

*TOPOGRAPHY OF SIGNAL-CENTERED
BEHAVIOR IN THE RAT: EFFECTS OF
DEPRIVATION STATE AND REINFORCER TYPE*

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In a series of three experiments, groups of food-deprived and water-deprived rats were given pairings of a retractable lever (CS⁺) with response-independent deliveries of either solid or liquid reinforcers. In Experiment 1 food-deprived rats given a solid-pellet reinforcer differentially tended to sniff, paw, mouth, and bite the CS⁺ lever more often than a lever that was not paired with food (CS⁻), whereas food-deprived rats given a liquid reinforcer tended to differentially sniff, paw, and lick the CS⁺ lever. 23½-hour water-deprived rats given liquid reinforcers showed very little CS⁺ contact. In Experiment 2 increasing the severity of water deprivation from 23½ to 47½ hours significantly increased CS⁺ contact. In Experiment 3, subjects that were simultaneously food and water deprived and given a water reinforcer failed to exhibit differential CS⁺ contact, but subjects that were simultaneously food and water deprived and given a food reinforcer did acquire differential CS⁺-contact behavior. These results suggest that (a) even under a single motivational state the nature of signal-centered behavior can be determined by type of reinforcer, (b) although water reinforcement produces less signal contact than food reinforcement, this can be facilitated with more severe water-deprivation levels, and (c) high CS-contact rates using food reinforcement are not simply a product of reductions in body weight with food deprivation.

Key words: autoshaping, sign-tracking, response topography, reinforcer type, deprivation state, rats

When a localized conditioned stimulus (CS) is paired with a response-independent appetitive reinforcer (unconditioned stimulus, UCS), animals will often learn to approach and contact the CS. This signal-directed behavior was first called autoshaping (Brown & Jenkins, 1968) but has since come to be known also as sign-tracking (Hearst & Jenkins, 1974) or as signal-centered behavior (Jenkins, Barrera, Ireland, & Woodside, 1978). The importance of this phenomenon lay in the fact that it demonstrated that directed skeletal activities could be conditioned by what were ostensibly Pavlovian contingencies, and much of the research in the years following 1968 was geared towards elaborating the associative substructure underlying signal-directed behavior (Hearst, 1979; Schwartz & Gamzu, 1977). However, an understanding of the associative relationships under-

lying signal-centered behavior is only one of the theoretical questions raised by the phenomenon of autoshaping. One could argue that understanding of the performance mechanisms that generate signal-centered behavior is equally important: Organisms not only approach localizable CSs, they also contact them with a range of species-specific behavior. Even in a single species such as the rat, the form of the signal-contact behavior can be quite varied (Davey, Oakley, & Cleland, 1981; Peterson, 1975; Timberlake, in press; Timberlake & Grant, 1975), and a knowledge of the associations underlying autoshaping does not, on its own, provide principles for the translation of learned associations into the signal-centered behavior we observe.

In recent years, at least two performance models have been proposed to account for signal-centered behavior. The earliest of these was a fairly simple adaptation of Pavlov's (1927) principle of stimulus substitution. This account maintains that the CS will act as a substitute or surrogate for the UCS, and an organism will direct towards the CS behavior that is involved in consumption of the UCS.

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Although there is evidence that animals often do treat the CS as they would the UCS (e.g., Jenkins & Moore, 1973; Peterson, 1975), there is also evidence to suggest that behavior not elicited by the UCS can become conditioned to the CS. For instance, reinforcers that require no obvious consummatory response (such as thermal reinforcement and electrical stimulation of the brain) can be used to develop signal-centered behavior (e.g., Peterson, 1975; Wasserman, Hunter, Gutowski, & Bader, 1975; Wilkie & McDonald, 1978). Similarly, dogs will direct species-specific food-soliciting and hunting behavior towards the CS (Jenkins et al., 1978), and rats will direct social behavior towards a conspecific that predicts food (Timberlake, in press; Timberlake & Grant, 1975). None of these are activities required to consume the reinforcer.

