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AUTOSHAPING IN THE RAT: THE EFFECTS OF LOCALIZABLE VISUAL AND AUDITORY SIGNALS FOR FOOD

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Two experiments investigated autoshaping in rats to localizable visual and auditory conditioned stimuli predicting response-independent food. In Experiment 1 considerable conditioned-stimulus approach behavior was generated by a localizable visual conditioned stimulus that was situated approximately 35 cm from the food tray. Using the same apparatus in Experiment 2 we found that the conditioned-stimulus approach was generated only to a visual conditioned stimulus and not to a localizable auditory conditioned stimulus even though subjects (1) could discriminate presentations of the auditory conditioned stimulus, (2) had associated it with food, (3) could localize it, and (4) would approach the auditory stimulus if this behavior constituted an instrumental response to food. The predominant conditioned responses to the auditory stimuli were goal tracking (entering the food tray) and orienting towards the food-paired conditioned stimulus by head turning and rearing and turning. These results imply that rats do not invariably approach a localizable appetitive Pavlovian conditioned stimulus but that stimulus-approach responses depend on the nature and modality of the conditioned stimulus.

Key words: autoshaping, visual conditioned stimulus, auditory conditioned stimulus, sign tracking, rats

When a localizable conditioned stimulus (CS) is scheduled to precede an appetitive unconditioned stimulus (UCS), animals frequently approach and contact the CS. This phenomenon has been called autoshaping (Brown & Jenkins, 1968), sign tracking (Hearst & Jenkins, 1974), and signal-centered behavior (Jenkins, Barrera, Ireland, & Woodside, 1978). Since the earliest description of the phenomenon in pigeons (Brown & Jenkins, 1968), it has been demonstrated in a wide variety of species using many kinds of reinforcers and localizable CSs (cf. Hearst & Jenkins, 1974; Schwartz & Gamzu, 1977). In studies that involve rats as subjects, reinforcers that have been used to generate sign tracking include liquid and solid foods (Davey & Cleland, 1982; Davey, Phillips, & Cleland, 1981), water (Davey & Cleland, 1982; Timberlake, 1983), and intracranial brain stimulation (Peterson, 1975; Wilkie & McDonald, 1978). The types of localizable CSs used range from retractable or illuminable levers (Atnip, 1977; Boakes, 1977; Davey, Oakley & Cleland, 1981; Locurto, Terrace, & Gibbon, 1976; Stiers & Silberberg, 1974) to static stimulus lamps (Holland, 1980) and even restrained conspecifics (Timberlake, 1983; Timberlake & Grant, 1975).

Only a handful of studies have used localizable auditory CSs as signals for food, and these have tended to produce conflicting results. Hearst and Jenkins (1974) and Steinhauer, Davol, and Lee (1977) report that pigeons will peck in the direction of the speaker emitting a localizable auditory CS, but Bilbrey and Winokur (1973) found no such CS-directed behavior in pigeons. Furthermore, Grastyán and Vereczkei (1974) found that cats would readily approach and contact a speaker emitting a localizable auditory CS for food, whereas Harrison (1979) found that rats would not approach a localized noise CS. A resolution to these conflicting findings is important from a theoretical point of view since they may reflect species differences in response to auditory CSs. For instance, approaches to the explanation of signal-directed behavior that emphasize the release of behavior systems related to feeding (e.g., Timberlake, 1983) would suggest that the nature of the CS is important in that it acts as a natural releaser for species-specific appetitive

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behavior—some of which involves approach to, and contact with, the CS. Hence an auditory CS might elicit CS-directed behavior only if it is a natural releaser for approach responses in that particular species. However, certain other theories of signal-directed behavior stress that the ability of the CS to evoke an orienting response (Buzsáki, 1982; Grastyán & Vereczkei, 1974; Holland, 1980) is crucial in generating sign tracking. Thus, this view would predict that if an auditory CS is as capable as a visual CS of generating a localized orienting response, then it should generate CS-approach responses to the same extent that would be expected from a localized visual CS.

The present study compares the ability of localized visual and auditory CSs to produce signal-directed behavior in the rat. Experiment 1 demonstrates that rats will readily approach a localizable visual CS in an apparatus built for studying auditory stimuli. Experiment 2 is a direct comparison of the ability of a localizable visual CS (an illuminable keylight) and a localizable auditory CS (10-Hz clicks) to generate CS approach.

