

Transfer across CS-US intervals and sensory modalities in classical conditioning of the rabbit

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Two experiments investigated transfer of the rabbit's conditioned nictitating membrane response (NMR) from shorter to longer CS-US intervals in conjunction with a change in CS modality, for example, light to tone. In Experiment 1, three experimental groups received initial training with a 400-msec CS-US interval, which produced substantial CR acquisition, and three control groups received initial training with a 2,800-msec CS-US interval, which produced minimal CR acquisition. Subsequently, the experimental and control groups received training with an 800-, 1,800-, or 2,800-msec CS-US trace interval. At the same time, the modality of the CS was changed from tone to light (or vice versa). Experiment 2 contained three groups that received initial exposure to a 400-msec CS-US interval, a 2,800-msec CS-US interval, or just the experimental chambers. Subsequently, all three groups received training with an 800-msec CS-US interval in a different CS modality. The results of both experiments revealed substantial positive transfer across CS modalities from the 400-msec CS-US interval to the 800-msec CS-US interval. There was also significant transfer to the 1,800-msec but not the 2,800-msec CS-US interval. The transfer did not appear immediately on test presentations of the second CS. Rather, the transfer appeared as an enhancement in the rate of CR acquisition after reinforced training with the second CS had commenced. The results are discussed with respect to mechanisms of transfer and facilitation of trace conditioning.

The present experiments examined transfer of training in classical conditioning of the rabbit's nictitating membrane response (NMR) under a combined manipulation of CS-US intervals and CS modality.

Many associative learning paradigms display trace conditioning over relatively brief intervals. However, the use of a serial compound procedure (CSA-CSB-US) substantially facilitates response acquisition to CSA over relatively long trace intervals (e.g., Bolles, Collier, Bouton, & Marlin, 1978; Kaplan & Hearst, 1982; Kehoe, Feyer, & Moses, 1981; Kehoe, Gibbs, Garcia, & Gormezano, 1979; Kehoe & Morrow, 1984; Pearce, Nicholas, & Dickinson, 1981; Rescorla, 1982). Research with serial compounds has focused primarily on the role of the CSA-CSB relation, but the substantial trace conditioning of CSA may arise in part from transfer between the CSB-US and CSA-US relations (Kehoe, 1982). Just as acquisition of an easy discrimination facilitates subsequent acquisition

of a hard discrimination (Lawrence, 1952; Pavlov, 1927, pp. 121-122; Seraganian, 1979), experience with one CS at a short, "easy" CS-US interval may facilitate acquisition to another CS at a long, "hard" CS-US interval (Kehoe et al., 1981). Recently, Westbrook and Homewood (1982) have found that toxicosis conditioning with one flavor (e.g., sucrose) at a relatively brief CS-US interval (e.g., 15 min) facilitates the subsequent acquisition of an aversion to a new flavor (e.g., salt) at a longer interval (e.g., 3 h).

The boundary conditions that yield transfer across CS-US intervals and/or sensory modalities in classical conditioning of the rabbit are not well delineated. First, abrupt shifts from a shorter to a longer CS-US interval have resulted in dramatic drops in performance, even when the same CS was used throughout training (Coleman & Gormezano, 1971; Prokasy & Papsdorf, 1965). However, gradual increases in CS-US intervals were found to sustain high levels of responding at long, otherwise ineffective CS-US intervals (Prokasy & Papsdorf, 1965). Second, in examining transfer across CS modalities, Yehle and Ward (1969) found positive transfer from a discrimination between two pulsed tones to a discrimination between two pulsed light stimuli (and vice versa). Third, in a joint manipulation of CS-US intervals and CS modalities, Kehoe et al. (1979, Experiment 3) found no evidence of transfer when they

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intermixed 400-msec light-shock trials (CSB-US) with 1,800-msec tone-shock trials (CSA-US). The course of acquisition to the tone CSA in the intermixed training group appeared identical to that of a group trained with only the 1,800-msec CSA-US trace interval. However, Kehoe and Morrow (1984) found that intermixed training (400-msec CSB-US/2,800-msec CSA-US) produced higher levels of responding to CSA in the intermixed training group than in a corresponding CSA-US trace conditioning group. Finally, there is some evidence of negative transfer across sensory modalities. Specifically, Hinson and Siegel (1980, Experiment 1) reported that initial training with one CS (e.g., tone) at a 10,600-msec CS-US interval subsequently retarded the rate of CR acquisition to another CS (e.g., light) at a 500-msec CS-US interval. Also, Scavio (1975) reported that prior tone-water pairings retarded the rate of CR acquisition under subsequent light-shock pairings. Investigations of cross-modal transfer in other species and paradigms have yielded equally complex results (cf. Church & Meck, in press; Rodgers & Thomas, 1982; Von Wright, 1970).