These apparent contradictions to stimulus substitution theory have fostered accounts of signal-centered behavior that assume that, because of the association formed between CS and food, the CS comes to "conditionally release" species-specific behavior related to feeding in general (e.g., Jenkins et al., 1978; Timberlake, in press; Williams, 1981; Woodruff & Williams, 1976). Hence, the nature of signal-centered behavior will depend primarily on the organism's deprivation state (e.g., hunger), the variety of species-specific behavior systems controlled by this state and environmental support for them, and *not* necessarily by the specific nature of the reinforcer used to generate learning.

The present study describes three experiments designed to supplement our knowledge of the contribution of deprivation state and reinforcer type to signal-centered topography. The results of such experiments should also help to clarify the effectiveness of both stimulus substitution and conditioned-release hypotheses in predicting the nature of signal-centered behavior.

EXPERIMENT 1

In a preliminary study, Davey, Phillips, and Cleland (1981) found that even under a single motivational state (hunger), some of the signal-centered behavior of rats could be determined by the nature of the reinforcer. In a within-subject design, a liquid reinforcer (condensed milk solution) that was preceded by a retract-

able lever (CS₁) produced significantly more CS-directed licking than a solid reinforcer (food pellet) that was paired with a second retractable lever (CS₂). This result is quite consistent with stimulus substitution theory, but consistent with a conditional release account only if one assumes that different types of reinforcers from a single motivational state can endeavor to selectively release different responses. Experiment 1 is designed to extend the finding of Davey, Phillips, and Cleland (1981) to cover interactions between reinforcer type and motivational state. For instance, a strong version of stimulus substitution theory would predict that the activity required to consume the reinforcer would be the prime determinant of signal-centered activity, whereas the underlying motivational state of the animal would play no direct role. Hence a liquid reinforcer would produce identical CS-directed behavior under conditions of either food or water deprivation.

METHOD

Subjects

The subjects were 16 male Hooded Lister rats approximately 90 days old at the outset of the experiment. All were experimentally naive.

Apparatus

The experiment was conducted in specially built chambers marketed by Campden Instruments Ltd., the internal dimensions of which are reported in Davey, Oakley, and Cleland (1981). Situated in one wall of the chamber was a central reinforcer-tray recess that was 5.0 cm high and 4.0 cm wide. A perspex flap covered this recess which, when pushed, recorded tray entries via a microswitch connected to the top of the flap. Reinforcement was provided either in the form of a single 45-mg food pellet delivered into the reinforcer tray, or as .8 ml of water or a 20% sucrose solution delivered by a dipper mechanism to the floor of the tray. In its normal resting position the dipper was flush with the floor of the tray. All reinforcer deliveries were accompanied by a brief flash of the tray light. Situated 3.0 cm to either side of the tray were two retractable levers. When extended, the levers projected 2.2 cm into the chamber, were 3.8 cm wide, and were located 13.5 cm from the ceiling and 4.0 cm from the grid floor. When retracted they were flush with the wall of the chamber, and when extended into the chamber, lever contacts

could be recorded by means of drinkometer circuits connected to the levers. A lever took approximately .5 sec to extend fully into the chamber, and trials were timed from the onset of insertion to the onset of retraction.

A small houselight situated on the ceiling of the chamber provided general illumination throughout each session. The chambers were housed in sound-attenuating boxes with the front door open to permit observation of the subjects through closed-circuit TV. A closed-circuit TV camera was positioned in front of each box throughout the whole of the experiment, and this relayed TV pictures of the subjects to observers in an adjoining room. The experiment was controlled and data were collected by solid-state logic programming equipment situated in the adjoining room.