EXPERIMENT 1

Experiment 1 was designed to investigate the acquisition of signal-directed behavior to a visual signal that was located some distance from the site of UCS delivery. Since other studies have demonstrated that signal approach is an inverse function of the distance between CS and food site (e.g., Holland, 1980), it was important to establish that reasonably reliable CS-approach responses to a visual CS could be developed in apparatus that was purposely built for the study of localizable auditory CSs in the rat.

Method

Subjects

The subjects were 4 male Hooded Lister rats, approximately 100 days old and maintained at 80% of their ad lib body weights throughout the experiment.

Apparatus

The test box (see Figure 1) was a converted metal alleyway, 70 cm in length and 20 cm in width. Each wall was 25 cm high. A 3.5-cm diameter perspex disc, 4 cm from the floor and which could be illuminated from behind by a white light, was located in each end wall. Hidden behind the disc was a small 5.5-cm diameter speaker from which clicks with a frequency of 10 per sec could be delivered and which had an intensity of 73± 2 db as measured in the center of the alleyway. A white noise generator produced ambient noise at 60± 2 db intensity when measured in the center of the alleyway.

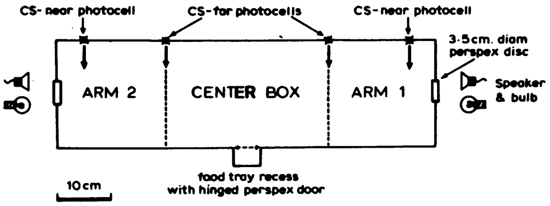

Fig. 1. A scale plan of the experimental apparatus used in both experiments presented in this paper. See text for further explanation.

On one of the walls in the center of the alleyway, situated 37 cm from each perspex disc, was a small aperture into which 45-mg food pellets could be delivered. A perspex door hinged at the top covered this food tray and tray entries could be measured by a microswitch located at the hinge. Food deliveries were associated with the brief click of the relay operating the food dispenser and by the sound of the pellet falling into the food tray. Photocell beams were positioned along the alleyway 5 cm and 20 cm from the perspex disc on the end of each wall. The photocells were termed CS-near (when 5 cm from a CS perspex disc at the end of the alleyway) and CS-far (when 20 cm from a CS perspex disc). For the purposes of gathering data, the area from the right hand perspex disc to its CS-far photocell was called "ARM 1," the central area between the two CS-far photocells was called the "CENTER BOX," and the area between the left hand perspex disc and its CS-far photocell was called "ARM 2." Background illumination was provided by a 60-W lamp situated 65 cm above the alleyway and directed away from it. The experiment was controlled and data collected by solid state logic units mounted on a rack system.

Procedure

The experiment consisted of three phases, which were preceded by adaptation to the experimental chamber. During adaptation each subject was placed in the chamber for 30 min with 10 food pellets present in the food tray.

Magazine training. After adaptation, each subject was given four sessions of magazine training in which food pellets were delivered into the food tray on a variable time (VT) 60-sec schedule. This schedule had a minimum interval of 20 sec and a maximum interval of 100 sec. Each session lasted for 40 food deliveries.

Acquisition. For the following 22 sessions, food delivery was paired with each of 40 illuminations of the perspex disc presented on a VT 60-sec schedule as for magazine training. For half the subjects the paired keylight was in ARM 1 and for the other half in ARM 2. The keylight was illuminated for 10 sec and was extinguished on delivery of the food pellet.

Differentiation. During this phase of the experiment (10 sessions), pairings of keylight with food remained as they had been during acquisition, but the keylight at the end of the opposite arm was illuminated for 10-sec periods, though independently of food. Such uncorrelated CS presentations were programmed on a VT 60-sec schedule identical to, but independent of, the schedule controlling food delivery. On no trials were correlated (CS+) and uncorrelated (CS−) keylights present at the same time. Subjects received 40 CS+ and 40 CS− presentations per session.

Observations

In order to supplement the quantitative data obtained from photocell activity, the behavior of all subjects was observed during the final session of acquisition and the final session of differentiation. Observations were made via a closed-circuit television (CCTV) that transmitted pictures of the animal to observers in an adjoining room. The behavior of the subjects during CS+ and CS− presentations was analyzed according to preselected topographic categories, which were defined on the basis of casual observations made during early sessions of acquisition. Each category was scored on the basis of the percentage of trials in which at least one instance of the behavior occurred. The categories were of two basic types, topography and position within the apparatus, and consisted of the following:

Topography. (1) *CS orienting:* standing motionless on all four legs and turning the head in the direction of the CS stimulus; (2) *CS approach:* walking towards the CS until at least the front paws crossed a line drawn between the ARM appropriate to the illuminated CS and the CENTER BOX. If the subject was already in the ARM appropriate to the CS at CS onset and remained there throughout CS presentation, this was not counted as CS approach. However, instances of the latter were rare because subjects spent the majority of the intertrial time in the CENTER BOX beside the food tray. Both orienting and approach were recorded only if there was an interval of at least 2 sec between the subject turning its head toward the CS and then moving toward the CS. If the animal turned and moved immediately towards the CS, this was scored only as CS approach; (3) *rear and turn:* rearing up on the hind legs either with or without a wall for support and turning in the direction of the CS.

