lie below the corresponding confidence-rating lines. For one subject (E.R.) all five yes-no points were substantially below the confidence-rating lines, which suggests that this subject had considerable difficulty in complying with the instruction to report her confidence at the time of response. For this reason, d_T was based on an ROC line drawn through the yes-no point alone.

The tables of Elliott (*14*), which are based on the assumption that ROC lines have unit slope, were not used because the slope may vary with d'. When the slope of the ROC line is a function of d', the d' estimates obtained from the tables are biased. In calculating d_T, the confidence-rating data were used to calculate the most likely slope of the ROC line passing through the yes-no point. First, an ROC line was fitted to each set of confidence-rating points. As in calculating d_a (*13*), the regression coefficient of ln slope on d_s was computed from these lines for each subject. Each family of lines thus generated includes a unique line through every point in the ROC plane, including a line through each yes-no point. The absolute value (in standard deviates) of the x-intercept of that line is d_T.

The speed-accuracy results shown in Fig. 2 invite a comparison between the detection-theoretic processes underlying retrieval from memory and those previously found in perceptual discrimination experiments (*5, 15*). In discrimination experiments involving the method of forced reaction times, $(d')^2$ was found to be a linear function of T. The data presented here suggest that the recognition memory d' stops growing when the retrieval time exceeds about 4 seconds. Some experimenters studying perceptual discrimination with other methods found similar asymptotes (*12*). Although models accounting for this behavior have been developed, their derivation would be out of place in a brief report (*16*). One model, based on the assumption that the memory trace continues to decay during retrieval, predicts that d', as a function of time, should follow the equation

$$d' = \frac{m[1 - e^{-\alpha (T - \eta)}]}{\alpha(T - \eta)\,[\sigma^2 + (T - \eta)^{-1}]^{1/2}} \quad (1)$$

where T is the measured total recognition time, and η, m, α, and σ are constants. Equation 1 is represented by the curves in Fig. 2. This model predicts an eventual decrease in accuracy with additional retrieval time, and a small decrease was found when the probe display time was increased from 4 to 8 seconds. The decrease was not significant in this experiment, but the possibility of an optimum retrieval time should be kept open. The method presented in this report should facilitate additional quantitative investigations of accuracy as a function of available time.

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References and Notes

1. In a prior study B. B. Murdock [*Quart. J. Exp. Psychol.* **20**, 79 (1968)] investigated speed-accuracy trade-off in paired-associate recall by means of explicit prior limits on reaction time. J. M. Swanson and G. E. Briggs [*J. Exp. Psychol.* **81**, 232 (1968)] demonstrated a trade-off in stimulus categorization by manipulating response latency with differential instructions and payoffs, for accuracy and speed. Differential payoffs were also used by B. L. Lively [*ibid.* **96**, 97 (1972)] to demonstrate a trade-off in the memory search task described by S. Sternberg [*Science* **153**, 652 (1966)]. None of these studies used methods capable of excluding the fast-guess hypothesis (*11*).
2. The subjects were paid female undergraduates meeting the usual requirements (right-handed, native speakers of English, and so forth).
3. The consonants were chosen from b, c, d, f, g, h, k, l, m, n, p, r, s, t, v, and z.
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7. This is not meant to imply that the two methods of controlling processing time are mutually exclusive. Procedures combining the two methods may be devised, and no doubt will be.
8. The design was also balanced for frequency of occurrence of consonants and order within trigram. Four additional sessions were used for training.
9. This corresponds to standard errors ranging from 2 to 8 msec in the mean latencies shown in Fig. 1.
10. Data are available in tabular form from the author.
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13. W. A. Wickelgren, *J. Math. Psychol.* **9**, 418 (1972). The regression coefficients of ln slope on d_s were negative (corresponding to slopes less than 1.0) for all three subjects, ranging from $-.09$ for N.V. and E.R. to $-.35$ for L.S. No consistent relationship was found between d' and the yes-no criterion parameter (β).
14. P. B. Elliott, in *Signal Detection and Recognition by Human Observers*, J. A. Swets, Ed. (Wiley, New York, 1964), p. 651.
15. M. M. Taylor, P. H. Lindsay, S. M. Forbes, *Acta Psychol.* **27**, 223 (1967).
16. These models will be adequately documented elsewhere (A. V. Reed, in preparation). In the meantime a summary of model derivation and parameter fitting will be available from the author. In the model of Eq. 1, $(T - \eta)$ is the retrieval integration time; m is the strength of the memory trace, relative to retrieval noise, at the start of retrieval; α is the decay coefficient of the trace; and σ is the standard deviation of threshold jitter.
17. The author is a National Science Foundation Graduate Fellow. This research was also supported by NIMH grant MH 17958-03 to W. A. Wickelgren. I thank Professor Wickelgren for his advice and supervision of this work.