Procedure

Before magazine training, eight subjects were placed on a food deprivation schedule that maintained their weight throughout the experiment at 80% of their free-feeding weights. The remaining eight subjects were given a 23½-hr water-deprivation schedule but allowed free access to food in the home cage. Each of these subjects was only given ½-hr access to water daily following each experimental session. All subjects were then divided into four experimental groups each consisting of four rats. The food-deprived subjects were divided into Group F/P (food deprived-pellet reinforcer) and Group F/S (food deprived-sucrose reinforcer), and the water-deprived subjects into Group W/S (water deprived-sucrose reinforcer) and Group W/W (water deprived-water reinforcer).

Magazine training. For the first 5 days each subject received magazine training in which the reinforcer appropriate to its group (food pellet, 20% sucrose solution, or water) was delivered into the reinforcer tray on a variable-time (VT) 100-sec schedule. Each session lasted for approximately 30 min, and at the end of these five sessions all subjects were reliably taking the reinforcer soon after it was delivered.

Autoshaping acquisition. For the following five sessions, reinforcer delivery was paired with each of 25 insertions into the chamber of the left lever (LL). In this phase, LL (CS+) was inserted into the chamber 10 sec prior to reinforcer delivery and was retracted on delivery of the reinforcer (a CS-UCS interval of 10

sec). CS contact had no effect on reinforcer delivery in this or any other phase of the experiment.

Autoshaping differentiation. For the next 10 sessions, pairings of LL (CS+) and reinforcer remained as they were during acquisition, but the right lever (RL) was now inserted into the chamber for 10-sec periods independently of the reinforcer. Right-lever insertions (CS-) were programmed on a VT 100-sec schedule identical to, but independent of, the schedule controlling reinforcer delivery. These programs were arranged such that only one lever could be present in the chamber at any one time.

Autoshaping reversal. A further 10 sessions consisted of reversing the lever-reinforcer relationships such that the RL (now CS+) preceded reinforcer delivery and the LL (now CS-) was inserted into the chamber on an independent VT 100-sec schedule.

Observation procedures. The final session of both the autoshaping differentiation and autoshaping reversal were video recorded and the lever-directed behavior of subjects was analyzed according to preselected topographic categories. These categories were as follows and a number of the important ones are illustrated in Figure 1: *Orienting*: a rapid movement of the head towards the lever without contacting the lever; *sniffing*: moving the nose around the lever with movement of the vibrissae characteristic of sniffing an object; *mouthing*: touching the lever with the mouth and making small nibbling movements; *licking*: contacting the lever with the tongue; *biting*: grasping the lever between the teeth; *pawing*: placing a paw on top of the lever or grasping the lever between the paws. In addition, note was also made during the lever presentations of two reinforcer-tray directed responses; *tray entry*: entering the tray, and *tray orienting*: a response similar to lever orienting but directed towards the tray without actually entering it. Each category was scored on the basis of the percentage of trials on which at least one instance of the response occurred. Although the observational data described in the results section represent the observations of one observer, as a test of reliability three observers independently scored the responses for one recorded session with 85% agreement among them, suggesting that the selected categories were reliable and objectively definable.