EXPERIMENT 1

The present experiment was conducted to determine whether trace conditioning could be facilitated by prior training with another CS in a different sensory modality at a shorter, more efficacious CS-US interval. To this end, six groups of animals were used. Three of the groups received initial training with one CS (e.g., tone) at a 400-msec CS-US interval and subsequent training with another CS (e.g., light) at an 800-, 1,800-, or 2,800-msec CS-US interval. As baselines for the detection of transfer effects, three control groups received initial training with a 2,800-msec CS-US interval followed by training with an 800-, 1,800-, or 2,800-msec CS-US interval. The baseline condition was designed to fulfill two criteria: (1) equal exposure to the handling, apparatus, CSs, and US as experienced by the experimental groups, and (2) minimal excitatory or inhibitory conditioning during Stage 1. The 2,800-msec CS-US interval was chosen as the baseline condition, because it clearly meets the first criterion and typically produces a low level of excitatory conditioning in the rabbit NMR preparation (cf. Kehoe et al., 1979, 1981). Thus, any differences between the experimental and baseline conditions would provide a conservative estimate of positive transfer.

Conventionally, two forms of transfer are recognized, namely "immediate transfer" and "general transfer." In immediate transfer, the alteration in responding appears on the initial presentation of the second CS. In general transfer, savings emerge over the course of training in the rate or asymptote of re-

sponse acquisition to the second CS (Meck & Church, 1982; Seraganian, 1979). Accordingly, the procedure of the present experiment was designed to detect both immediate transfer and general transfer.

Method

Subjects. The subjects were 46 naive, female albino rabbits (*Oryctolagus cuniculus*). On arrival, each rabbit was 70-80 days old and weighed approximately 1.5 kg. All rabbits had free access to food and water in their home cages.

Apparatus. The apparatus and recording procedure for the nictitating membrane response were patterned after those of Gormezano (1966) as detailed in Kehoe et al. (1981). In brief, the subjects were trained individually in eight sound-attenuating, ventilated conditioning chambers. During training, each rabbit was restrained in a Perspex box, which was held in place within each chamber between metal stays screwed to the floor. A speaker was mounted at a 45-deg angle, 8 cm anterior to and 16 cm above the subject's head. The speaker provided both white noise and an aural CS, which was a 1,000-Hz, 88-dB (SPL) tone superimposed on an 82-dB ambient noise level provided by white noise and an exhaust fan. An 8-W frosted neon light tube was mounted 4 cm above the speaker. The light tube served as a houselight and was flashed at a rate of 20 Hz in order to provide a visual CS. The duration of both CSs was 400 msec, regardless of the CS-US interval. The US was a 50-msec, 3-mA, 50-Hz ac shock delivered via stainless steel Autoclip wound clips positioned 10 mm apart and 15 mm posterior to the dorsal canthus of the right eye. The sequence and timing of stimulus events were controlled by an Apple II computer equipped with interfaces and software developed by Scandrett and Gormezano (1980).

Each rabbit's right external eyelids were held open by No. 3 tailor hooks mounted on a Velcro strap that fitted about the head. A muzzle-like headset, fitted about the snout, supported a transducer for monitoring movements of the nictitating membrane. A small hook was attached to a silk loop sutured in the nictitating membrane of the rabbit's right eye. The hook was connected by a thread to one end of an L-shaped wire lever, which mechanically transmitted the movement of the nictitating membrane to the transducer. Inside the transducer, movement of the lever rotated a disk of polarized filter that was interposed between a light-emitting diode and a photo transistor covered by a fixed polarized filter. Thus, rotation of the disk produced changes in the intensity of the light reaching the transistor through the fixed filter. The signal from the transistor was amplified and transmitted to an analog/digital converter attached to the Apple II computer.

