The percentage of SWS increased on both nights 1 and 2 (Fig. 2) $[F(4, 20) = 44.0, P < .001]$. This is predominately due to a marked increase in stage 4 (the deepest stage) on night 1 but is more equally divided between stages 3 and 4 on night 2 (Fig. 2). Significant increases were shown for both stages 3 and 4 individually on night 2, but only for stage 4 on night 1. When expressed as a percentage of total sleep time, neither SWS nor stages 3 or 4 individually was significantly raised on nights 3 and 4.

The increase in SWS on nights 1 and 2 (Fig. 1) is more remarkable because of the extended sleep period and is accompanied by a decrease in rapid eye movement (REM) sleep particularly. A relative decrease in stage 2 sleep occurred on nights 1 to 3. Sleep onset latency (timed from lights out to first appearance of stage 2) was significantly shorter on night 1 [Friedman two-way analysis of variance, $\chi_r^2(4) = 11.7, P < .05$]; stage 4 (but not stage 3) onset was also significantly shortened on night 1 $[\chi_r^2(4) = 12.1, P < .05]$. There were no changes in sleep onset latency on any of the subsequent nights.

We conclude that in a group of highly fit subjects SWS increases after an extreme metabolic load. This increase appears to have components of both time and intensity. Intensity factors are suggested by the dominance of stage 4 sleep and the decrease of stage 4 onset latency on night 1 but a surge of stage 3 on night 2. Temporal aspects are shown by the significantly raised percentages and absolute amounts of SWS on nights 1 and 2 and the decline over the next 2 days. The possibility that recovery after severe exercise in the form of SWS does not occur completely on the first night was suggested to us by a pilot study on a single subject in whom the typical decline in SWS throughout the night to very low levels toward the end of the sleep period did not occur; that is, the last third of the night after a heavy exercise load still had a high percentage of SWS. We have shown a relationship between a measured amount of exercise and SWS (*11*). Most studies in which fit subjects have been tested show an increase in SWS after exercise (*9*), but this is not the case with unfit subjects (*10*). It may be that an inadequate exercise load was used with unfit subjects, or the strain caused by an adequate load may have disrupted sleep as it did to some extent on postmarathon night 1 of this study. Increased metabolism has been shown to be related to an increase in SWS under a variety of circumstances (*17*).

The quantitative increase in total sleep time and particularly in SWS and the qualitative shift toward more stage 4 sleep immediately after metabolic stress support the theory that sleep (particularly SWS) is a recovery period for daily activity. This conclusion does not imply that restoration is an exclusive function of sleep, and several hypotheses of the function of REM sleep are still tenable (*3, 18*).

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Retroactive Interference in Discrimination Learning

Abstract. *In stage 1 of this experiment pigeons were trained to discriminate between two levels of noise or two colors by pecking on one of two disks. In stage 2 the discriminative stimuli were not presented, but pecking on the disks was rewarded on a random schedule. The second procedure caused the pigeons to forget the discrimination they had learned.*

Events that affect an organism after it has learned something new may cause it to forget what it learned. This retroactive interference (RI) has been studied in many experiments with human subjects. In most of these, the event considered the possible cause of forgetting is a second learning experience. The usual experimental procedure involves two groups of subjects and three treatment phases. During phase 1 the two groups are trained identically, for example, to recite a list of words or nonsense syllables. During phase 2 the control group rests while the experimental group learns a second task, and during phase 3 both groups are tested for retention of what they learned in phase 1.

Numerous experiments on RI have also been done with animal subjects. Most of the more recent ones have been concerned with the effects of events that intervene between the presentation of a single stimulus and the opportunity to make a learned response to that stimulus (the delayed matching-to-sample paradigm) (*1*). Such experiments differ from the work with humans in two important ways. (i) They deal with short-term rather than long-term memory, and (ii) the postlearning event examined as a possible cause of forgetting is usually a simple stimulus change, such as the extinction of a light source. Only a few experiments with animals have examined the effect of a relatively protracted learning experience upon the retention of previously learned behavior (*2–5*).

Several of the experimenters who studied RI in situations involving long-term memory in animals used a simple spatial discrimination as the first task and its reversal as the second (interfering) task (*4*, *5*). It would aid in understanding the processes responsible for RI to know whether two tasks that do not involve the identical stimuli and responses in different relationships may also interfere with each other and what principles determine the amount of interference that may occur. These matters have been examined in a large number of experiments with human subjects, but it is not known whether the generalizations derived from these experiments can be extended to some of the nonhuman subjects widely used in studies of learning.