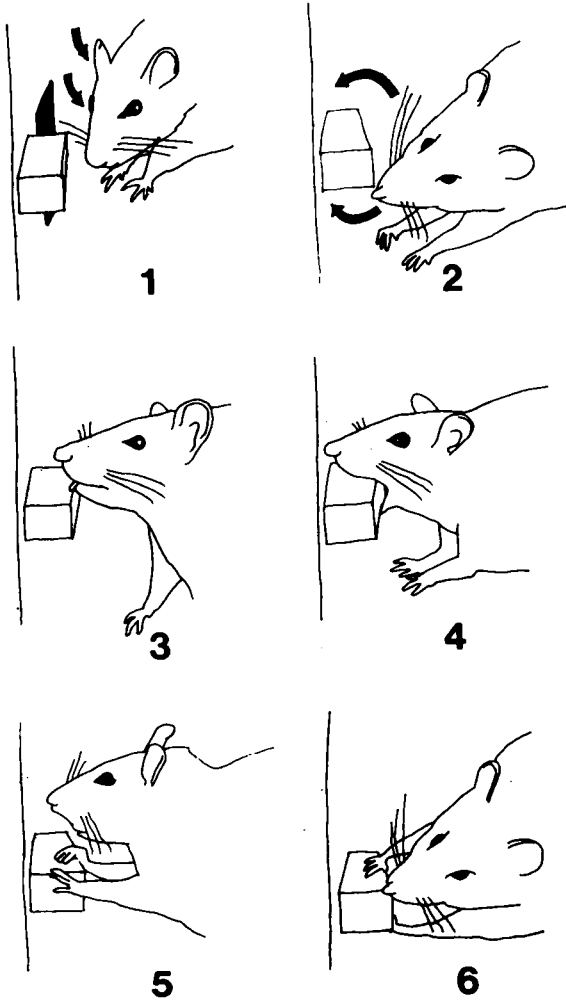


Fig. 1. Illustrations of the response topography categories used in Experiment 1. (1) Orient, (2) sniffing, (3) licking, (4) biting, and finally two distinctive methods of pawing the lever (5) paw "support"—resting paws on the lever, and (6) paw "grip"—gripping the lever between the paws as in holding an object (see text for further explanation).

RESULTS

Table 1 shows the mean number of contacts to CS⁺ and CS⁻ for the last three sessions of differentiation and reversal. This shows that for the two food-deprived groups (F/P and F/S), subjects primarily contacted the lever paired with the reinforcer and switched their approach and contact tendencies when the predictive significance of the levers was reversed. Wilcoxon tests on contact rates indicated greater responding to CS⁺ than CS⁻ at the end of both differentiation and reversal for the food-deprived groups (F/P and F/S combined) (Diff, $T = 0$, $p < .01$; Rev, $T = 0$, $p < .01$).

However, the water-deprived subjects (W/S and W/W combined) showed no differential tendency to contact CS⁺ rather than CS⁻, either at the end of differentiation ($T = 6$, $p > .05$) or reversal ($T = 16$, $p > .05$). Page's L-test for trend revealed no upward or downward trend in rate of CS⁺ contact for any of the water- or food-deprived groups over the last five sessions of both differentiation and reversal, suggesting that performance had reached asymptote during these periods of training.

When rate of CS⁺-contact data from the last three sessions of differentiation and reversal are compounded, a Kruskal-Wallis between-groups analysis was significant [$H(3) = 11.84$, $p < .01$]. Furthermore, Dunn's multiple comparisons test showed that Group W/W made significantly fewer contacts than either of Groups F/P ($|D| = 9.25$, $p < .05$) or F/S ($|D| = 9.25$, $p < .05$) but was not significantly different from Group W/S ($|D| = 2.5$, $p > .05$). In addition no significant difference was observed between Groups F/S and F/P ($|D| = 0$, $p > .05$). Although Group W/S exhibited a lower CS⁺-contact rate than food-deprived groups, comparison between W/S and F/S ($|D| = 6.75$, $p > .05$), and W/S and F/P ($|D| = 6.75$, $p > .05$) just failed to reach statistical significance at the 5% level.

Table 1 also shows the mean number of tray entries during CS⁺ and CS⁻ for sessions at the end of differentiation and reversal. From these data only Groups W/W and W/S exhibited a consistently higher rate of tray entry during CS⁺ than during CS⁻, both at the end of differentiation ($T = 0$, $p < .01$) and reversal ($T = 0$, $p < .01$). There were no significant differences between groups in rate of tray entry [$H(3) = 3.596$, $p > .05$].

Table 2 catalogs the results of the observational procedures by presenting the percentage of CS⁺ and CS⁻ trials on which a particular topography occurred. These results are summarized in Figure 2 where differential CS⁺ response tendencies are indicated by subtracting CS⁻ scores from CS⁺ scores. Whereas all groups equally show a differential tendency to tray entry during CS⁺, the topography of CS⁺-directed activities differs between groups.

