Inhibitory stimulus control of the classically conditioned nictitating membrane response of the rabbit*

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Pavlovian conditioned inhibition training provides a method for investigating inhibitory dimensional stimulus control of the rabbit's conditioned nictitating membrane response. The basic technique consists of reinforcing a burst of white noise while a compound made up of white noise and a tone is systematically not reinforced. Generalization tests to the white noise and a series of test tones result in a U-shaped gradient which remains relatively stable over a series of training-test phases.

Hullian theories of discrimination learning postulate the existence of two opposing processes which interact through stimulus generalization to determine the observed strength of a conditioned response at each point on a stimulus dimension (cf. Spence, 1937). A stimulus associated with reinforcement develops excitation, and a stimulus associated with extinction develops inhibition. In order to evaluate this theory, it is desirable to examine excitatory and inhibitory stimulus control in isolation and from this analysis derive the generalization gradient obtained following discrimination training (e.g., Hearst, 1968). While suitable methods of analyzing excitatory stimulus control are available in both operant and Pavlovian situations, the development of satisfactory procedures for analyzing inhibitory stimulus control has proved a more refractory problem. Part of the difficulty lies in realizing an experimental arrangement in which excitation is constant at all points on the stimulus dimension while inhibition alone varies (cf. Jenkins, 1965).

This report describes a technique for investigating inhibitory control of the auditory frequency dimension using the classically conditioned nictitating membrane response (NMR) of the rabbit. The basic procedure consists of two stages: (1) differential conditioning using a burst of white noise as CS+ and white noise plus a tone as CS— (i.e., Pavlovian conditioned inhibition training, Pavlov, 1927, p. 76), and (2) stimulus generalization test in extinction in which the frequency of the tone is varied randomly while the noise remains constant. The resulting U-shaped gradient provides an index of inhibitory dimensional control of the conditioned inhibitor. The above procedures are analogous to those employed in operant conditioning situations for obtaining inhibitory gradients (e.g., Weisman, 1969; Hearst, Besley, & Farthing, 1970). The method differs from that described by Moore (1972) in which rabbits received differential conditioning to tones of the same frequency but of different intensity (CS+ < CS—). With the latter procedure, inhibitory gradients emerged from generalization tests to other tones of the same intensity as CS—.

EXPERIMENT 1

Experiment 1 illustrates the conditioned inhibition procedure for obtaining inhibitory gradients and compares these gradients with those obtained with the tone in the role of a conditioned excitor, i.e., when noise plus tone is trained as CS+ while noise alone is CS—.

Method

Subjects and apparatus. Four groups of four albino rabbits received NMR conditioning using procedures described by Gormezano (1966) in apparatus described in detail elsewhere (e.g., Hupka, Kwaterski, & Moore, 1970). A CR was defined as a 1-mm deflection of the oscillograph pen recording the NMR occurring within the CS-US interval.

Procedure. The following procedures held throughout the experiment: (1) CS duration was 450 msec, (2) the US was a 50-msec ac shock of 2 mA intensity applied via clips to the infraorbital region of the right (recorded) eye, (3) the CS-US interval on reinforced trials was 400 msec, (4) the intertrial interval was a constant 30 sec, and (5) 120 trials were given in each daily session.

On Day 1, the animals were sutured for NMR recording and adapted to the restraining box and experimental enclosure for ½ h. Days 2-7 consisted of differential conditioning (Phase 1) to white noise alone and white noise plus a 1,200-Hz tone (see Table 1). For two groups (LL,CS— and SS,CS—), the former was CS+ and the latter was CS— (60 trials to each per day in a random order), while the reinforcement contingency was reversed for the two remaining groups (LL,CS+ and SS,CS+). The designations L and S refer to acoustic stimuli of 86 and 76 dB SPL, respectively. The first letter refers to the tone and the second to the noise. The intensity of the noise on CS+ trials was always equal to that on CS— trials. Days 8-9 were generalization test days carried out in extinction to noise plus tones of 400, 800, 1,200, 1,600, and 2,000 Hz, each presented 24 times per day in a random order.