The specific purpose of the research reported here was to determine whether pigeons trained to discriminate between two acoustic or visual stimuli will retain the discrimination if they are given a second phase of training during which the stimuli they were taught to discriminate are never presented, but in which the responses are rewarded on a probabilistic basis.

We worked with four groups of white carneau pigeons. In phase 1, two groups [experimental noise (N_e) and control noise (N_c)] were trained to discriminate between white noise at 65 and 95 dB sound pressure level. The remaining groups [experimental color (C_e) and control color (C_c)] were trained to discriminate between two lights, approximately equal in luminance, that appeared red or orange to human observers. The birds were maintained at 80 percent of their free-feeding weight and were trained in a test chamber that contained three translucent disks arranged in a horizontal row at the approximate height of the pigeon's head, a loudspeaker, and a device for presenting food. Daily training sessions consisted of 80 trials, separated from each other by intervals of 10 seconds. During the interval between trials the disks were not illuminated. At the start of a trial the center disk was illuminated by white light. For groups N_e and N_c, a single peck on the illuminated center disk caused the white noise to come on at either 65 or 90 dB, whereas for groups C_e and C_c, a peck on the center disk caused its color to change from white to either red or orange. For all groups a peck on the center disk also caused the two side disks to be illuminated by white light. A single peck on one of the illuminated side disks was considered a correct response if it occurred in the presence of one of the noise or color stimuli (for example, 95-dB noise or red light), and a peck on the other disk was considered correct for the remaining member of the stimulus pair. Correct responses were rewarded by a 2.5-second period of access to a tray of mixed grain. Incorrect responses were followed after 10 seconds by a repetition of the trial.

The birds in the experimental groups received three phases of training. Phases 1 and 3 each consisted of 30 sessions of discrimination training. During phase 2, the white noise or color stimuli were not presented. Instead, both groups received 100 trials per day on which a reward was scheduled randomly and with equal probability for a peck on the left or right disk (probability learning). Each trial was repeated until the scheduled reward was collected. These trials were mixed with additional trials on which no reward was scheduled for either response (to prevent the birds from getting satiated during a training session or gaining