Three of the four subjects in Group F/P exhibited a differential tendency to mouth, bite, and paw the CS⁺, one subject showed a marginal tendency to lick the CS⁺, and all four subjects differentially sniffed CS⁺. In con-

Table 1

Mean contacts/trial and tray entries/trial to CS⁺ and CS⁻ for all groups in Experiment 1. Data are means of the last three sessions for each phase.

Group	Subjects	Rate of Contact		Rate of Tray Entry		Experimental Phase
		CS ⁺	CS ⁻	CS ⁺	CS ⁻	
F/P	R181	6.37	0.47	0.17	0.20	Differentiation
	R182	0.10	0.03	0.83	0.17	
	R183	4.07	1.30	0.10	0.73	
	R184	3.47	0.10	0.10	0.83	
	MEAN ± SEM	3.50 ± 1.30	0.48 ± 0.29	0.30 ± 0.18	0.48 ± 0.18	
F/S	R181	6.22	2.92	0.45	0.23	Reversal
	R182	0.65	0.09	4.46	0.98	
	R183	3.07	3.00	0.05	0.15	
	R184	0.86	0.60	0.53	0.41	
	Mean ± SEM	2.40 ± 1.45	1.65 ± 0.76	1.37 ± 1.04	0.44 ± 0.19	
W/S	R185	4.30	1.00	1.40	1.67	Differentiation
	R186	0.96	0.10	2.73	2.13	
	R187	2.00	0.17	1.43	0.40	
	R188	0.57	0.27	2.57	2.00	
	MEAN ± SEM	1.74 ± 0.95	0.39 ± 0.21	2.03 ± 0.36	1.40 ± 0.41	
W/W	R185	9.89	0.35	0.21	0.65	Reversal
	R186	0.28	0.03	0.18	0.18	
	R187	3.40	1.07	0.83	0.31	
	R188	5.23	1.03	0.89	1.31	
	MEAN ± SEM	4.65 ± 2.05	0.62 ± 0.26	0.53 ± 0.19	0.61 ± 0.26	
F/S	R189	0.10	0.03	1.73	0.63	Differentiation
	R190	0.13	0.03	0.83	0.53	
	R191	0.17	0.33	0.06	0.00	
	R192	0.23	0.03	0.80	0.50	
	MEAN ± SEM	0.16 ± 0.03	0.11 ± 0.08	0.64 ± 0.38	0.42 ± 0.14	
W/S	R189	0.36	0.31	2.56	1.02	Reversal
	R190	0.00	0.10	1.76	1.11	
	R191	0.72	0.42	0.06	0.00	
	R192	0.61	0.12	0.84	0.48	
	MEAN ± SEM	0.42 ± 0.16	0.24 ± 0.08	1.16 ± 0.60	0.65 ± 0.26	
F/S	R193	0.05	0.08	1.24	0.42	Differentiation
	R194	0.07	0.00	2.09	1.16	
	R213	0.45	0.18	2.67	1.09	
	R214	4.66	0.06	2.84	1.20	
	MEAN ± SEM	1.31 ± 1.12	0.06 ± 0.04	2.21 ± 0.36	0.97 ± 0.19	
W/W	R193	0.00	0.08	0.82	0.79	Reversal
	R194	0.01	0.15	2.49	1.63	
	R213	0.37	0.34	2.39	1.32	
	R214	0.09	0.78	1.33	0.51	
	MEAN ± SEM	0.12 ± 0.09	0.34 ± 0.16	1.76 ± 0.41	1.06 ± 0.26	

trast, three of the four subjects in Group F/S showed a differential tendency to lick CS⁺, and two subjects showed differential pawing to CS⁺. None of the subjects in Group F/P exhibited CS⁺-directed biting, and only one subject exhibited mouthing of the CS⁺ and this on a small minority of trials. All subjects in

Group F/S differentially sniffed CS⁺. Water-deprived subjects (Groups W/S and W/W) did differentially sniff CS⁺ but generally failed to exhibit any other kinds of CS⁺-directed behavior (other than simple CS⁺ orienting). One subject in Group W/W (R214) did show pawing of CS⁺ on 27.5% of trials, but these ap-

Table 2

Mean percentage trials with at least one occurrence of a particular response topography in Experiment 1. Data are calculated by combining observations from the last session of differentiation and reversal.