Procedure. All rabbits received 1 day of preparation, 2 days of rest, 1 day of adaptation, 4 days of Stage 1 training, and 5 days of Stage 2 training. On the preparation day, hair surrounding the rabbit's right eye was removed, and a small loop of silk (000 Dynex) was sutured into the nictitating membrane. On the adaptation day, the animals were placed in the conditioning apparatus for 70 min, but neither a CS nor a US was presented.

Following the adaptation day, the animals were assigned to one of six groups ($n=8$) according to a 2×3 manipulation of the CS-US intervals in Stages 1 and 2, respectively. The term "CS-US interval" refers to the interval between the onset of the CS and the onset of the US. In Stage 1, the CS-US interval was either 400 or 2,800 msec. In Stage 2, the CS-US interval was 800, 1,800, or 2,800 msec. The groups were designated by the significant digits of the CS-US intervals in Stages 1 and 2, respectively. Thus, the groups were labeled 4-8, 4-18, 4-28, 28-8, 28-18, and 28-28. For example, Group 4-8 received a 400-msec CS-US interval in Stage 1 and an 800-msec CS-US interval in Stage 2. Half the animals in each group received tone as the CS in Stage 1 and flashing light as the CS in Stage 2. The other half of each group received the light in Stage 1 and the tone in Stage 2. With the exception of the first day in Stage 2 training, all training days consisted of 70 CS-

US trials separated by a mean intertrial interval of 60 sec (± 20 sec). On the first day in Stage 2 training, Trials 1, 2, 3, and 4 were CS-alone trials that provided a test for immediate transfer from Stage 1 to the new stimulus in Stage 2.

A conditioned response (CR) was defined as any extension of the nictitating membrane exceeding .5 mm which occurred following the onset of the CS but prior to the onset of the US. To analyze the data, a set of planned orthogonal contrasts was written (Miller, 1966). The rejection level was set according to a Type I error rate of .05 for a family of contrasts.

Results

Figure 1 shows the mean percentage of CRs in Stage 1 for each group plotted as a function of 35-trial blocks. A fault in the data disk prevented recovery of all the data from Stage 1. Thus, the data for Stage 1 are based on $n_s=4, 8, 3, 4, 8,$ and 3 for Group 4-8, 4-18, 4-28, 28-8, 28-18, and 28-28, respectively. The curves in Figure 1 clearly indicate that the 400-msec CS-US interval produced faster and higher levels of CR acquisition than the 2,800-msec CS-US interval did. Responding in the groups trained with the 400-msec CS-US interval attained terminal levels exceeding 75% CRs, whereas responding in the groups trained with the 2,800-msec CS-US interval rose only slightly over training, reaching a mean terminal level no higher than 24% CRs. Statistical analysis confirmed that there was a significant main effect of CS-US interval [$F(1,24)=28.23$], which interacted with the linear trend over trials [$F(1,24)=36.96$]. Any

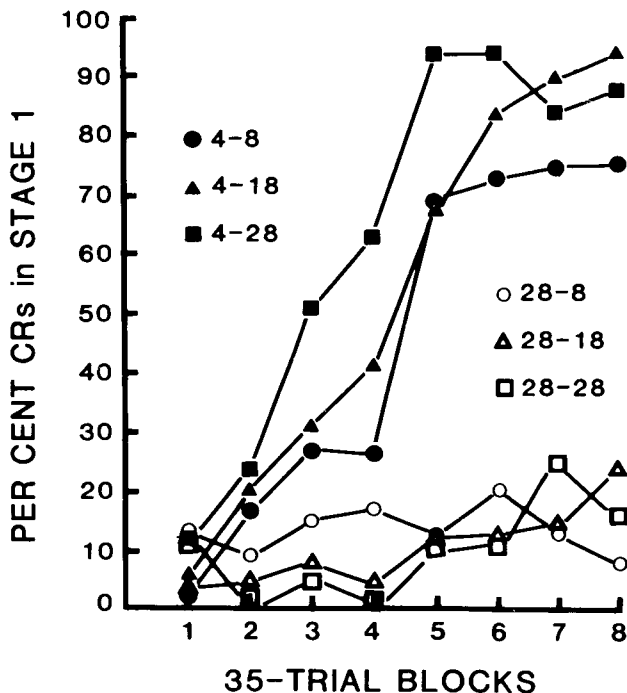


Figure 1. Mean percentage of CRs in Stage 1 of Experiment 1 plotted as a function of 35-trial blocks. Groups 4-8, 4-18, and 4-28 received training with a 400-msec CS-US interval, and Groups 28-8, 28-18, and 28-28 received training with a 2,800-msec CS-US interval.

other apparent differences between groups failed to attain statistical significance.

