The Effect of Reinstatement Stimulus Conditions on the Maintenance of Long-Term Memory

BYRON A. CAMPBELL PATRICK K. RANDALL Department of Psychology Princeton University Princeton, New Jersey

Weanling rats trained on an appetitive S^DS^Δ discrimination were subsequently exposed to different components of the training stimulus for 15 min each week for 10 successive weeks. On the week following the final stimulus exposure retention was measured by a 2-hr relearning test. Those subjects exposed to all acquisition cues (S^DS^Δ) with reinforcement, as well as those exposed to S^Δ conditions alone, demonstrated enhanced retention relative to a control group receiving no reinstatement experience. All other exposure conditions including presentation of S^D with reinforcement were either ineffective or impaired retention.

Studies of both human and animal development generally agree that early experience exerts a profound influence on adult behavior but that many types of learned behaviors acquired under laboratory conditions are forgotten more rapidly in young animals than adults (Campbell & Spear, 1972; Campbell & Coulter, in press). Similarly man's inability to recall little, if anything, of the first few years of life-often called the period of infantile amnesia by analysts of child development-is in direct contrast to the importance of those early years for adult character and personality formation. In an attempt to resolve this apparent paradox, Campbell & Jaynes (1966) introduced the concept of reinstatement, loosely defined as periodic partial repetition of early events such as to maintain the effects of those experiences which would otherwise dissipate with time. Operationally, reinstatement is defined as the maintenance over time of learned behavior by periodic exposure to cues associated with the original learning. Two critical assumptions underlie the significance of this phenomenon: First, the reinstatement conditions themselves are insufficient to establish learning. This has been confirmed repeatedly by several investigators (Campbell & Jaynes, 1966, 1969; Shubat & Whitehouse, 1968; and Silvestri, Rohrbaugh, & Riccio, 1970). Second, the effectiveness of reinstatement is not merely the result of additional training, but occurs by virtue of the temporal distribution of re-exposure periods. This supposition was supported by Greenfield and Riccio (1972), who demonstrated that reinstatement periods massed early in the retention interval are less effective than distributed exposures or massed exposures late in the retention interval.

Received for publication 26 March 1975 Revised for publication 19 November 1975 Developmental Psychobiology, 9(4):325-333 (1976) © 1976 by John Wiley & Sons, Inc. Given the basic phenomenon, a number of questions arise regarding the relative importance of different aspects of the reinstatement periods. Must all of the conditions of original learning be reinstated? If not, which aspects of the training are necessary and sufficient to decrease retention loss?

In the 1st experiment directed toward these questions, Silvestri et al. (1970) reported that retention of conditioned fear was a reliable function of the duration of exposure to the conditioned stimulus (CS) alone during the reinstatement periods, whereas exposure to the unconditioned stimulus (UCS) or to a "new" aversive stimulus during reinstatement was ineffective at any duration. More recently, Greenfield and Riccio (1972), using a spatial avoidance task, examined the efficacy of CS exposure more extensively. They demonstrated that reinstatement of the CS+ (cues associated with shock) was sufficient to enhance retention. They also noted—but with some ambiguity—increased retention following expsoure to the CS- (cues associated with safety). Apparently, the critical factor in reinstatement of an aversively motivated task is re-exposure, not to the shock itself, but to the CS, with shock-associated cues being somewhat more effective than safety cues.

Although reinstatement in an appetitive situation has been demonstrated (Campbell & Jaynes, 1969), the relative effectiveness of various reinstatement conditions associated with a food-reinforced task has not been investigated. What is the relative importance of exposure to the S^D (positive discriminative stimulus present) or the S^Δ (negative discriminative stimulus present) in an appetitive discrimination? Do brief presentations of S^D and S^Δ without reinforcement maintain memory? What analogies can be drawn between the appetitive and aversive situation? This experiment was designed to investigate the effectiveness of a variety of such reinstatement conditions for appetitive discriminations.

Method

Subjects

The subjects were 150 21-25-day-old female rats of the Wistar strain (*Rattus norvegicus*) purchased from Perfection Breeders, Douglassville, Pennsylvania. The rats were housed in group cages for 2-3 days prior to the experimental treatment, and then individually in small cages during the retention interval. Thirteen to 22 subjects were run in each of the groups described below. The rats were maintained on a 16-hr light: 8-hr dark cycle except during the period of original training when they were housed under the described experimental conditions.