	Subjects	Tray Entry	Tray Orient	Latency	Orient	Sniff	Lick	Mouth	Bite	Paw
F/P	R181	0.0	12.5	0.7	10.0	62.5	2.5	90.0	85.0	92.5
	CS, R182	85.0	85.0	0.9	87.5	52.5	0.0	0.0	0.0	0.0
	R183	5.0	15.0	1.2	0.0	32.5	60.0	75.0	50.0	100.0
	R184	47.5	47.5	0.6	47.5	80.0	0.0	52.5	47.5	57.5
	MEAN/ SEM	34.4 ±15.6	40.0 ±14.0	0.9 ±0.1	36.3 ±15.9	56.9 ±11.8	15.6 ±11.2	54.4 ±16.0	45.6 ±16.0	62.5 ±16.5
	R181	10.0	30.0		40.0	57.5	5.0	12.5	10.0	15.0
	CS, R182	17.5	62.5		75.0	7.5	0.0	0.0	0.0	0.0
	R183	2.5	25.0		22.5	30.0	52.5	32.5	10.0	75.0
	R184	52.5	52.5		67.5	25.0	10.0	10.0	0.0	15.0
	MEAN/ SEM	20.6 ±8.2	42.5 ±6.7		51.3 ±10.0	30.0 ±9.7	16.9 ±11.5	13.8 ±4.9	5.0 ±2.8	26.3 ±12.2
F/S	R185	45.0	27.5	0.4	37.5	87.5	37.5	5.0	0.0	60.0
	CS, R186	62.5	65.0	0.3	72.5	27.5	0.0	0.0	0.0	0.0
	R187	70.0	50.0	0.7	42.5	90.0	25.0	0.0	0.0	25.0
	R188	67.5	77.5	0.5	42.5	95.0	32.5	0.0	0.0	0.0
	MEAN/ SEM	61.3 ±6.4	55.0 ±8.6	0.5 ±0.1	48.8 ±8.2	75.0 ±10.6	23.8 ±9.1	1.2 ±1.2	0.0 ±0.0	21.3 ±11.2
	R185	62.5	25.0		25.0	20.0	0.0	0.0	0.0	0.0
	CS, R186	35.0	62.5		57.5	22.5	0.0	0.0	0.0	0.0
	R187	17.5	52.5		32.5	40.0	0.0	0.0	0.0	2.5
	R188	67.5	35.0		35.0	47.5	17.5	0.0	0.0	0.0
	MEAN/ SEM	45.6 ±10.0	43.8 ±8.6		37.5 ±8.1	33.8 ±7.7	4.4 ±3.7	0.0 ±0.0	0.0 ±0.0	0.6 ±0.6
W/S	R189	82.5	2.5	0.3	60.0	67.5	0.0	0.0	0.0	0.0
	CS, R190	67.5	47.5	0.6	85.0	52.5	0.0	0.0	0.0	0.0
	R191	0.0	25.0	0.7	30.0	22.5	2.5	0.0	0.0	0.0
	R192	35.0	72.5	1.1	55.0	60.0	0.0	0.0	0.0	0.0
	MEAN/ SEM	46.3 ±12.6	36.9 ±9.9	0.7 ±0.2	57.5 ±8.6	50.6 ±8.0	0.6 ±0.6	0.0 ±0.0	0.0 ±0.0	0.0 ±0.0
	R189	45.0	20.0		37.5	15.0	0.0	0.0	0.0	0.0
	CS, R190	62.5	47.5		55.0	12.5	2.5	0.0	0.0	0.0
	R191	0.0	22.5		15.0	22.5	2.5	0.0	0.0	2.5
	R192	30.0	52.5		55.0	15.0	0.0	0.0	0.0	0.0
	MEAN/ SEM	34.4 ±9.4	35.6 ±6.2		40.6 ±9.8	16.3 ±12.7	1.3 ±0.8	0.0 ±0.0	0.0 ±0.0	0.6 ±0.6
W/W	R193	90.0	17.5	0.6	90.0	82.5	2.5	0.0	0.0	0.0
	CS, R194	97.5	15.0	0.4	72.5	30.0	0.0	0.0	0.0	2.5
	R213	90.0	40.0	0.2	82.5	67.5	0.0	0.0	0.0	0.0
	R214	70.0	65.0	0.8	72.5	47.5	0.0	2.5	0.0	27.5
	MEAN/ SEM	86.9 ±4.5	34.4 ±11.1	0.5 ±0.1	79.4 ±4.6	56.9 ±11.1	0.6 ±0.6	0.6 ±0.6	0.0 ±0.0	7.5 ±6.8
	R193	62.5	32.5		30.0	5.0	2.5	0.0	0.0	0.0
	CS, R194	97.5	27.5		25.0	7.5	2.5	0.0	0.0	5.0
	R213	72.5	30.0		35.0	15.0	0.0	0.0	0.0	0.0
	R214	45.0	62.5		35.0	15.0	0.0	0.0	0.0	0.0
	MEAN/ SEM	69.4 ±9.6	38.1 ±7.3		31.3 ±6.1	10.6 ±2.9	1.3 ±2.9	0.0 ±0.0	0.0 ±0.0	1.2 ±1.2

