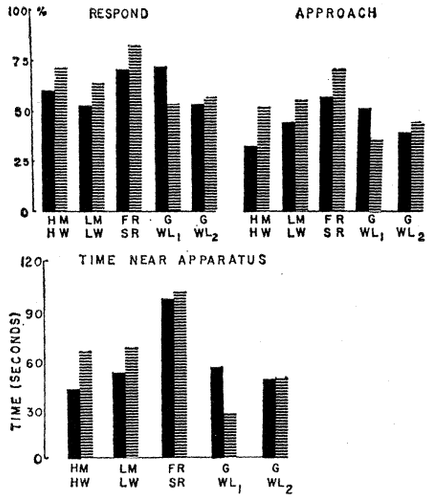

Fig. 1. Average response to, approach to, and time spent near the imprinting apparatus by purebreds (solid bars) and crossbreds (striped bars); *N*, 669.

and off. A continuous tape recording of the clucking of a broody hen furnished an auditory stimulus. The temperature in the testing room was maintained at about 30°C. Each chick was given one 5-minute test.

Each chick was transported from its isolation box to the testing compartment 24 ± 2 hours after hatching and placed in a circle, 5 cm in diameter, drawn on the floor of the compartment opposite the visual stimulus. Time before response toward the stimulus, time before approach to the stimulus (within 15 cm), and time spent near the apparatus (within 15 cm) during the test period were the behavior traits measured.

A trend is obvious in response, approach, and stay-near tendencies of purebred and crossbred chicks (Fig. 1). In four of the five comparisons crossbreds were superior to purebreds in response and approach tendencies. Chi-squares (variances were heterogeneous) comparing all crossbreds with all purebreds showed that significantly more crossbreds than purebreds responded and approached. Differences within mating sets were not significant, but this fact is not surprising since variances for these traits are large. Essentially the same pattern is seen for the tendency of chicks, 24 hours after hatching, to stay near the imprinting apparatus; variances were homogeneous for this trait but still very large. Results of *F* tests comparing crossbreds and purebreds within 2 × 2 sets were not significant, but pooling of data over sets showed that crossbreds spent significantly more time near the apparatus than did purebreds.

Although the degree of inbreeding of the lines employed was low in most instances (*3*), results showed that tendencies to respond toward, to approach, and to stay near a distant imprinting apparatus 24 hours after hatching are heterotically inherited traits. The results do not preclude additive inheritance, which has a low but significant effect on response tendencies (*5*).

Fisher's fundamental theorem of natural selection (*6*) predicts that traits that are major components of fitness contain little additive genetic variation (σ_A^2) when the population concerned is in relative equilibrium with its environment. Such traits will have been subjected to extensive prior selection that reduces σ_A^2 but favors the accumulation of (or evolution of) nonadditive genetic variation. According to this theory the traits measured by us were probably adaptive during development of the domestic fowl.

Correlations between selected and unselected traits may change during the course of selection, and genetic correlations may in fact change sign during a selection experiment (*7*). For this reason the FR and SR (*3*) and their reciprocal crosses were excluded from the correlation analysis.

Table 1 shows weighted phenotypic correlations among the traits studied; both quantitative and qualitative measurements of response and approach tendencies are shown. The fact that response toward the imprinting apparatus correlated highly with approach and with time spent near the apparatus indicates that chicks that respond generally follow a pattern of approach and stay-near behavior. This sequence of steps seems to be meaningless except in terms of the concept of imprinting. The evidence that nonadditive gene action has evolved for response, approach, and stay-near behavior during the critical period for imprinting in this neonatal species, coupled with evidence that such behaviors are highly related, supports the idea that these traits indicate tendencies to imprint.