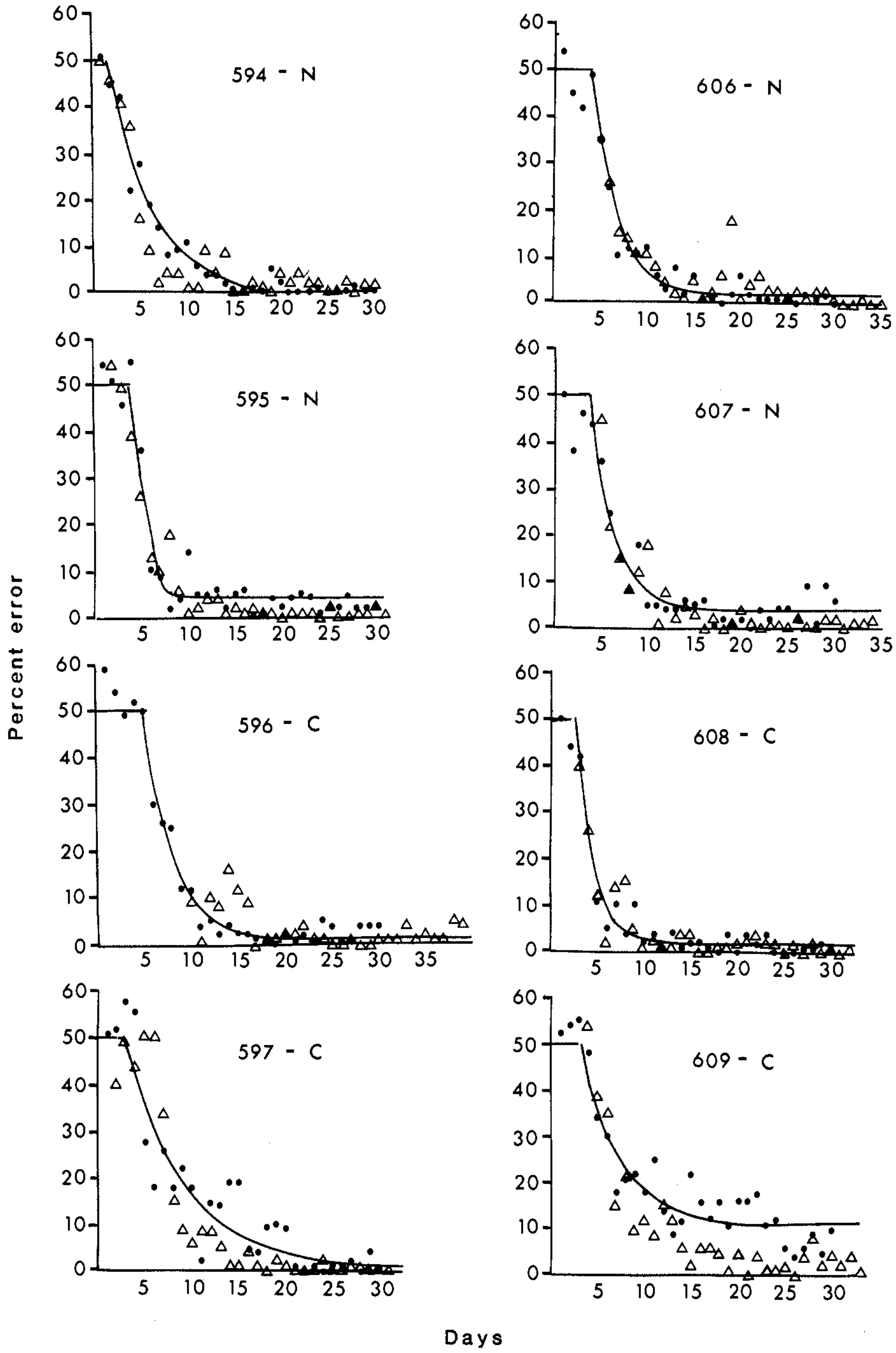

Fig. 1. The course of learning a discrimination (circles) and relearning the same discrimination (triangles) by individual pigeons in the experimental groups; *N* indicates a discrimination between noise intensities and *C* indicates a discrimination between colors.

weight over the long run). The proportion of trials on which a reward was scheduled was reduced gradually from 1.0 to 0.2 and remained there through phase 2. Altogether, phase 2 consisted of 47 daily sessions during which there were on the average a total of 40,500 trials.

We wanted to examine the effect of phase 2 on the memory for the task learned in phase 1. Groups N_c and C_c served as controls for the forgetting that may occur in the absence of any experimental treatment. While the experimental groups were in phase 2, the birds in the control groups were maintained at 80 percent of their free-feeding weights. They remained in their living cages except when being weighed daily.

Figures 1 and 2 show the proportion of errors made by the individual birds during successive training sessions. An empirical learning curve consisting of two segments was fitted to these results. A horizontal line at $P = .5$ represents a period of chance performance, the presolution period, and is followed by a decay curve. The fitting process consisted of a computer-aided search for the length of the horizontal line (0 to 30 days), and the parameters of the decay curve that together yielded the least sum of squared deviations of the points from the fitted function.

The position of the unfilled points (representing relearning) with respect to the horizontal axis (Figs. 1 and 2) was determined by, in effect, sliding them parallel to that axis and finding the position for which the sum of the squared deviations of the points from the learning curve fitted to the phase 1 results was minimized.

Six of the eight birds in the experimental group performed at roughly chance levels (50 percent errors) at the beginning of the reacquisition period and then improved with continued training as they did during the original acquisition period. In other words, most of the birds in the experimental groups lost the discrimination completely, and none of them performed as well as they did at the end of phase 1. A few birds in the control groups show some forgetting also (for example, birds 600 and 604), but others performed as well at the beginning of the reacquisition period as they had at the end of the original acquisition period (for example, birds 598 and 605). The mean proportion of errors made on the first day of reacquisition is 0.40 for the experimental groups and 0.15 for the control groups [t-test on the difference between the arcsine square root transforms of the proportions, $t(13) = 3.67$, $P < .01$]. The treatment given the experimental groups interfered with the retention of the discrimination.