There was no evidence of immediate transfer from Stage 1 to Stage 2. On the first four trials of Stage 2 training, Groups 4-8, 4-18, and 4-28 showed mean levels of only 3%, 3%, and 0% CRs, respectively. Groups 28-8, 28-18, and 28-28 showed slightly higher mean levels of 9%, 19%, and 10% CRs, respectively. If anything, the training with 400-msec CS-US interval in one modality may have slightly inhibited responding on the first exposures to the stimulus in the other modality. However, the apparent difference between 400- and 2,800-msec CS-US intervals failed to attain statistical significance [$F(1,38)=3.61, p=.06$].

Figure 2 shows the mean percentage of CRs in Stage 2 plotted across 35-trial blocks. Panel A shows acquisition curves for Groups 4-8 and 28-8, Panel B shows the curves for Groups 4-18 and 28-18, and Panel C shows the curves for Groups 4-28 and 28-28. Inspection of the figure reveals clear evidence of positive transfer across sensory modalities. For each pair of groups, the group initially trained with the 400-msec CS-US interval showed a higher level of responding in Stage 2 than that of its control group initially trained with a 2,800-msec CS-US interval. Positive transfer was the greatest in the pair of groups trained with the 800-msec CS-US in Stage 2 and diminished in magnitude across the 1,800- and 2,800-msec CS-US intervals. The statistical analysis confirmed that the level of responding in Stage 2 was facilitated by prior training with the 400-msec CS-US interval relative to the 2,800-msec CS-US interval [$F(1,40)=9.96$]. Moreover, there was a significant linear trend across Stage 2's CS-US intervals [$F(1,40)=5.82$], which interacted with the linear trend over training trials [$F(1,40)=13.34$].

Further inspection of Figure 2 reveals that the positive transfer effect was apparent from the first block of training trials in Stage 2 and continued throughout Stage 2, particularly in the groups trained with the 800- and 1,800-msec CS-US intervals. As a measure of the rate of CR acquisition, we used the trial numbers of the 1st, 2nd, 3rd, 5th, and 10th CRs in Stage 2. Figure 3 shows the mean trial for each of the designated CRs. Since $i^{\text{th}} + 1$ CR must necessarily occur at least one trial later than the i^{th} CR, there would have to be a linear trend across the series of designated CRs. To remove this necessary linear trend from the measure of initial acquisition, the trial numbers of the 2nd, 3rd, 5th, and 10th CRs were adjusted downward by 1, 2, 4, and 9, respectively. For example, if a subject started responding in Stage 2 by making a series of 10 consecutive CRs beginning on Trial 13, then that subject would be assigned a value of 13 for each of the designated CRs. In practice, no subject started responding with 10 consecutive CRs, but 26 of the 46 subjects did show at least two of their