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1 March 1968

Reinforcement Magnitude as a Determinant of Performance Decrement after Electroconvulsive Shock

Abstract. *The intensity of a foot shock may be a determinant of the rate at which an avoidance response becomes resistant to disruption by electroconvulsive shock. Mice were trained, one trial a day, in a passive avoidance learning task, with one of three foot-shock intensities. Electroconvulsive shock was administered at various intervals after each trial. At all foot-shock intensities, electroconvulsive shock given 10 seconds after each training trial was effective in disrupting learning. Where electroconvulsive shock was given at longer intervals after each trial, those animals learning at low intensities of foot shock showed greater impairment of performance than those learning at high intensities.*

The relationship between retention of a learned behavior and the administration of electroconvulsive shock (ECS) has been studied extensively. Primary emphasis has been on the interval between training and ECS delivery. Typically, the longer this interval, the less performance is disrupted when the animals are later tested. There is debate, however, over the duration of the period after learning during which ECS disrupts memory consolidation (that is, causes retrograde amnesia). Chorover and Schiller (*1*) place an upper limit of 10 seconds on the interval during which ECS can produce retrograde amnesia. Quartermain *et al.* (*2*) have suggested a 30-second limit; Mc-

Gaugh (*3*), a 1- to 3- hour interval. Kopp *et al.* (*4*) report production of some retrograde amnesia with intervals up to 6 hours.

We varied the intensity of foot shocks and also the interval between training and delivery of ECS (training-ECS interval) to investigate whether both of these factors are determinants of the rate at which an avoidance response becomes resistant to disruption by ECS. Previous studies in which foot-shock (FS) intensity was varied used single intervals of less than 20 seconds (*5*) between training and delivery of ECS; there was no change in performance decrement related to FS intensity. One study (*1*) varied the duration of the FS as well as the training-ECS interval. As the duration of the FS increased, there was a decrease in the training-ECS interval which would result in a disruption of retest performance.

Naive male mice (325; Carworth Farms strain 1) approximately 60 days old were housed four to a cage and had unrestricted access to food and water. Subjects were randomly assigned to 17 groups (at least 18 in each group) and trained in a passive avoidance learning task for 5 successive days, one trial per day. Only the data from day 1 and day 2 are reported here.

The passive avoidance learning apparatus was similar to that used by Kopp *et al.* (*4*). In vertical cross section, the box was V-shaped, 11.5 cm wide at the top and narrowing to 3.75 cm wide at the floor level. The box was 33 cm long and divided by a partition into a 10-cm-long compartment with clear plastic sides in which the subject was placed, and a 23-cm-long compartment with metal sides in which shock could be delivered. A square opening (3.75 by 3.75 cm) in the bottom of the partition gave access from the start to the shock compartment. The floor of the box consisted of two strips of aluminum separated by a 0.8-cm gap. Foot shock was delivered by way of these floor strips.

The start compartment was brightly illuminated by two 28-volt lamps outside the base of one wall, and the shock compartment was made as dark as possible by extending the dividing partition beyond the chamber wall and by placing the box in a darkened room. A contact relay circuit was used such that as soon as the subject was dropped into the start compartment, facing away from the dark compartment, a timing circuit was activated. When the mouse moved through the partition into the dark compartment, a photocell beam positioned 7.75 cm into the dark compartment was interrupted, causing foot shock, turning off the lights illuminating the start box, and stopping the timing circuit.

Foot shock was 60-cycle a-c regulated by an autotransformer. A resistor (270 kohms) in series with the subject provided relatively constant current in the FS circuit. The intensity of the FS was measured at the box with a milliammeter substituted for an animal. Intensities of FS used were 0.3, 1.5, and 2.8 ma. Shock duration was 0.15 seconds.

After moving through the partition and receiving FS, subjects were removed from the apparatus and given either no ECS, or ECS 10, 160, 640, or 1600 seconds after FS. Control groups received no FS and either no ECS or ECS 10 seconds after entry into the dark compartment. Animals receiving no ECS were replaced in their home cages immediately after the training trial; animals receiving ECS 10 seconds later were given ECS and allowed to recover in their home cages; those receiving ECS 160, 640, or 1600 seconds later were removed from the avoidance box immediately after the trial and placed in a holding cage until 160, 640, or 1600 seconds had elapsed, at which time they were removed from the holding box, given ECS, and replaced in their home cages. Subjects were held by hand, and the ECS was administered by means of saline-soaked, cup-shaped electrodes applied to the cornea of each eye at a constant current of 50 ma for 0.25 seconds. This elicited, in all animals, a full tonic extension seizure. After each daily training trial ECS was applied. No mice were lost because of the ECS treatments.