Apparatus

The apparatus consisted of 8 typical operant conditioning units, housed in individually sound-insulated chambers. Each unit was 20 x 23 x 19 cm and contained a 5 x 1.9-cm bar which projected 5.7 cm from the wall above the grid floor. Depression of a lever (approximately 15 g force required) delivered the food pellet to a food cup situated 2.54 cm to the left of the lever. Water was available ad lib. The discrimination

stimulus was a 7½-W white light, located 8.9 cm above the bar. A dim house light located over the cage produced an illumination level of approximately 1 lux when the discrimination light was off.

Design

The basic plan of this experiment was to train experimental animals on a simple light-dark discrimination for 4 successive days, and then to give each animal one 15-min reinstatement session per week for 10 successive weeks, with separate groups receiving different conditions of reinstatement. On the week following the 10th week of reinstatement training, the animals were tested for retention using a relearning procedure. The effects of reinstatement training on retention of the original discrimination were compared to control groups which received either original training (O.T.) and no reinstatement training or no original training (N.O.T.) and equal amounts of reinstatement training.

Discrimination Training

The discrimination training consisted of 4 days in the lever boxes and was the same procedurally for all groups. The animals were placed in the boxes at 1600 hours each day and left in the boxes overnight until 1000 hours the next morning. During this time they had ad libitum access to food-via the lever-pressing response-and water. At 1600 hours on the 1st day each rat was weighed and placed in the lever box. At 1000 hours on the following day the animal was removed from the box and placed in an individual cage without access to either food or water where it remained until 1600 hours when it was weighed and replaced in the lever box. The procedure was repeated for 4 successive days. The N.O.T. control animals were removed from their home cages for the same period of time each day and left in holding cages from 1000 to 1600 hours daily without food and water just as were the experimental animals. Throughout training, the light above the bar was on for 2 min and off for 2 min, the animal being rewarded only during the light-off (dark) period. During this 2-min positive interval, bar presses were reinforced on a VI 15-sec schedule, such that an animal could receive a maximum of 8 pellets (20 mg; J. P. Noyes) during a single positive period. The numbers of responses during the positive and negative periods were recorded every 4 hr on electromagnetic counters.

Reinstatement Training

Following 4 days of discrimination training or control procedures the animals were assigned to 1 of 8 reinstatement or control conditions. Reinstatement itself consisted of 10 weekly 15-min exposures to one or more of the original training conditions. Two groups, one with prior discrimination training (O.T., $S^D S^\Delta$, S^r) and the other without training (N.O.T., $S^D S^\Delta$, S^r) were exposed to both the positive and negative stimuli during the weekly reinstatement periods, identical to the conditions of training, including the *ad libitum* feeding conditions in the home cage and the VI 15-sec reinforcement schedule during S^D . (Presentation of reinforcement during S^D is denoted as S^r ; absence of reinforcement during S^D as S^r .) Another group with prior

discrimination training (O.T., S^DS^Δ , $-S^r$) was given 15-min weekly exposures to both stimuli but without reinforcement during the S^D period. Two groups with (O.T., S^Δ , $-S^r$) and without (N.O.T., S^Δ , $-S^r$) prior discrimination training, were exposed to only the negative (S^Δ) stimulus during the 15-min reinstatement periods whereas 2 other groups, with (O.T., S^D , S^r) and without (N.O.T., S^D , S^r) prior training, received 15-min weekly exposures to only the positive stimulus (S^D) reinforced on the original VI 15-sec schedule. The final group (O.T., no reinstatement) received original training but no interpolated exposures of any kind except for weekly handling comparable to that received by the O.T. and N.O.T. subjects. The experimental design and a portion of the experimental results are summarized in Table 1.

Retention Test

Retraining consisted of placing the animals in the lever boxes with all conditions identical to those of original training, including the delivery of reinforcement on a VI 15-sec schedule. Bar presses during both the positive and negative stimulus periods were recorded every 20 min for 2 hr.

Results

The main results of this experiment are summarized in Table 1 which shows the percentage of responses to S^D during the 2 hr of the relearning test. Of the experimental groups, total reinstatement of the original training conditions including reinforcement on a VI 15-sec schedule during S^D (O.T., S^DS^Δ , S^r) was most effective in maintaining the discrimination. Surprisingly, the next most effective treatment was exposure to S^Δ without reinforcement (O.T., S^Δ , S^r). The 3rd most effective condition was the no reinstatement control (O.T., no reinstatement) demonstrating modest retention of the original discrimination. All other reinstatement conditions employed, including the O.T., S^D , S^r group, appeared to impair retention rather than enhance it, relative to the group receiving original training but no reinstatement training.