Position. The differing locations of the rat within the box (i.e., ARM 1, CENTER BOX, ARM 2) were noted during CS presentation and scored as the percentage of trials in which the rat was present at least once in that part of the apparatus. Two observers scored the first observation session with 85% agreement. Scores given in the results represent observations made by a single observer throughout.

RESULTS AND DISCUSSION

Table 1 summarizes the individual goal-tracking and sign-tracking data, as obtained from the rate of tray entry and photocell crossings per min. At the end of differentiation, all subjects were entering the food tray more frequently during CS+ than CS− [t (3) = 9.069, $p < .01$], were triggering the CS-near photocell more frequently during CS+ than CS− [t (3) = 10.749, $p < .01$], and were triggering the CS-far photocell more frequently during CS+ than CS− [t (3) = 8.546, $p < .01$]. A comparison between the first four sessions and the last four sessions of acquisition shows a significant increase in the tendency to trigger the CS+ -near photocell [$t(3) = 4.232$, $p < .05$], suggesting that activity in the area of the CS+ stimulus increased with training.

Table 2 summarizes the observational data from Experiment 1. These data indicate that subjects tended to be in the CENTER BOX during CS presentations, though in addition they did approach the CS+ arm on 44% of CS+ trials and approached the CS− arm on only 21% of CS− trials. This suggests that the CS+ -near and CS+ -far photocell data in Table 1 represent approach to the CS+ stimulus during its presentation. All subjects oriented towards CS+ more frequently than to CS−, but only two of four subjects demonstrated rear and turn towards the CS. All subjects showed a greater tendency to be in the CS+ box during CS+ presentation than in the CS− box during CS− presentation.

The results of this experiment suggest that rats will orient towards a visual CS+ and leave the vicinity of imminent food delivery to make close approaches to this localizable visual CS, even though it is up to 35 cm from the site of food delivery.

EXPERIMENT 2

Having demonstrated in Experiment 1 that rats will approach distally placed food-correlated visual CSs, we conducted Experiment 2 to compare the ability of localizable visual and auditory CSs to evoke such signal-directed behavior.

METHOD

Subjects

The subjects were six naive female Hooded Lister rats, maintained at 80% of their ad lib body weights throughout the experiment.

Apparatus

The test box was the same as that used in Experiment 1 (Figure 1).

Procedure

The experiment consisted of four phases, which were preceded by adaptation to the experimental chamber. During adaptation each subject was placed in the chamber for 30 min with 10 food pellets present in the food tray.

Magazine training. After adaptation each subject was given four sessions of magazine training in which food pellets were delivered into the food tray on a VT 60-sec schedule. This schedule had a minimum interval of 20 sec and a maximum interval of 100 sec. Each session lasted for 40 food deliveries.

Table 1

Experiment 1. Individual data plus mean (and standard error of the mean) of tray entry, near-photocell activity, and far-photocell activity, expressed as responses per min during CS+, ITI, and CS−. Data are calculated from the final three sessions of Acquisition and Differentiation. Photocell data represent photocell triggerings/min.

		ACQUISITION		*DIFFERENTIATION*		
	Rat	*CS+*	*ITI*	*CS+*	*ITI*	*CS−*
TRAY ENTRIES	147	3.4		4.1	0.7	1.3
	148	6.7	*	5.8	0.9	1.0
	149	17.5		13.7	0.2	0.8
	150	8.9		6.7	2.1	4.1
	MEAN	9.1	—	7.6	1.0	1.8
	± SEM	3.0	—	2.2	0.4	0.8
CS NEAR PHOTOCELL	147	13.8	1.6	12.9	0.6	4.1
	148	15.2	1.0	13.8	0.4	4.2
	149	19.6	1.4	13.1	1.1	4.4
	150	12.9	0.4	12.1	0.4	3.4
	MEAN	15.4	1.1	13.0	0.6	4.0
	± SEM	1.5	0.3	0.4	0.2	0.2
CS FAR PHOTOCELL	147	4.0	1.6	2.2	1.5	0.7
	148	3.8	2.4	4.1	2.3	1.5
	149	12.2	3.5	11.0	2.6	3.4
	150	3.8	1.6	5.2	2.1	1.4
	MEAN	6.0	2.3	5.6	2.1	1.8
	± SEM	2.1	0.5	1.9	0.2	0.6

*Data lost due to equipment failure.