On the first day of training, any mouse that remained in the start compartment for more than 40 seconds was discarded from the study, for a total of 15 mice. On subsequent days, if an animal remained in the start compartment for more than 300 seconds, the trial was terminated, and the animal was removed and given a latency score of 300.

Figure 1 plots day 2 medians and interquartile ranges (IQR) for all 17 groups. The range of the medians for these groups on day 1 was 16 to 28 seconds.

Raw score latencies were analyzed with analyses of variance. There were no significant differences between the groups on day 1. An analysis of variance on day 2 latencies yielded significant differences ($P < .01$) for both main effects—foot-shock intensity and electroconvulsive-shock interval—and a nonsignificant interaction (Fig. 1). Thus, the intensity of foot shock did differentially affect learning of the avoidance response, and disruption of this learned response was related to the training-ECS interval.

One-way analysis of variance for each ECS condition across the three foot-shock intensities showed a significant difference ($P < .05$) when no ECS was given, no significant differences when the ECS was delivered 10 or 160 seconds later, and significant differences when the ECS was delivered 640 ($P < .025$) or 1600 seconds ($P < .05$) later.

When ECS is delivered 10 seconds

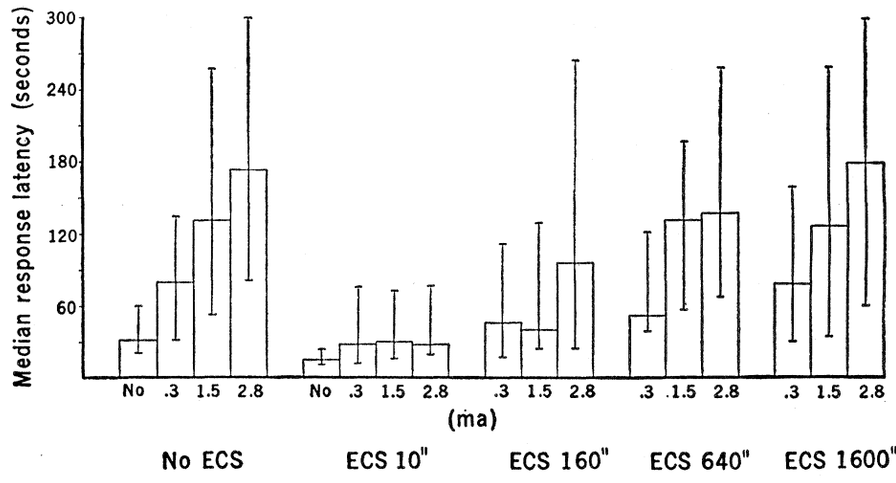

Fig. 1. Effect of foot-shock intensity and training-ECS interval on acquisition of a passive avoidance response by 60-day-old male mice (Carworth Farms strain 1).

Table 1. Significance of the differences among ECS conditions at the three intensities of foot shock on day 2.

Training-ECS interval (sec)	Training-ECS interval (sec)			
	10	160	640	1600
	Foot shock, 0.3 ma			
No ECS	.01	.07	NS*	NS
10		.05	.05	.05
160			NS	NS
640				NS
	Foot shock, 1.5 ma			
No ECS	.01	.02	NS	NS
10		NS	.01	.01
160			.025	.05
640				NS
	Foot shock, 2.8 ma			
No ECS	.01	NS	NS	NS
10		.05	.01	.01
160			NS	NS
640				NS

* Not significant.

after the response when no FS is given, response latencies on day 2 are shorter ($P < .01$) than those of mice given no FS and no ECS (Fig. 1). (All comparisons reported between two groups were made with median tests.) This result suggests that ECS is not acting as an aversive stimulus in this situation, or latencies of the first group would have been longer than those of the second.