TABLE 1.	Experimental	Conditions and	Group Designations.
----------	--------------	----------------	---------------------

Group designation	Original training	Reinstatement conditions	n	Percent responses to S ^D during test (1st 2 hr)
O.T., S^D , S^Δ , S^r	yes	S^{D}, S^{Δ}, S^{r}	21	78.9
O.T., S^{Δ} , S^{r}	yes	$egin{array}{l} \mathbf{S^D}, \mathbf{S^\Delta}, \mathbf{S^r} \ \mathbf{S^\Delta}, -\mathbf{S^r} \end{array}$	24	73.9
O.T., no reinst.	yes	none	18	65.3
O.T., S^D , S^Δ , $-S^r$	yes	$S^{D}, S^{\Delta}, -S^{r}$	23	62.9
O.T., S ^D , S ^r	yes	S^{D}, S^{r}	20	56.9
N.O.T., S^D , S^Δ , S^r	no	S^{D}, S^{Δ}, S^{r}	18	55.3
N.O.T., S^{Δ} , $-S^{\Gamma}$	no	S^{D}, S^{r} S^{D}, S^{Δ}, S^{r} $S^{\Delta}, = S^{r}$	13	56.6
N.O.T., S ^D , S ^r	no	S^{D}, S^{r}	13	51.7

A 1-way analysis of variance confirmed the differential effects of the different treatments (F = 20.06, df = 7,140, p < .01). Newman-Keuls comparisons between individual groups revealed that the O.T., S^D , S^A , S^r and the O.T., $S^A - S^r$ groups were not significantly different, and that they in turn were superior to all other groups (all differences, p < .05). Furthermore, the O.T. group exposed to S^D with reinforcement (O.T., S^D , S^r) was inferior (p < .05) to all other groups receiving original training, including the group given extinction during the 10 reinstatement sessions (O.T., S^DS^A , $-S^r$). No significant differences existed among the N.O.T. control groups; differences did exist between these and all groups receiving original training except the O.T., S^D , S^r group.

The salient findings of this research are the superior performance of the group receiving S^{Δ} (without reinforcement) as a reinstatement condition $(O.T., S^{\Delta}, -S^r)$ and the inferior performance of the group receiving S^D (with reinforcement) as reinstatement $(O.T., S^D, S^r)$. Ten 15-min exposures to the negative stimulus (S^{Δ}) at weekly intervals were effective in maintaining the original discrimination whereas an equal number of exposures to the positive stimulus (S^D) accompanied by reinforcement on a VI 15-sec schedule as in original training impaired performance during the 2-hr relearning test of retention.

The data also show that 15-min of reinstatement each week for 10 weeks with stimulus and reinforcement conditions identical to those of original training, but without the 4 days of original training received by the O.T. groups, produced only 55.3% responding to S^D during the 2-hr retention test. This percentage of correct responding was significantly lower than that of all O.T. groups except the O.T., SD, Sr group. Unfortunately, a group receiving neither original training nor reinstatement was not included in the design for budget and time reasons; thus, whether or not some minimal amount of learning did occur could not be determined. If learning did occur, however, it was inconsequential relative to the effects of the same reinstatement condition or retention of the criterion response in the O.T., $S^D S^{\Delta}$, S^r group. In addition, the lack of a difference between the reinforced group (N.O.T., S^D , S^{Δ} , S^{τ}) and the other non-reinforced groups suggests that the reinstatement training sessions were too brief to produce measureable learning. This confirms the results of a previous study (Campbell & Jaynes, 1969) which reported no effects of reinstatement under identical conditions relative to a group which received no original training and no reinstatement.