Acquisition. For this phase the subjects were divided into two groups of three. The first group (CS+ LIGHT group) was presented with keylights paired with food and unpaired auditory clicks. The second group (CS+ CLICKER group) was presented with auditory clicks paired with food and unpaired keylights. *CS+ LIGHT Group:* For the 24 sessions of acquisition all food deliveries were preceded by a 10-sec illumination of the perspex disc (CS+) at the end of ARM 1. These were presented on a VT 60-sec schedule as for magazine training. In addition, these subjects received 10-sec presentations of a 10-Hz clicker (CS−) from the speaker situated at the end of ARM 2. These clicker presentations were scheduled on a VT 60-sec schedule identical to, but independent of, that which controlled the illuminations of the perspex key at the end of ARM 1. These auditory clicks were not paired with food and CS+ and CS− were never presented simultaneously. *CS+ CLICKER Group:* In this group the keylight presented in ARM 1 was never paired with food (CS−), whereas the auditory clicker presented in ARM 2 was used as the CS+ signaling food delivery. This group received 26 sessions of acquisition. In all other respects the CS+ CLICKER group was identical to the CS+ LIGHT group.

Reversal. During this phase both groups received two sessions in which the ARM locations of CS+ and CS− were reversed.

Instrumental Phase. Only the CS+

Table 2

Experiment 1. Percentage of trials with at least one instance of each of the four observational categories: orienting, approach, tray entry, and rearing. Also percentage of trials in which the subject was observed in the CS+ ARM, the CENTER BOX, or the CS− ARM during a trial. Data were taken from the last session of each phase.

		ACQUISITION				*DIFFERENTIAL*							
		Orienting	*Approach*	*Tray Entry*	*Rearing*	*Orienting*		*Approach*		*Tray Entry*		*Rearing*	
	Rat	*CS+*	*CS+*	*CS+*	*CS+*	*CS+*	*CS−*	*CS+*	*CS−*	*CS+*	*CS−*	*CS+*	*CS−*
RESPONSE TOPOGRAPHY (%)	147	32	52	72	8	73	13	32	17	63	26	10	7
	148	28	32	84	4	90	20	48	23	97	30	7	3
	149	24	64	100	0	57	10	59	20	100	20	0	3
	150	36	52	96	0	47	20	38	25	100	50	0	3
	MEAN	30	50	88	3	67	16	44	21	90	31	4.3	4.0
	± SEM	2.6	6.7	6.3	1.9	9.4	2.6	5.8	1.8	9.1	6.5	2.3	1.0
		CS+ Box	*Center Box*	*CS− Box*		*CS+ Box*		*Center Box*		*CS− Box*			
	Rat	*CS+*	*CS+*	*CS+*		*CS+*	*CS−*	*CS+*	*CS−*	*CS+*	*CS−*		
LOCATION (%)	147	60	100	32		65	43	85	100	25	33		
	148	60	100	32		60	37	100	100	13	23		
	149	84	92	24		80	28	100	93	17	27		
	150	64	96	36		62	50	100	93	10	27		
	MEAN	67	97	31		67	40	96	97	16	28		
	± SEM	5.7	1.9	2.5		4.5	4.7	3.8	2.0	3.3	2.2		

CLICKER group experienced this phase. Each subject was given five sessions of 60 trials each, during which the clicks could be sounded at the end of either ARM on a random basis (mean ITI of 60 sec). Each trial commenced when the subject was in the CENTER BOX and food was delivered only if the subject broke the CS-far photocell in the ARM in which the clicks were presented. On the final of these five sessions, approach to the wrong ARM during a trial terminated the trial without food. Thus, food could be obtained only by approaching the correct ARM without previously approaching the incorrect ARM.

Observations

Observations as described in Experiment 1 were made during both CS+ and CS− trials on the last two sessions of acquisition and the two sessions of reversal.