Table 1 contains, for day 2, the significance levels of the differences in response latencies between the ECS conditions for each foot-shock intensity. An ECS delivered 10 seconds after FS disrupted the avoidance response at all three FS intensities. An ECS given 160 seconds after FS disrupted only the groups given 0.3- and 1.5-ma foot shocks whereas an ECS given 640 or 1600 seconds later did not cause a significant disruption in any of the groups. The response latency of the group given 2.8-ma foot shock increased when ECS was delayed 160 seconds, whereas there was no increase in that of the group given a 1.5-ma foot shock until the ECS was delayed 640 seconds. The group given 0.3-ma foot shock never shows a single large increase in response latency. When ECS is delayed 1600 seconds, all FS groups have response latencies very similar to those when no ECS is given. It seems then that, as the FS intensity increased, the interval during which ECS caused a significant disruption of the learned response decreased.

Failure in previous studies (*5*) to find this interaction between FS intensity and effectiveness of ECS in causing performance decrement seems to have been due to the use of only a single short training-ECS interval. Our study shows that, with short training-ECS intervals, ECS is effective in producing performance decrement over a wide range of reinforcement intensities, whereas with long training-ECS intervals only responses followed by low intensities of foot shock are disrupted. This result seems compatible with both the results of Kopp *et al.* (*4*) who used a 0.32-ma, 0.8-second FS and obtained disruption with long training-ECS intervals, and with the data of Chorover and Schiller (*1*) who used a 0.75-ma FS with durations of 0.5 to 4.0 seconds and obtained disruption only at short training-ECS intervals when long FS durations were used.

There seem to be some performance changes which are independent of FS intensity and some which are not. These data may support a two-part theory of memory consolidation. One component of the trace might be based on simple contiguity of the conditioned stimulus and the unconditioned stimulus; this component does not vary with reinforcement magnitude and is not subject to disruption by ECS. The second component of the trace seems to be time dependent (and may be a performance factor) and varies both in size and in resistance to disruption with reinforcement magnitude.

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On the Discovery of Actin

The initial isolation and characterization of actin is commonly ascribed to F. B. Straub (*1*). Actin actually was isolated and characterized under the name "myosin-ferment" 55 years before Straub's studies were published.

W. D. Halliburton, at the time a physician acting as assistant professor of physiology at University College in London, was attempting to extend Kühne's observations on frog muscle proteins (*2*) to those of the rabbit and cat. Halliburton's observations (*3*) included the following comments, captioned "The preparation and properties of myosin-ferment."

> We now turn to the full consideration of the ferment which brings about the coagulation of myosin, and to which allusion has been several times made in the foregoing pages.
>
> I have prepared three specimens in all; and the method of preparation is almost precisely that adopted by Schmidt in the preparation of the fibrin-ferment from blood.
>
> Muscle was first allowed to undergo rigor; it was then chopped up into small pieces and kept under absolute alcohol for a long time.
>
> The first preparation made from cat's muscle was kept under alcohol for ten months; and two preparations from rabbit's muscle were kept under alcohol for three months.
>
> The pieces of muscle after having been thus treated were then dried over sulphuric acid, and powdered. An aqueous extract of this powder contained the myosin-ferment, as shown by the fact that dilution of muscle-plasma, or a solution of myosin with it brought about coagulation much more quickly than dilution with distilled water.
>
> The chemical properties of the aqueous extract were as follows:
>
> 1. Alcohol gave a precipitate soluble in water.
> 2. Boiling gave no precipitate.
> 3. The xanthoproteic reaction showed that a small amount of proteid was present.
> 4. Nitric acid gave a slight precipitate in the cold; this disappeared on boiling, and reappeared on cooling.

This description and other experiments described in Halliburton's long article indicate that he was dealing with the protein now known as actin. It also seems clear that Halliburton was able to distinguish operationally between myosin A (actin-free myosin) and myosin B (natural actomyosin).

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