The number of responses to S^D and S^Δ during successive 20-min periods of the 2-hr retention test are shown in Figure 1. Only relevant groups are shown. The 1st (left) panel shows the performance of the no reinstatement group. Number of responses and percentage correct responding were low and increased only gradually. In contrast, the total reinstatement group $(O.T., S^DS^\Delta, S^r)$ shown in the 2nd panel started and remained high on both criteria. The 3rd panel shows the performance of the S^Δ , S^r group on the retention test. Here, the rate of responding to S^Δ remained low throughout the first 2 hr whereas responding to S^D began low but increased rapidly after the first 20 min to produce the high level of correct responding reported in Table 1. Finally (right panel), the O.T., S^D , S^r group showed a relatively high level of responding to both stimuli, and differential responding appeared very gradually. These results indicate that S^Δ training during the reinstatement session served to maintain

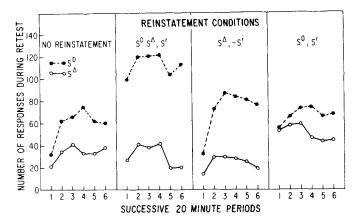


Fig. 1. The effect of 4 reinstatement conditions on performance during the 2-hr relearning retention test.

inhibition of responding to S^{Δ} . The S^D responding, although initially low, returned to a high level once the reinforcement condition was reinstituted. In contrast, S^D reinstatement training maintained a high level of responding to S^D , but weakened inhibition of responding to S^{Δ} .

The pattern of results obtained for the various reinstatement conditions following original training can be traced directly to the effects of those conditions on rate of responding during reinstatement. Figure 2 shows the number of responses to S^D and S^Δ during the reinstatement procedure for 3 reinstatement groups that received original training. The left panel shows the number of responses to S^D and S^Δ for the O.T., $S^\Delta S^D$, S^r group. Clearly, the animals continued to respond more to S^D than S^Δ . Reinstatement is thus effective in maintaining the original discrimination, although as noted earlier the same amount of training (N.O.T., $S^D S^\Delta$, S^r group) did not lead to

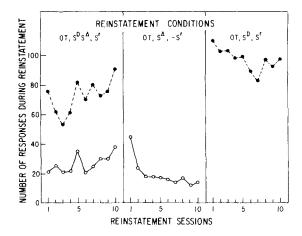


Fig. 2. Performance (number of bar-presses) during the 10 reinstatement sessions for 3 reinstatement groups.

acquisition of the discrimination. Given 15 min of S^{Δ} each week the rats showed a gradual decline in responding over the 10 reinstatement sessions. In interpreting this figure, remember that the graph portrays number of responses during the entire 15-min period and not rate of responding. Because the S^{Δ} group was exposed to 15 min of the negative stimulus instead of the 7.5 min for the $S^{D}S^{\Delta}$ group, rate of responding was about equal for the 2 groups on the 1st day of reinstatement. Similarly, note for the S^{D} group (right panel) that the rate of responding during S^{D} , although high, was somewhat lower than in the O.T., S^{D} , S^{r} group.

Discussion

The present study substantiates again the phenomenon of reinstatement. Brief periods of interpolated training during a long retention interval, insufficient in themselves to establish the criterion response, can serve to maintain a previously learned response that would otherwise be forgotten. The major outcome of the research, however, is the finding that reinstatement training consisting of exposure to S^{Δ} is more effective than interpolated training on S^D in maintaining retention of an S^DS^{Δ} discrimination. Exposure to the S^DS^{Δ} stimulus condition without reinforcement (O.T., S^DS^{Δ} , $-S^r$) was ineffective in maintaining the discrimination, at least with the reinstatement durations used in this study. This finding that periodic exposure to only a portion of the original stimulus conditions can maintain responses that would otherwise be forgotten may have profound implications for future analysis of the conditions necessary to retain desired aspects of early experience.

A major question raised by the study concerns the mechanism responsible for the superiority of the S^{Δ} reinstatement group relative to the S^{D} group. One possibility may be the extent to which responding to S^D and inhibition of responding to S^{Δ} generalize. As noted in Figure 1, rate of responding to SD for the O.T., SD, Sr group continued high during relearning and declined only gradually during S^{Δ} . In contrast, the low rate of responding to S^{Δ} acquired during reinstatement for the S^{Δ} , $-S^{r}$ group did not depress responding to S^{D} after the first 20 min of the relearning test. Descriptively, the S^D behavior seemed to generalize to S^Δ conditions. Empirical evidence regarding the form and amplitude of inhibitory and excitatory gradients has only recently appeared and is far from conclusive (see Hearst, Besley, & Farthing, 1970) though the problem has long been of great theoretical interest (Hull, 1943; Spence, 1936). This study appears to provide empirical support for the frequently postulated notion that an excitatory gradient is less steep than its inhibitory counterpart. Further studies are clearly necessary in that the generalization gradients obtained here are undoubtedly confounded with age, retention, and attentional factors. Thus, the nature and stability of inhibitory and excitatory control in young animals is of primary importance to the interpretation of the present results. In one of the few experiments directed to this problem, Bacon (1971) has reported data strongly suggesting that neonatal dogs are under control of the S^D , but not of S^Δ in a successive go:no-go tactile discrimination. If inhibitory control in young animals is lacking at the end of the original training, the S^{Δ} and the $S^{D}S^{\Delta}$ reinstatement groups may have received S^{\Delta} training at ages where inhibitory stimuli are effective, whereas the S^D group had no S^{Δ} training at the critical development stages.