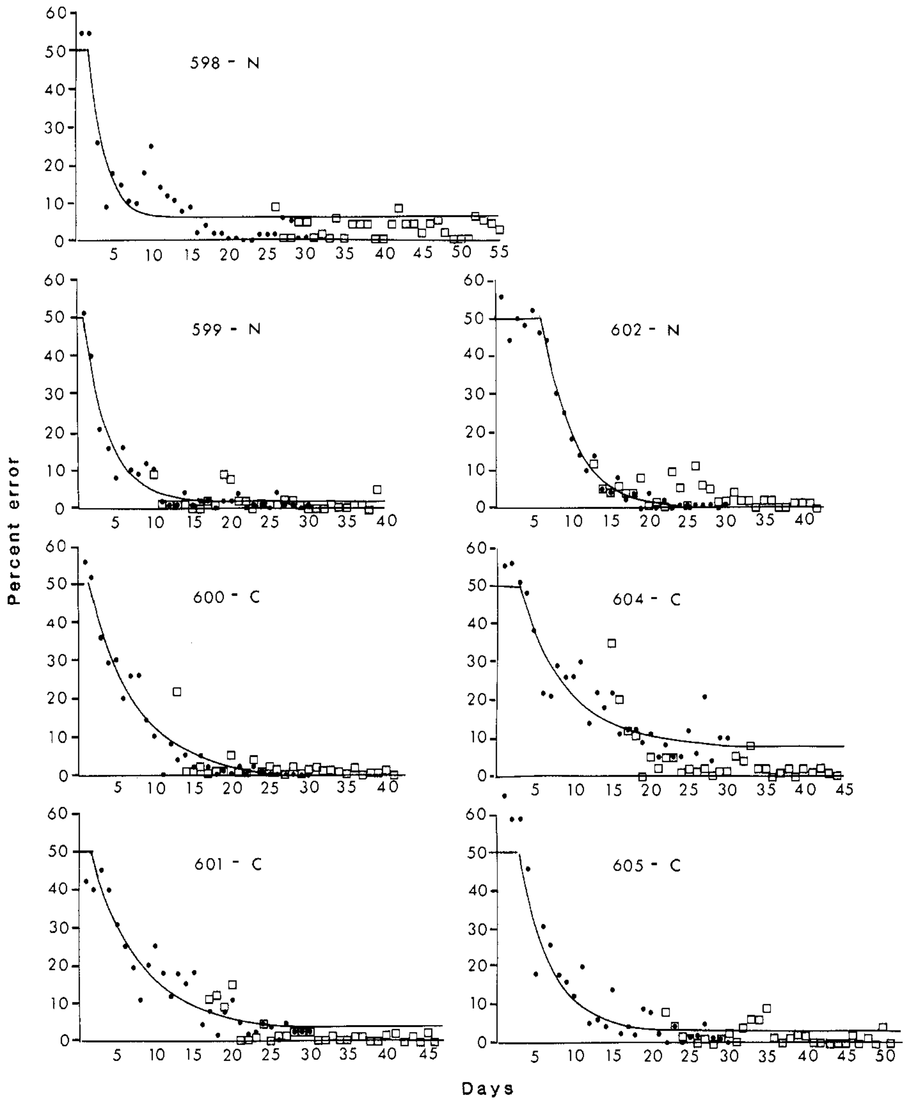

Fig. 2. The course of learning a discrimination (circles) and relearning the same discrimination (squares) by individual pigeons in the control groups.

This conclusion is supported by an alternative analysis based on a measure of forgetting provided by our procedure for superimposing the reacquisition data on the learning curve fitted to the original acquisition data. The procedure used amounts to finding, for each subject, a constant, D_0, which must be added to each abscissa value (day) when plotting the reacquisition data. If reacquisition were identical to original acquisition—if forgetting were complete—D_0 would equal zero. The fitting procedure yielded mean D_0 values of 3.25 days for the experimental groups and 13.29 days for the control groups. Thus, the average performance of the subjects in the experimental groups on the first day of reacquisition was equivalent to that seen after 3.25 days of the original acquisition procedure. Similarly, the average performance of the subjects in the control groups was equivalent to that seen after 13.29 days during original acquisition. The difference between these two values of D_0 is significant [$t(13) = 6.25$, $P < .001$].

For birds that performed at chance levels at the beginning of reacquisition training, the course of reacquisition was similar to that of original acquisition except that the period of chance performance was shorter. As estimated by our curve-fitting method, the mean duration of the period of chance performance for the experimental groups during phase 1 was 3 days. Thus the mean D_0 of 3.25 days corresponds almost perfectly to the end of the presolution period observed during phase 1.

The results do not show any systematic differences between the groups trained to discriminate between noise intensities and those trained to discriminate between colored lights. That retention of the two discriminations was affected equally by the tasks the birds performed during phase 2 and, indeed, that the phase 2 activity should cause any forgetting at all would not be expected from what is known of RI in human long-term memory. One of the most widely accepted generalizations (6) holds that little or no interference occurs unless the discriminative stimuli that control responding in the first and second phases of training are reasonably similar. In our experiments the stimuli that controlled responding during phase 1 were completely absent during phase 2.