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Imprinting: Lasting Effects on Uracil Incorporation into Chick Brain

Abstract. *On the first day after hatching, domestic chicks were trained for 20, 60, 120, or 240 minutes with an imprinting stimulus. On the second day, they were all retrained for 60 minutes. The greater the chicks' experience on the first day, the lower the rate of incorporation of tritiated uracil into macromolecules in the anterior part of the forebrain roof on the second day. Such effects were not found in other brain regions, nor in any brain region of chicks that received similar treatment on the first day but were not retrained on the second.*

When split-brain chicks had one eye covered during exposure to a rotating, flashing light to which they became socially attached, incorporation of [^{3}H]-uracil into macromolecules was 15.2 percent higher on the trained side of the forebrain than on the untrained side. No such differences were found in any other region of the brain (*1*). The forebrain roof has been implicated not only as the site of most rapid incorporation of uracil into presumed RNA during an imprinting procedure, but also as the region where the activity of RNA polymerase and incorporation of lysine into presumed protein first increases after imprinting (*2, 3*). The results for the split-brain chicks indicate that certain general effects of the imprinting procedure, such as a change in concentration of hormone, are not likely to be solely responsible for the increased incorporation of uracil into macromolecules, since such general effects would be expected to influence both sides of the brain to the same extent. However, the biochemical changes produced by the rotating flash-

ing light used for imprinting the chicks could result from other nonspecific consequences of exposure, such as general sensory stimulation at the time of training (*4*).

In the present study, we have attempted to dissociate the longer-lasting effects of training, in which we are primarily interested, from short-term changes which might arise from sensory stimulation. Experience with the imprinting stimulus was varied on the first day after hatching but kept constant after [^{3}H]uracil had been injected on the second. If incorporation of uracil is exclusively related to the training procedure, the amount of incorporation on the second day should be inversely related to the length of training on the first. The design of the experiment presupposes that the process by which chicks form social attachments is not instantaneous, but is cumulative; the longer the period of exposure, the more the young bird learns and the stronger the bond with the familiar object (*5*). It is assumed, however, that the amount learned is not linearly related to duration of training, and the longer the period of training on the first day, the less the bird will learn on the second.

We first exposed 64 socially isolated Ross chicks from four batches to a constant overhead light for 60 minutes a few hours after hatching. This was done to maximize the effects of subsequent training (*6*). The chicks were placed in activity wheels and trained at 30°C with an orange flashing rotating light for 20, 60, 120, or 240 minutes at 24 to 27 hours after hatching (*7*). The bouts of training lasted 20 minutes and were interspersed by 20 minutes in a dark incubator. The bouts of training of the 20-, 60-, and 120-minute groups were arranged symmetrically between the beginning and end of training of the 240-minute group. Apart from the periods of exposure to light, the chicks were kept in dark incubators in social isolation and were only handled in the dark or under dim green light.

The extent to which the four groups approached the training stimulus is shown in Fig. 1. The chicks' preference for the familiar object was then measured in a choice test in which the novel object was a red patterned cylinder rotating around a light (*7*). The mean preferences of the four groups are shown in Fig. 1. The strength of