The importance of original training in this research should be emphasized. Exposure to S^{Δ} during reinstatement improved performance on retest only in those animals that received training on the original S^DS^{Δ} discrimination. In this situation rats apparently do not acquire inhibition of responding to a stimulus unless that stimulus has been previously contrasted with a stimulus associated with reinforcement.

A further question raised by this experiment is the relationship between aversive and appetitive conditioning with respect to the characteristics of effective reinstatement treatments in each. Greenfield and Riccio (1972) report that in a spatial avoidance task, exposure to fear cues (i.e., CS+ without reinforcement) is a more effective reinstatement condition than is equal exposure to safety cues (CS-). Although the task required in that study was quite different from that used in the present research, the results suggest that effective reinstatement procedures may differ for appetively and aversively motivated tasks. In the aversively motivated tasks, cues associated with the primary reinforcer appear to be more effective than cues which are not, whereas in appetitive conditioning cues associated with the primary reinforcer are least effective (even deleterious) when presented alone. Note, however, that the effective stimuli in both cases were associated with "negative" consequences (i.e., shock, absence of food).

Finally, Silvestri et al. (1970) found that brief 10-15 sec exposures to the conditioned fear side of a black-white apparatus were effective in maintaining conditioned fear in the absence of the primary motivating stimulus, electric shock, but that both shorter and longer durations of reinstatement training were less effective. Short reinstatement sessions were interpreted as too brief to elicit the conditioned fear and longer durations were presumed to extinguish it. Possibly, therefore, shorter exposures to S^DS^Δ or S^D alone would have been effective in maintaining the discrimination in contrast to the present study where 15-min presentations of those stimuli impaired discrimination performance on re-test. The conditions under which reinstatement training without additional primary reinforcement can serve to maintain memory would appear to be a problem of considerable theoretical and practical importance.

Notes

This research was supported in part by Grant MH-01562 from the National Institute of Mental Health.

Request reprints from Dr. Bryon A. Campbell, Department of Psychology, Princeton University, Princeton, New Jersey 08540, U.S.A.

References

Bacon, W. (1971). Stimulus control of discriminated behavior in neonatal dogs. J. Comp. Physiot. Psychol., 76:424-433.

Campbell, B. A., and Jaynes, J. (1966). Reinstatement. Psychol. Rev., 73:478-480.

Campbell, B. A., and Jaynes, J. (1969). Effect of duration of reinstatement on retention of a visual discrimination learned in infancy. *Dev. Psychol.*, 1:71-74.

Campbell, B. A., and Spear, N. E. (1972). Ontogeny of memory. Psychol. Rev., 79:215-236.

Campbell, B. A., and Coulter, X. (in press). Ontogeny of learning and memory. In M. R. Rosenzweig and E. L. Bennett (Eds.), *Neural Mechanisms of Learning and Memory*. Cambridge, Massachusetts Institute of Technology Press.

- Greenfield, A., and Riccio, D. C. (1972). Conditioned reinstatement in rats: Effect of exposure distribution and cue. *Psychol. Rep.*, 31:79-83.
- Hearst, E., Besley, S., and Farthing, G. (1970). Inhibition and the stimulus control of operant behavior. J. Exp. Anal. Behav., 14:373-408.
- Hull, C. L. (1943). Principles of Behavior. New York: Appleton-Century.
- Shubat, E., and Whitehouse, J. M. (1968). Reinstatement: An attempt at replication. *Psychonom. Sci.*, 12:215-216.
- Silvestri, R., Rohrbaugh, M., and Riccio, D. C. (1970). Conditions influencing the retention of learned fear in young rats. Dev. Psychol., 2:389-395.
- Spence, K. (1936). The nature of discrimination learning in animals. Psychol. Rev., 43:427-449.