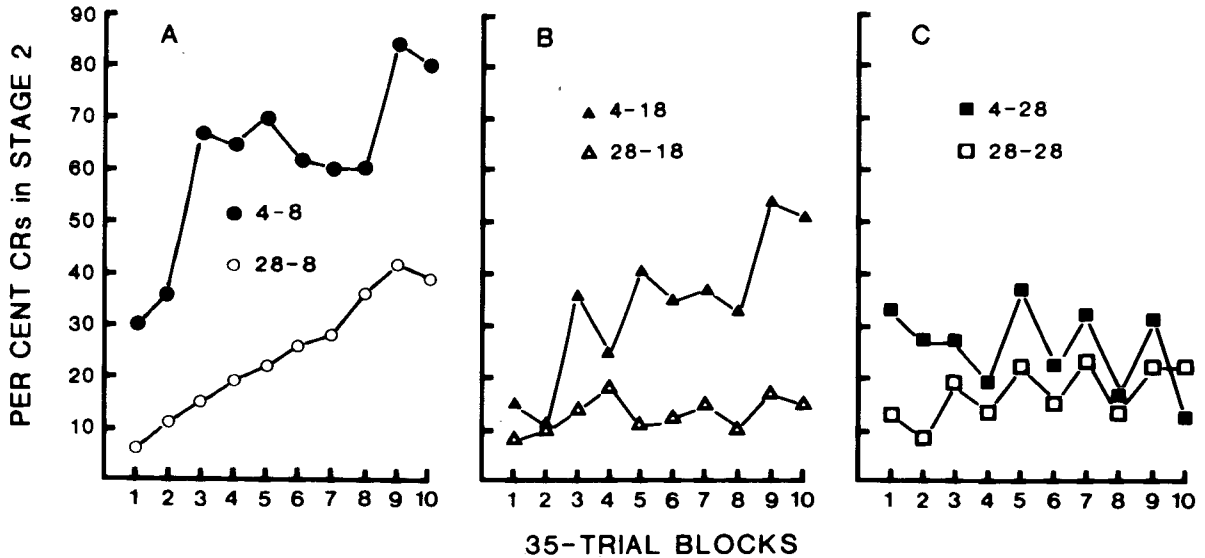


Figure 2. Mean percentage of CRs in Stage 2 of Experiment 1 plotted as a function of 35-trial blocks. Groups 4-8 and 28-8 were trained with an 800-msec CS-US interval (Panel A), Groups 4-18 and 28-18 with a 1,800-msec CS-US interval (Panel B), and Groups 4-28 and 28-28 with a 2,800-msec CS-US interval (Panel C).

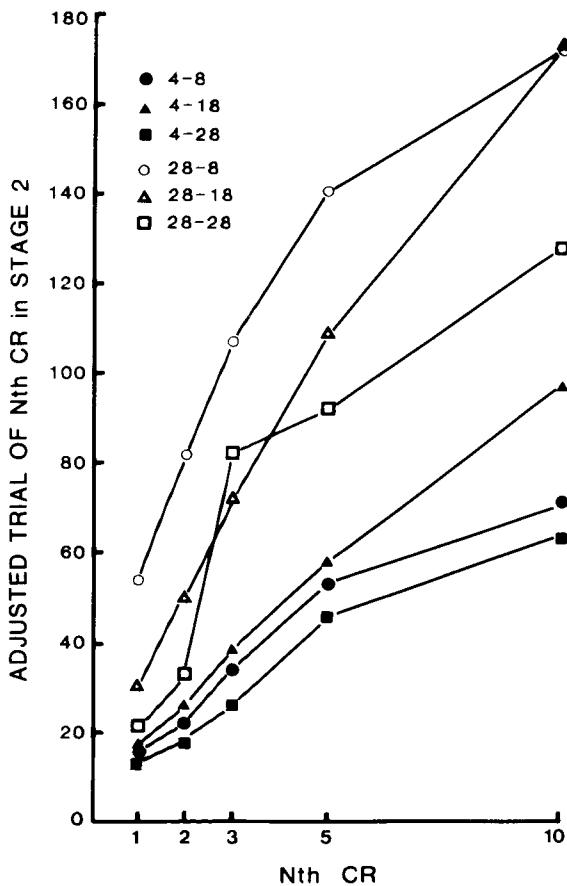


Figure 3. Mean trial of the 1st, 2nd, 3rd, 5th, and 10th CR in Stage 2 of Experiment 1. The trial number for each of the designated CRs has been adjusted downward to eliminate an upward trend necessitated by the fact that the trial of the $n^{\text{th}} + 1$ CR must be at least one trial greater than the n^{th} CR.

initial CRs on consecutive trials. The means shown in Figure 3 reflect this adjustment, and thus, the upward trends indicate that there were actual gaps between trials containing CRs. Figure 3 reveals that Groups 4-8, 4-18, and 4-28 generally showed significantly more rapid initial CR acquisition than did Groups 28-8, 28-18, and 28-28 [$F(1,40) = 6.47$]. However, the differences between the groups were relatively small for the 1st and 2nd CRs and grew more pronounced for the later CRs; this was confirmed statistically by a significant interaction between the Stage 1 CS-US interval and the linear trend across CRs [$F(1,40) = 4.41$].