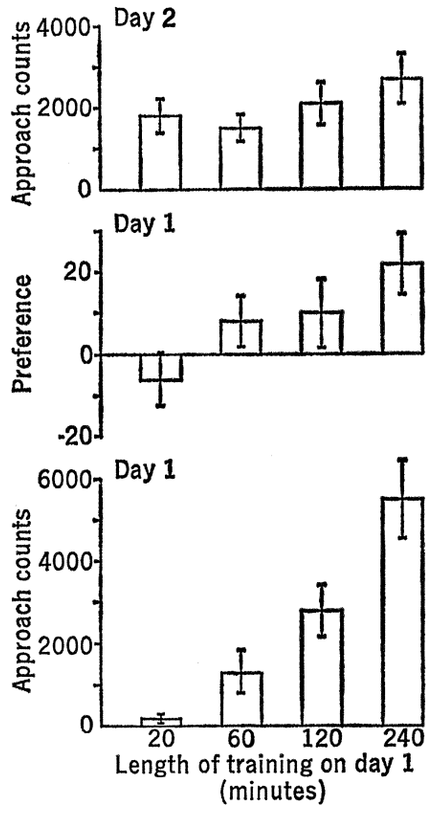

Fig. 1. Means and standard errors for total counts of chicks' approach activity toward a flashing rotating light and for their preferences for it in a choice test. The chicks were trained with the light for 20, 60, 120, or 240 minutes on the first day after hatching, given a choice test immediately afterward, and then retrained for 60 minutes on the second day. A chick obtained four approach counts for each revolution of an activity wheel 30 cm in diameter. A chick's preference was the maximum distance traveled (in centimeters) from the midpoint between the familiar light and a novel one. Each chick was placed in a specially geared wheel in which the bird's movements carried it away from the object that it tried to approach. When a chick had been carried sufficiently close to the less preferred light, it usually turned around and attempted to approach that one (*7*). A negative score means that a chick attempted to approach the novel stimulus.

their preference for the familiar object was clearly correlated with the length of exposure (Spearman $\rho = .325$, $P < .01$).

On the second day after hatching, all the chicks were given an injection into the heart region of 20 μc of [^{3}H]uracil (1000 mc/mmole) and placed in a dark incubator maintained at 30°C; 47 minutes later they were trained for a further, uninterrupted 60 minutes with the familiar flashing orange light. The approach activity of the chicks during this second period of training is shown in Fig. 1. The birds trained for longer periods on the previous day tended to be more active, but the trend was not statistically significant. The chicks were killed 150 minutes after injection, and the brains were dissected as in previous studies (*1*, *2*) except that the forebrain roof was further subdivided into anterior and posterior regions at the widest part of the section (*8*). The brain and liver samples were frozen, coded, and analyzed for acid-insoluble radioactivity

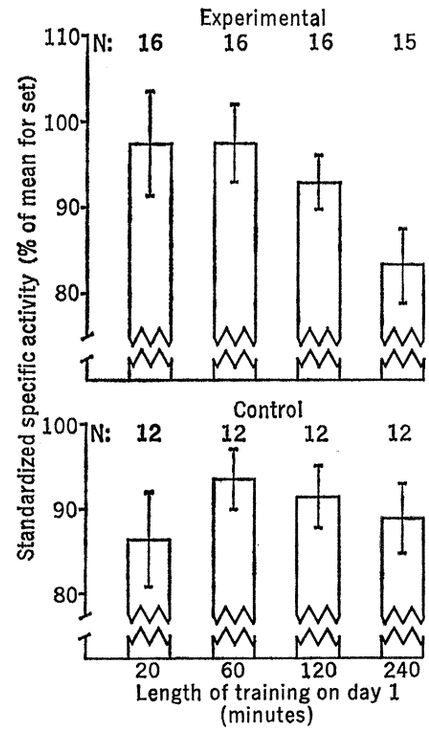

Fig. 2. Mean and standard error for specific activity of [^{3}H]uracil incorporated into macromolecules of the anterior forebrain roofs of 2-day-old domestic chicks. The experimental birds were trained with an imprinting stimulus for varying amounts of time on the first day after hatching, and were all retrained for 60 minutes on the second day. The control birds received the same treatment on the first day but were left in the dark on the second. The data have been standardized by expressing each value as a percentage of the mean for all brain samples from the set with which it was analyzed (*9*). The decline in the experimentals as training on day 1 increased from 20 to 240 minutes is statistically significant (Spearman $\rho = -.311$ corrected for ties; $t = 2.56$; $P < .02$), whereas no such relation can be detected in the controls (Spearman $\rho = +.106$).

Table 1. Mean standardized specific activities and standard errors for samples from liver, midbrain, base of forebrain, and posterior roof of forebrain of experimental and control chicks. The correlations between these values and the length of training on the first day after hatching are also given and are corrected for ties; N, number of animals.