Days 10-11 consisted of additional differential conditioning (Phase 2) for each group, but under altered circumstances: (1) Group LL,CS— was switched to an SS,CS— treatment in Phase 2 of differential conditioning, i.e., both the noise and tone were lowered 10 dB in intensity. (2) Group LL,CS+ was switched to lower CS intensity in a similar way. (3) Group SS,CS— was switched to an LS treatment, i.e., tone intensity was increased 10 dB while noise remained the same as in Phase 1. (4) Group SS,CS+ was switched in a similar way. Finally, Days 12-13 were generalization test sessions like Days 8-9, but with the intensity of noise and tone the same as in Phase 2 of differential conditioning.

Table 1
Summary of Experimental Design for Phase 1 of Experiment 1

Group	Conditioning	
LL, CS—	White Noise (86 dB) and Tone (86 dB)	= CS—
	White Noise (86 dB)	= CS+
SS, CS—	White Noise (76 dB) and Tone (76 dB)	= CS+
	White Noise (76 dB)	= CS+
LL, CS+	White Noise (86 dB) and Tone (86 dB)	= CS+
	White Noise (86 dB)	= CS—
SS, CS+	White Noise (76 dB) and Tone (76 dB)	= CS+
	White Noise (76 dB)	= CS—

**Note—S = soft, L = loud*

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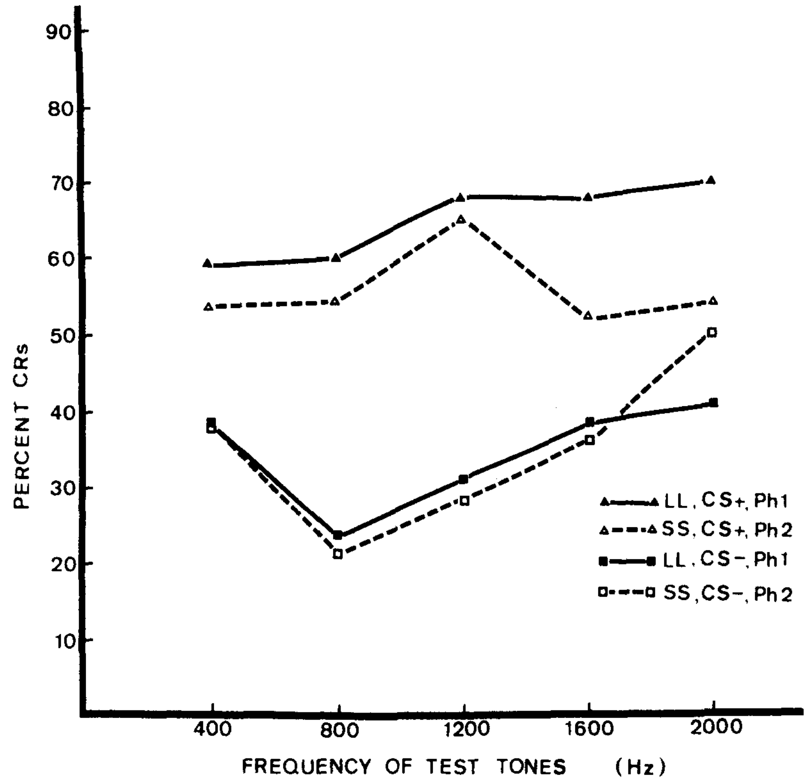

Fig. 1. Mean percentage of CRs during 2 days of generalization tests in Phase 1 and Phase 2 for Groups LL,CS+ and LL,CS−.

ratio on the two types of gradients: This manipulation elevated the excitatory gradient, but lowered the inhibitory gradient. This suggests that inhibitory potential may be directly related to CS intensity, as predicted by a recently elaborated neural theory of stimulus control (Schneiderman, Pearl, Wilson, Metcalf, Moore, & Swadlow, 1971). Schneiderman et al postulate the existence of higher order detector units which modulate the strength of the conditioned response by integrating excitatory and inhibitory inputs recruited at lower levels. A strong nonreinforced CS presumably recruits more inhibitory inputs than does a weaker nonreinforced CS, while holding the number of excitatory inputs constant.

EXPERIMENT 2

Experiment 2 provides data on the effect of repeated training and testing on inhibitory control of the conditioned NMR.