The statistical analysis of Stages 1 and 2 included tests to determine whether there were any differences in the conditionability of the particular tone and light stimuli used in the present experiment. In fact, there were no significant main effects or interactions involving the tone and light stimuli. Inspection of the data revealed that differences between responding to the tone and light were small and inconsistent.

EXPERIMENT 2

The present experiment was conducted to replicate the cross-modal transfer from the 400- to the 800-msec CS-US intervals. A rest control group was added in order to determine whether there was negative or positive transfer from the 2,800- to the 800-msec CS-US interval (cf. Hinson & Siegel, 1980).

Method

The subjects were 24 female albino rabbits of the same age and weight as used in Experiment 1. The apparatus and procedures were identical to those used in Experiment 1. The subjects were

assigned to three groups (n=8) designated 4-8, 28-8, and R-8. However, the death of one subject reduced Group R-8 to seven subjects. Groups 4-8 and 28-8 received training identical to that of their counterparts in Experiment 1. Group R-8 received only restraint and exposure to the chambers for 70 min/day during Stage 1. During restraint, Group R-8 was used to observe spontaneous responses during intervals corresponding to those of the training trials in Group 28-8. In Stage 2, Group R-8 received training with an 800-msec CS-US interval in the same manner as the other two groups.

Results

Figure 4 shows the mean percentage of CRs in Stage 1 as a function of 35-trial blocks. Examination of Figure 4 reveals that Group 4-8 showed rapid CR acquisition to an asymptote near 100% CRs, which was significantly higher than the level of responding displayed by either Group 28-8 [F(1,20)=123.16] or Group R-8 [F(1,20)=183.75]. In turn, Group 28-8 showed modest CR acquisition to an asymptote of 20% CRs, which was significantly greater than the level of spontaneous responding observed in Group R-8 [F(1,20)=8.03].

The results of Stage 2 confirmed those of Experiment 1; that is, there was no detectable immediate transfer across modalities, but there was substantial general transfer. On the first four trials of Stage 2, the mean percentage of CRs was 8%, 0%, and 5% for Groups 4-8, 28-8, and R-8, respectively. Figure 5 shows the mean percentage of CRs in Stage 2 plotted

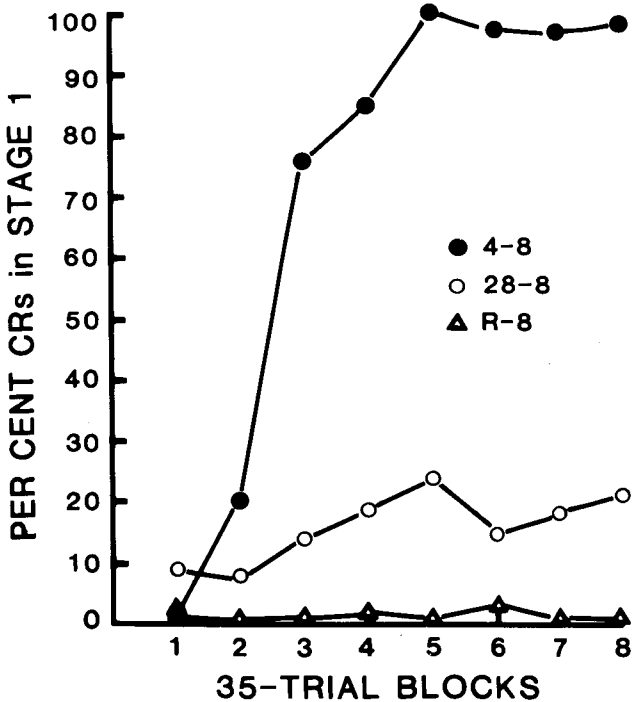


Figure 4. Mean percentage of CRs in Stage 1 of Experiment 2 plotted as a function of 35-trial blocks. Group 4-8 received training with a 400-msec CS-US interval, Group 28-8 received training with a 2,800-msec CS-US interval, and Group R-8 received restraint in the conditioning apparatus.

