

Fig. 1. Mean percentages of correct responses for (A and B) delayed matching and (C and D) discrimination learning. Closed circles represent data from trials containing dark delays and open circles represent data from trials containing delay-interval illumination. Data are presented for 8 days of discrimination learning and three preceding days during which no delay-interval illumination occurred (*10*) and discriminative stimuli were uncorrelated with reward and nonreward (S+, red disk or vertical line). The plotted means result from averaging the scores of ten birds per day.

Figure 1, C and D, shows the discrimination learning data in a manner analogous to those on matching. The data displayed are mean percentages of "correct" responses, that is, percentages of responses to each S+ of the total responses to S+ and S− from the same dimension. Scores close to 50 percent indicate little discrimination and a score of 100 percent indicates complete discrimination. During the last 3 days of uncorrelated training (*10*), the scores approximated 50 percent and none of the main effects or interactions were significant; all probabilities were > .05. During the eight discrimination sessions when discriminative stimuli differentially signaled food and no food, responding gradually came to occur only in the presence of those stimuli (S+) signaling food (scores approaching 100 percent), F (7, 56) = 57.23, $P < .001$. However, the presence or absence of delay-interval illumination did not affect the rate of discrimination learning, $F < 1$, and no other main effect or interaction was significant; all probabilities were > .50 (*11*). Thus, as assessed by discrimination learning, the houselight did not interfere with the establishment of associations (in LTM) even though it drastically interfered with the maintenance of STM.

This experiment is important for both methodological and theoretical reasons. First, the method of chaining delayed matching to discrimination learning trials is a way of measuring STM throughout the course of associative learning. The method presents opportunities to ask incisive questions about the relations between STM and animal learning. Second, the results suggest a dissociation between processes involved in the maintenance of STM and those involved in 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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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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