RESULTS AND DISCUSSION

Table 3 shows the rate at which the CS-near and CS-far photocells were triggered during CS+ and CS− for all subjects during acquisition. For the last five sessions of acquisition, there were no statistically significant differences in the rate of crossing the CS-near photocell ($p > .05$), either within groups (CS+ vs. CS−) or between groups (CS+ CLICKER vs. CS+ LIGHT). However, differences were observed in the frequency of crossing the CS-far photocell, dependent upon the nature of the CS+. For the CS+ LIGHT group, rate of crossing the CS+-far photocell during CS+ presentations was significantly higher than their rate of crossing the CS− -far photocell during CS− presentations [$t(2) = 5.751$, $p < .05$]. Furthermore, the CS+ LIGHT group crossed the CS+ -far photocell during CS+ more frequently than did the CS+ CLICKER group [$t(4) = 17.032$, $p < .001$]. This did not appear to be a result based simply on greater reactivity caused by visual stimulus changes, because the rate of CS -far photocell crossings to the visual CS− in the CS+ CLICKER group was significantly lower than that to the visual CS+ in the CS+ LIGHT group [$t(4) = 16.9307$, $p < .001$]. There was no significant difference between the rate of CS-far crossings during CS+ and CS− presentations in the CS+ CLICKER group [$t(2) = 1.262$, $p > .05$]. Table 3 also shows that the trends in photocell activity observed during the last five sessions of acquisition were similar to those that had developed in the first five sessions of acquisition. This suggests that rats in the CS+ CLICKER group did not approach the CS source on ini-

Table 3

Experiment 2. Individual data plus mean (and SEM) of far-photocell and near-photocell activity expressed as rate per min for both CS+ LIGHT and CS+ CLICKER groups during CS+ and CS– at the beginning and end of the Acquisition phase.

		CS– Far photocell				*CS– Near photocell*			
		First 5 Sessions		*Last 5 Sessions*		*First 5 Sessions*		*Last 5 Sessions*	
Group	*Rat*	*CS+*	*CS–*	*CS+*	*CS–*	*CS+*	*CS–*	*CS+*	*CS–*
CS+ LIGHT	91	2.5	0.7	4.1	1.0	0.4	0.9	0.8	0.5
	83	1.4	0.5	2.9	1.1	0.3	0.2	0.5	0.4
	84	3.1	0.7	5.2	2.7	0.6	0.6	1.4	1.4
	Mean	2.3	0.6	4.1	1.6	0.4	0.6	0.9	0.8
	± SEM	0.4	0.1	0.7	0.5	0.1	0.1	0.3	0.3
CS+ CLICKER	87	0.8	0.9	1.6	1.8	0.3	0.5	0.4	0.5
	92	1.1	1.5	1.1	1.3	0.5	0.5	0.2	0.6
	88	0.7	0.6	1.0	0.3	0.1	0.1	0.3	0.0
	Mean	0.9	1.0	1.2	1.1	0.3	0.4	0.3	0.4
	± SEM	0.1	0.3	0.2	0.4	0.1	0.1	0.1	0.2

tial acquisition sessions and then adopt a more efficient strategy of staying near the food tray. Differential CS+ CLICKER approach was never apparent during any stage of acquisition.

Figures 2 and 3 illustrate the observational data taken from the last two sessions of acquisition and the two sessions of reversal. From Figure 2 it can be seen that both the CS+ LIGHT and CS+ CLICKER groups showed orienting responses to their respective CS+s, but a differential tendency to approach CS+ was found only in the CS+ LIGHT group. This can also be seen in Figure 3, where subjects in the CS+ LIGHT group were more often found in their respective CS+ ARM than the CS+ CLICKER group. The CS+ approach behavior in the CS+ LIGHT group was not a motor pattern restricted to one arm of the alleyway, since subjects continued to approach CS+ when the CS+ ARM was reversed (Figures 2 and 3). These observational data suggest that the increased level of CS+ -far photocell crossing in the CS+ LIGHT group accurately reflected a tendency to approach the CS+.

From Figure 2 it can be seen that two of the CS+ CLICKER subjects exhibited differential rear and turn responses to the CS+ (Subjects 88 and 92). The third subject in that group (87) did not exhibit rear and turn but did show differential orienting reactions to CS+. The possibility that the CS+ CLICKER group could not differentially discriminate the clicks is discounted by the fact that differential CS+/CS– tray entry rates (bottom panel, Figure 2) were shown by this group. The further possibility that these subjects could not localize the clicks seems discounted by the fact that all CS+ CLICKER subjects learned to approach the ARM from which the clicks originated on more than 75% of the trials by Session 5 of instrumental training in Phase 4. Furthermore, the fact that all CS+ CLICKER subjects emitted orienting and rear and turn responses to CS+ both prior to and following reversal also suggests they were able to localize the auditory CS.