Training on day 1 (minutes)	N	Liver	Midbrain	Base	Posterior roof
		Experimental groups			
20	16	106.5 ± 11.0	117.5 ± 3.7	112.4 ± 7.5	81.9 ± 4.0
60	16	96.5 ± 7.7	112.9 ± 6.3	109.8 ± 5.5	87.8 ± 4.5
120	16	96.5 ± 12.3	112.5 ± 6.2	108.6 ± 5.3	86.3 ± 3.2
240	15	107.7 ± 10.9	110.5 ± 4.4	103.0 ± 4.6	81.7 ± 3.4
Spearman ρ		−.003	−.173	−.106	−.030
		Control groups			
20	12	83.8 ± 6.4	116.9 ± 5.8	103.6 ± 4.9	85.2 ± 4.7
60	12	77.8 ± 7.6	119.3 ± 5.6	107.8 ± 6.2	87.6 ± 5.7
120	12	93.0 ± 10.4	122.0 ± 5.3	116.3 ± 5.0	82.6 ± 4.7
240	12	89.3 ± 10.3	113.1 ± 4.7	108.6 ± 6.1	78.5 ± 3.5
Spearman ρ		+.077	−.058	+.120	−.145

(expressed as disintegrations per minute per milligram of protein in the sample) by the techniques described elsewhere (*2*). To eliminate variability between sets of samples analyzed at different times, each value has been expressed as standardized specific activity, that is, as a percentage of the mean for all the brain samples in the set with which the sample was analyzed (*9*).

In the anterior part of the forebrain roof, the incorporation of [^{3}H]uracil into presumed RNA (Fig. 2) was negatively correlated with the length of training on the previous day ($P < .02$). The difference in the anterior roof region between the group trained for 60 minutes and the group trained for 240 minutes is also statistically significant ($t = 2.31$, $P < .05$). None of the other differences in the other brain regions or the liver were statistically significant, nor were any of the other trends (Table 1).

The effect of training on day 1 on uracil incorporation into the anterior roof on day 2 could have occurred regardless of whether or not the birds had been trained on day 2, as a result of long-lasting depression in regions that were active the previous day (*10*). We therefore repeated the first part of the experiment with a further 48 Ross chicks from three batches. These control chicks were exposed to a constant overhead light shortly after hatching, and were trained for 20, 60, 120, or 240 minutes on the first day after hatching. However, on the second day, when incorporation of [^{3}H]uracil was measured, they were kept in the dark at 30°C from the time of precursor injection until they were killed. In every other respect, the birds were treated in the same way as the experimentals. The approach and preference scores during training and testing did not differ from the experimentals. In the control chicks, no significant differences were found between any of the groups in any of the brain regions or in the liver (Fig. 2 and Table 1). Thus, the duration of training on day 1 had no effect on incorporation into macromolecules on day 2 if the birds received no further training. This contrasted markedly with the incorporation in the anterior roof when birds were trained for 60 minutes on the second day after hatching.

We infer that those chicks trained for longer periods had learned more than those trained for shorter periods, because preference for the familiar object continued to be strengthened over the first 4 hours of training. If this is correct, it is reasonable to assume that the experimental birds trained for longer periods on day 1 would have had less to learn on day 2 about the object to which they were becoming attached than would those trained for shorter periods on day 1. Is this the explanation for the inverse relation between rate of incorporation of uracil into the anterior roof and the length of training on the preceding day? It is possible that the well-trained chicks were less attentive and therefore received less stimulation than the birds which had been trained for shorter periods on day 1. However, we think such a possibility is implausible because, if anything, the birds trained for longer periods on day 1 approached the familiar object more on day 2 than did the birds trained for shorter periods. When these new data are taken together with the results of our previous experiments, particularly those from split-brain chicks, they suggest that biochemical changes occurring in the anterior part of the forebrain roof are linked with acquisition processes involved in imprinting rather than with more general side effects of training (*11*). It remains possible, however, that general neuronal differentiation in the anterior roof is affected by the imprinting procedure—the further that development of the region had proceeded on the first day, the less that might have needed to occur on the second day when the experimental birds were once again trained.

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7. The apparatus used for training and testing the chicks and the methods of scoring are described elsewhere (*6*).
8. G. Horn, S. P. R. Rose, P. P. G. Bateson, *Science* **181**, 506 (1973).
9. Four brain samples and one liver sample from each of four chicks, one from each group, were analyzed as a set of 20 except when an experimental chick died before the end of an experiment and the size of the set was reduced to 16.
10. After 60 minutes of imprinting, incorporation of [^{3}H]uracil into the forebrain roof first increases and then falls below the resting level for several hours. However, after 24 hours no differences could be detected between trained and untrained chicks [P. P. G. Bateson, S. P. R. Rose, G. Horn, *Brain Res.* **42**, 552 (1972)].
11. The biochemical significance of these findings is discussed elsewhere (*8*).
12. We thank Joanna Jaeckel, Ann L. D. Horn, and Arun Sinha for assistance. Supported by grants from the Science Research Council to P.P.G.B. and G.H. and by a grant from the Medical Research Council to S.P.R.R.

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