Our results are compatible with a model (7) based on the assumption that all the information a pigeon acquires during the course of these experiments is stored in a single memory of limited capacity, and that newly entered information destroys information already stored. On an empirical level, this research yielded two surprising results: (i) our procedure produced virtually complete forgetting, and (ii) the learning and relearning curves are nearly identical.

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Disappearance of Stabilized Chromatic Gratings

Abstract. *When the image of a stationary, sinusoidal luminance grating is stabilized on the retina of a human subject, he becomes unable to detect this stimulus at contrasts that are readily visible in normal, unstabilized vision. At much higher contrasts, such stabilized gratings can still be seen over most of the normal range of spatial frequencies, although the threshold contrast may be increased by as much as 20 or 30 times. When the analogous experiment is performed with an isoluminance chromatic grating, however, there is no contrast that can restore the visibility of the stabilized grating; the threshold elevations for stabilized chromatic gratings are too great to measure. Saturated red/green gratings fade out and disappear at 100 percent contrast (even where this is 45 times the unstabilized threshold), and they do not reappear as long as stabilization is maintained. Without some kind of temporal variation of the proximal stimulus, the opponent-color pathways apparently do not respond to spatial patterns.*

The visual contrast sensitivity function for isoluminance chromatic gratings behaves differently from the luminous contrast sensitivity function measured under comparable conditions (1, 2). The two sensitivity curves cross each other, with the chromatic sensitivity being greater at low spatial frequencies and the luminous sensitivity being greater at high spatial frequencies. [This is analogous to the relation between luminous and chromatic flicker sensitivity curves (2, 3).] These results are believed to reflect the relatively coarse spatial organization of the opponent-color pathways, compared with that of the pathways that transmit achromatic information.

It has recently been shown that stabilizing the retinal image (that is, canceling the image motion due to eye movements) has profound effects on the luminous contrast sensitivity function. Although these effects vary somewhat with the experimental techniques used (4), complete absence of temporal variation greatly decreases sensitivity and changes the shape of the curve, moving the sensitivity peak to higher spatial frequencies (Fig. 1A).

I now report that attempts to measure the chromatic contrast sensitivity with image stabilization lead to a surprising result: Under stabilized-image conditions, the chromatic contrast sensitivity for isoluminance gratings cannot be measured because the stabilized chromatic threshold is always greater than 100 percent contrast. Chromatic gratings of the highest contrast that could be produced faded out and disappeared when the retinal image was stabilized and did not reappear as long as stabilization was maintained. This means that the chromatic threshold was elevated by a factor of more than 45 at low spatial frequencies (Fig. 1B). How much more, of course, is unknown.

This extreme behavior is not shown by the luminous contrast sensitivity under stabilized-image conditions. The maximum elevation of the luminous contrast threshold (Fig. 1A) is only 30 times, and this is the greatest elevation of the luminous contrast threshold so far reported (4).

To make the luminous and chromatic sensitivity measurements directly comparable, both were carried out with the same subject, under the same conditions, in the same apparatus. The only difference was a spatial phase shift of 180° between the red and green components of the two stimuli. When the red and green gratings were in phase, the stimulus was a yellow luminous grating, variable in contrast from 0 to 100 percent. When they were out of phase, the stimulus was an isoluminance red/green grating.

Because the maximum chromatic contrast obtainable under these conditions depends on the chromaticities of the red and green components, these primary colors were made as saturated as possible (5). Both were derived from the P22 phosphors of a standard (RCA) color television screen. The P22 red component is nearly a spectral color. The green is not, but its luminance is almost twice as great as that of the red. It was therefore possible to greatly increase the saturation of the green component while approximately balancing the red and green luminances by viewing the display through a yellow (Wratten 16) filter. The final setting of the red/green balance was then made by adjusting the modulation of the green component relative to that of the red; this was done by flicker photometry. Thus, the apparent color contrast of the chromatic gratings (viewed without stabilization) was very high, while their (flicker photometric) brightness contrast was imperceptible (6).

Once a stabilized chromatic grating of this kind has disappeared, a striking chromatic afterimage can be seen by suddenly reducing the stimulus contrast to zero. Although the subject is then viewing a uniform yellow field, he sees a red/green chromatic grating of opposite phase to the stimulus. The strength of these chromatic afterimages (as measured by the chromatic contrast required to produce a just-detectable afterimage) is generally less than that of comparable luminous afterimages (measured in the same way) (4, 7). This is the opposite of what might be expected from the data of Fig. 1 if the elevation of the stabilized threshold and the formation of the afterimage are merely different aspects of the same local adaptation process (8). Thus, there may be important differences between these two processes (in either the

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