These data, with those from Experiment 1, confirm that rats will approach a visual CS for food in this test apparatus, but only when it is correlated with food delivery. This signal-directed behavior, however, was not apparent in rats trained with an auditory click as the CS for food, even though the CS+ could be discriminated and localized by the subject. Subjects given an auditory CS+ did, however, direct orienting responses to the CS+ while remaining close to the food tray in the CENTER BOX.

GENERAL DISCUSSION

In this study it was found that rats would readily approach a localizable visual CS for food that was situated distally to the food site but would not approach a distal localizable auditory CS. In the latter case, CS-approach responses did not occur despite the fact that subjects (1) could discriminate presentations of the auditory CS+, (2) had associated this

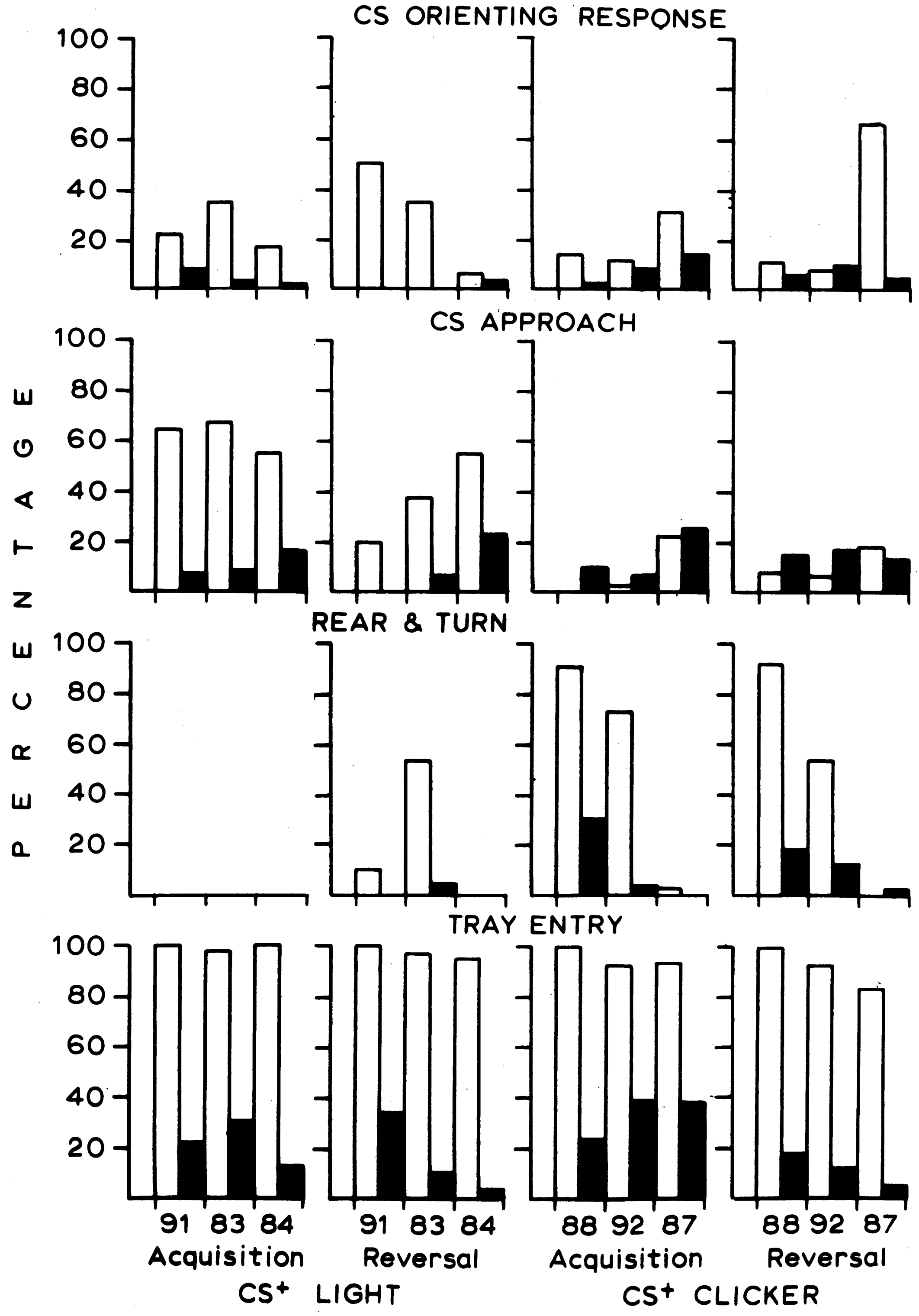

Fig. 2. The percentage of trials containing each of the four types of behavior during CS+ (unfilled bars) and CS− (filled bars) averaged for the two sessions ending acquisition and the two sessions of reversal. In Experiment 2, CS+ LIGHT subjects are represented in the two left-hand columns and CS+ CLICKER subjects in the two right-hand columns.