Method

Four naive albino rabbits were treated exactly like Group SS,CS− of Experiment 1, except that 2 days of generalization testing were given following only 2 days of conditioned inhibition training. This sequence was repeated four more times.

Results and Discussion

The mean absolute generalization gradients for Groups LL,CS+ and LL,CS−, pooled over two test sessions, are shown in Fig. 1. The functions in the upper portion of Fig. 1 depict the observed excitatory gradients as a consequence of the training procedure employed, while the lower functions are the observed inhibitory gradients obtained as a consequence of conditioned inhibition training to the tone. Lowering CS intensity from Phase 1 to Phase 2 had no discernible effect on the inhibitory gradient, but this treatment did lower and sharpen the excitatory gradient generated by conditioned excitation training.

The inhibitory gradients show a displaced minimum located at 800 Hz instead of 1,200 Hz. Inspection of data from individual Ss indicated that this bias was genuine. (The mean gradient is quite representative of individual rabbits.) The source of this bias is not known, but it may have been caused by unknown acoustic factors such as differential masking by noise.

Figure 2 shows the mean absolute generalization gradients for Phases 1 and 2 of Groups SS,CS− and SS,CS+. These gradients are similar to those shown in Fig. 1. The most interesting aspect of the data is the differential effect of increasing the tone-to-noise

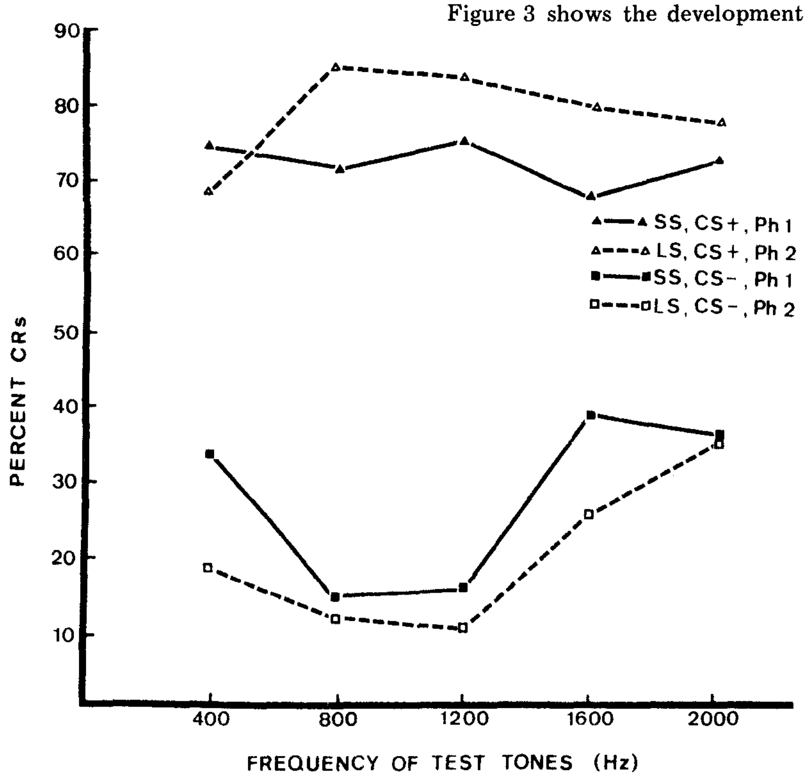

Fig. 2. Mean percentage of CRs during 2 days of generalization tests in Phase 1 and Phase 2 for Groups SS,CS+ and SS,CS−.