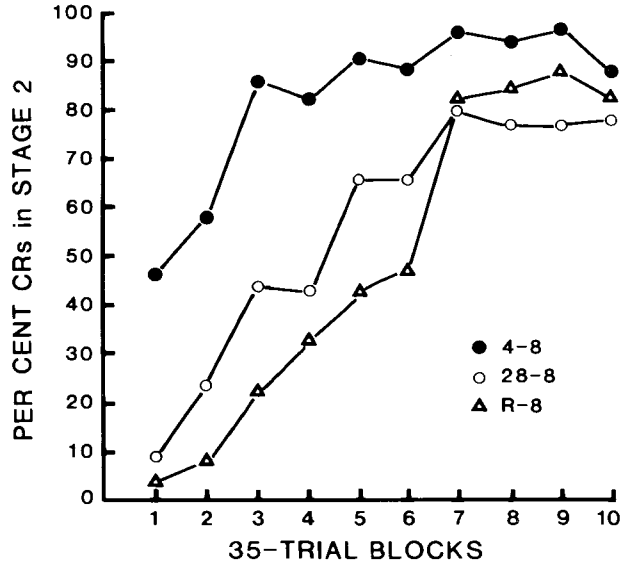


Figure 5. Mean percentage of CRs in Stage 2 of Experiment 2 plotted as a function of 35-trial blocks. All groups were trained with an 800-msec CS-US interval.

across 35-trial blocks. Group 4-8 showed rapid acquisition, particularly in the first block of trials, whereas Groups 28-8 and R-8 showed more gradual acquisition. All three groups appeared to converge at an asymptote around 85% CRs. The overall level of responding in Group 4-8 was higher than the collective performance of Groups 28-8 and R-8 [F(1,20)=10.12]. Although Group 28-8 displayed a slightly higher level of responding than Group R-8, the difference was not significant.

Figure 6 shows the mean adjusted trial of the 1st, 2nd, 3rd, 5th, and 10th CRs for Groups 4-8, 28-8, and R-8. Examination of Figure 6 reveals that Group 4-8 showed very rapid CR acquisition, requiring approximately 16 trials to attain the first CR and only a few more to attain the 10th CR. Thus, the relatively flat curve for Group 4-8 indicates that there was a rapid transition in performance from no CRs to virtually 100% CRs. Groups 28-8 and R-8 showed slower rates of CR acquisition. As seen in Experiment 1, the differences between Group 4-8 and the other two groups were smallest for the 1st CR and grew more pronounced for the later CRs. Statistical analysis confirmed that there was a significant difference between the linear trend of Group 4-8 and that of Groups 28-8 and R-8 taken together [F(1,20)=6.91]. Although Group 28-8 showed some slight savings relative to Group R-8, the apparent differences failed to attain significance.

GENERAL DISCUSSION

The present experiments clearly demonstrated positive transfer across a combined increase in CS-US interval and change in CS modality. Specifically,

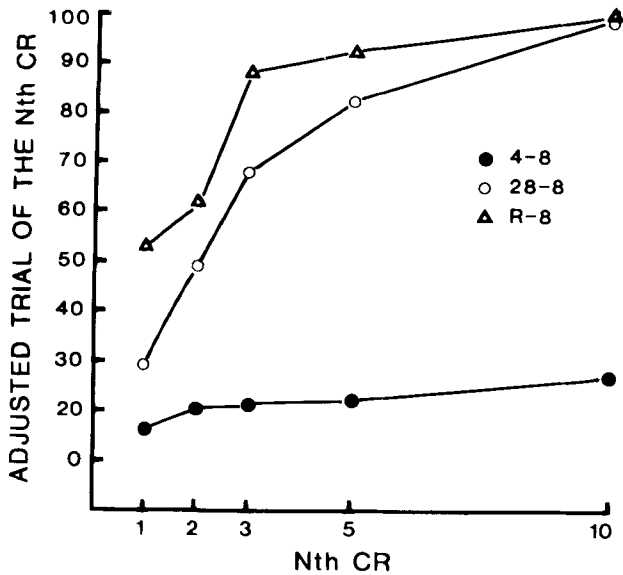


Figure 6. Mean trial of the 1st, 2nd, 3rd, 5th, and 10th CR in Stage 2 of Experiment 2. The trial number for each of the designated CRs has been adjusted downward to eliminate an upward trend necessitated by the fact that the trial of the $n^{\text{th}} + 1$ CR must be at least one trial greater than the n^{th} CR.