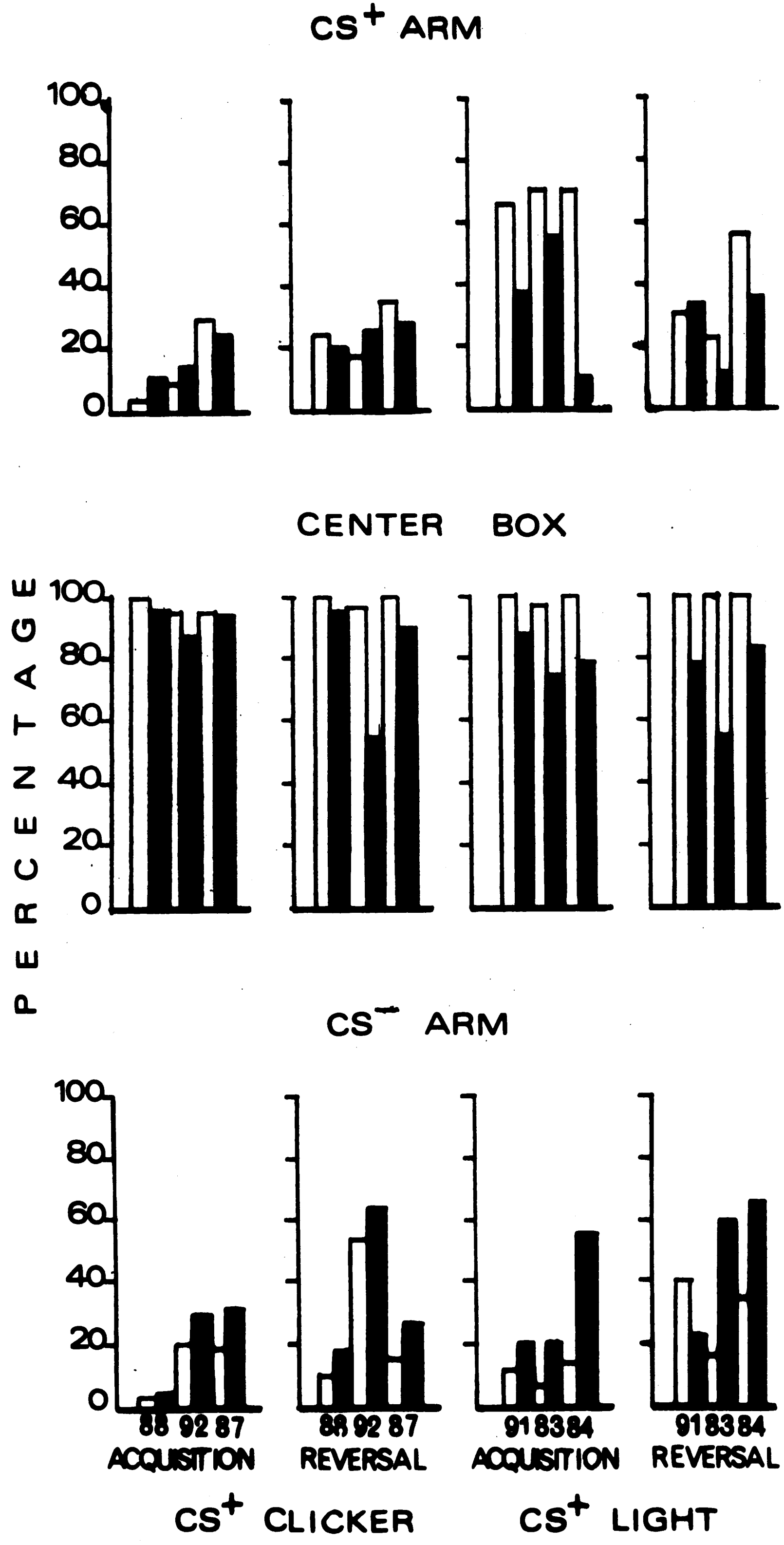

Fig. 3. Percentage of trials in which each subject was observed in the CS+ BOX, the CENTER BOX, or the CS− BOX during CS+ trials (unfilled bars) and CS− trials (filled bars) in Experiment 2. Data are taken from the last two sessions of acquisition and the last two sessions of reversal.