Results and Discussion

Figure 3 shows the development of

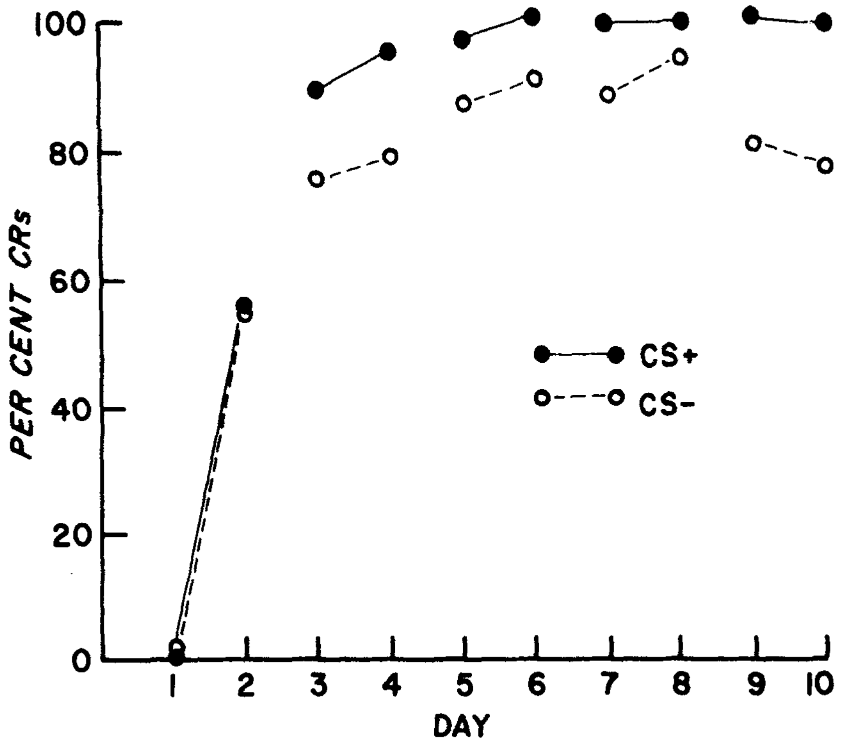

Fig. 3. Mean percentage of CRs to CS+ and CS— as a function of day of conditioned inhibition training. The breaks in the curves represent interpolated generalization test sessions.

Table 2
Mean Percentage of CRs to Each Test Tone and Mean Index of Inhibitory Control as a Function of Test Phase

Test Tone (Hz)	Phase 1	2	3	4	5
400	23	61	53	54	45
800	19	47	47	32	31
1200 (CS—)	15	53	45	51	45
1600	20	59	55	58	56
2000	21	59	63	62	52
Index	.28	.39	.38	.32	.34

differential conditioning as a function of amount of training, with four interpolated generalization tests at 2-day intervals. The corresponding mean absolute generalization gradients are presented in Table 2 together with a mean "index of inhibitory control" computed from inhibitory gradients of each rabbit as follows: Index = (minimum % CR)/(minimum % CR + maximum % CR). Table 2 shows that inhibitory gradients remained remarkably stable over five test phases, and the value of the mean "index of inhibitory control" nicely paralleled the degree of differential conditioning obtained in the immediately preceding phase of differential conditioning.

As in Experiment 2, the observed inhibitory gradients tended to show a minimum at 800 Hz rather than at 1,200 Hz.

The finding that inhibitory gradients remained relatively stable as a function of amount of training may have methodological implications for research on inhibitory control, where such stability would be desirable, e.g., within-Ss pharmacological manipulations using scopolamine or other agents which presumably work selectively on inhibitory processes.

GENERAL DISCUSSION

A Pavlovian conditioned inhibition paradigm provides a suitable method of investigating inhibitory stimulus control along an audio-frequency dimension. The observed gradients following conditioned inhibition training with a noise burst as CS+ and the same noise burst plus a tone as CS— are stable over repeated training and test series and appear to be more symmetrical than the inhibitory gradients reported by Moore (1972, p. 219). In the latter case, the observed lack of symmetry along the audio-frequency dimension (gradients were steeper on the low-frequency end of the dimension than on the high-frequency end) following intensity differentiation was most probably due to a lack of orthogonality between the intensity and frequency dimensions rather than some basic peculiarity of audio-frequency generalization. Thus, the asymmetry of Moore's (1972) inhibitory gradients was likely the result of greater generalized excitation from the soft CS+ to loud test tones at the lower end of the frequency scale than at the higher end.

We are presently employing the conditioned inhibition technique to derive inhibitory generalization gradients which, in conjunction with independent excitatory gradients, provide an exact quantitative evaluation of Hullian theory of discrimination learning in classical conditioning of the rabbit's NMR.

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