after CR acquisition had occurred with a CS from one sensory modality at a 400-msec CS-US interval, the rate of CR acquisition to a CS from another modality was facilitated at CS-US intervals of 800 and 1,800 msec but not 2,800 msec. There was no discernible immediate transfer on the initial presentations of the second CS. Instead, the transfer effect appeared to be an entirely general transfer inasmuch as the rate of CR acquisition to the new CS was enhanced after reinforced training had begun.

A fundamental interpretative issue concerns whether the transfer effects represent a form of stimulus generalization or an enhancement in the formation of a new association in the second stage. A stimulus generalization hypothesis would contend that the observed transfer reflects the ability of the association formed in Stage 1 to withstand alterations in the CS-US interval and CS modality so as to raise CR performance in the second stage. In fact, there have been demonstrations that generalization across sensory modalities can occur on the basis of temporal patterns shared by the otherwise distinctive CSs (Friedes, 1974; Meck & Church, 1982; Seraganian & Popova, 1976). However, no such transfer appeared in the present results. On the operational side, there were minimal similarities in the temporal characteristics of the auditory and visual stimuli. The auditory CS consisted of a sharp onset of a pure, constant tone, whereas the visual CS consisted of the offset of the houselight followed by repeated cycles of on-off flashes. More importantly, there was no evidence of immediate transfer that would be expected had

the subjects shown stimulus generalization along any conceivable dimension of similarity between the auditory and visual CSs.

Since the transfer effects were localized entirely in the rate of CR acquisition to the second CS, there appears to have been an enhancement in the acquisition of a new association. It is tempting to infer that the observed general transfer reflects a global change in the efficiency of the organism's learning system. However, such a spectacular conclusion does not even adequately describe the data. In particular, an interpretation in terms of a vague, but global, change in the organism's learning capacity offers little basis for explaining both the positive transfer at the shorter CS-US intervals, 800 and 1,800 msec, and its absence at the longest interval, 2,800 msec. Moreover, there are more prosaic accounts of transfer which contend that Stage 1 training neutralizes the background stimuli as a source of competition for the processing resources of the animal (Mackintosh, 1977; Seraganian, 1979; Westbrook & Homewood, 1982). In particular, Mackintosh's (1975) model of associative learning assumes that there is a tradeoff between concurrent stimuli in which the stimulus with the greatest associative strength on a trial gains a proportional increment in its growth rate parameter while all other stimuli suffer a proportional decrement in their growth rate parameters. According to this model, exposure in Stage 1 to the paired relation between a salient CS and US generates both increases in the CS's associative strength and increases in that CS's growth rate parameter. Concomitantly, the concurrent, but less salient, background stimuli presumably gain associative strength less slowly and suffer progressive decreases in growth rate. In Stage 2, the reduction in the growth rate for the background stimuli would benefit the new, salient CS by permitting its associative strength to exceed that of the background stimuli sooner than it would otherwise. However, this benefit would appear only if the new CS began with an appreciable growth rate. If the new CS had a low growth rate, as in the case of a long CS-US interval, then the neutralization of the background stimuli would be of no value to the new CS.

The present results themselves offer only indirect support for the hypothesis that prior training neutralizes the background stimuli. However, the case for the neutralization of background stimuli becomes more persuasive when viewed in conjunction with evidence that background stimuli can acquire something like excitatory associative strength when they are "paired" with a US in the absence of an explicit CS. Although background stimuli themselves do not evoke overt CRs in rabbit conditioning preparations, background stimuli do seem to acquire associative properties such as the capacity to "block" subsequent acquisition to an added explicit CS (Mis & Moore, 1973; Randich & LoLordo, 1978). Specif-

ically, exposures to the US alone subsequently retard CR acquisition to an explicit CS, provided that the background stimuli do not undergo large changes between the US-alone exposures and CS-US pairings (Hinson, 1982). By the same token, a change in context between the first and second stage in experiments of the present type might be expected to eliminate the observed transfer.

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