CS+ with food, (3) could localize the CS+, and (4) would approach the CS+ if this behavior constituted an instrumental response for food. The predominant CRs to the auditory CS were goal tracking (entering the food tray) and CS+ -orienting responses characterized by head turning or rearing and turning. CRs characteristic of the visual CS+ were goal tracking, CS+ orienting, and CS approach. These observations do not appear to be consistent with views that consider sign tracking to be functionally equivalent to the CS-orienting response (e.g., Buzsáki, 1982; Holland, 1980). Although both visual and auditory CSs elicited orienting responses, only the visual CS generated active CS approach. Thus, if an appetitive CS elicits an orienting reaction, this is not a sufficient condition for active CS approach to ensue; this latter response is presumably determined by other factors, perhaps related to the nature of the CS. However, this argument does beg the question of what constitutes an orienting response to auditory and visual stimuli. Since no note was taken of reactions to the auditory and visual CSs prior to conditioning (e.g., Holland, 1977), it is difficult to determine whether the approach to the visual CS+ represents a component of the orienting reaction to visual stimuli or whether it results from the conditioned pairing of a visual CS with food. However, if CS approach were part of the orienting reaction to the visual CS, one might have expected the CS+ CLICKER group to show approach behavior to the visual CS− on early acquisition trials (when that stimulus is still relatively novel), which habituates to a low level by the end of acquisition. Table 3 suggests that this was not the case: Levels of CS− approach in the CS+ CLICKER group were much the same between the first and last five sessions of acquisition and in both cases lower than visual CS approach in the CS+ LIGHT group. It is plausible that CS+ approach in the CS+ LIGHT group was influenced by adventitious reinforcement of this response, but this does not explain why CS-approach responses should occur initially to the visual CS and not the auditory CS; approach responses must be generated by other factors (e.g., the CS-UCS contingency) before such responses can be adventitiously reinforced.

Consideration of the present results in the context of other studies that have used localizable auditory CSs suggests that the ecological relevance of CS modality may be important in determining the CS approach. For instance, the results of the present study are consistent with those of Harrison (1979) who also found that rats would approach a localizable tone CS for food if that behavior was part of an instrumental response sequence, but would not approach the auditory CS if it signaled response-independent food. However, both the present results and those of Harrison (1979) are contrary to findings reported by Grastyán and Vereczkei (1974), who used cats as subjects. They found that cats would readily approach a localizable auditory clicking CS (10 Hz) that predicted response-independent food. Even when the CS was spatially discontiguous with the food site, hungry cats would readily approach the CS even if this resulted in the loss of food on that trial. Grastyán and Vereczkei observed that their subjects "approached the CS and performed a thorough investigation around it—sniffing and searching. Some of the animals also used their paws and teeth, and exploration often assumed a definitely aggressive manner" (1974, p. 126).

The differing results obtained from rats and cats may reflect a species difference based on natural feeding habits. Timberlake (1983) has suggested that the nature of signal-centered behavior will depend on the nature of the CS and whether the CS is a natural releaser for appetitive behavior systems in that species. The cat is primarily a carnivorous predator whose repertoire of appetitive behavior includes phylogenetically preorganized predatory responses. Since the prey of cats is often located on the basis of auditory signals, it seems reasonable to suppose that such signals will release stalking and aggressive responses related to prey killing. Consistent with this analysis, aggressive responses appear to be a prominent part of the signal-centered topographies of cats observed by Grastyán and Vereczkei.

However, rats are mainly omnivorous foragers who, even when preying, rarely detect food on the basis of auditory signals (cf. Ewer, 1971). Hungry rats generally exhibit investigative foraging responses that include sniffing and manipulating any small objects in the environment—whether they be food or not (Barnett, 1956; Ewer, 1971). The retractable and illuminable levers normally used as appetitive CSs in autoshaping studies with rats are quite suitable for releasing and supporting these manipulative responses, but auditory CSs possess neither an ecological relevance for the rat (in that rats do not normally detect food through auditory cues) nor the physical properties necessary for supporting species-specific appetitive responses. Although subjects in the present study were observed on a casual basis to approach, paw, and nose the illuminated perspex disc that constituted the visual CS, other studies show that even when a visual CS is made obviously nonmanipulable by increasing its diffuseness (while maintaining its localizability), rats cease to sign track and predominantly direct their behavior towards the food tray during CS presentation (Holland, 1980). Such converging evidence suggests that manual and oral manipulability may be a property of appetitive CSs that is important in generating and maintaining active CS approach in the rat.

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