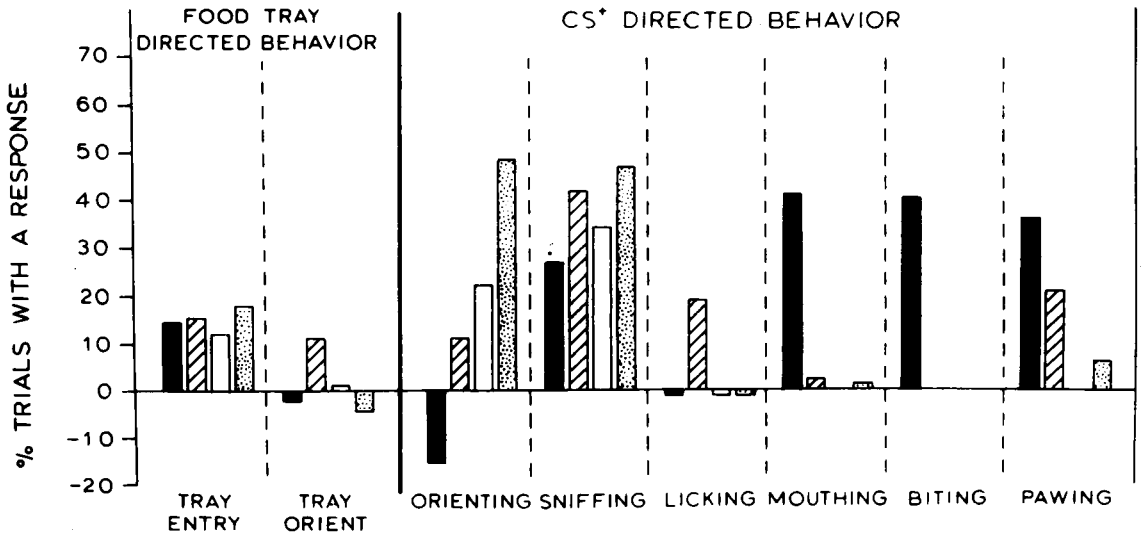


Fig. 2. Differential CS⁺-directed behavior for all four groups of subjects. Group F/P = filled bars, Group F/S = hatched bars, Group W/S-unfilled bars, Group W/W = stippled bars. Differential scores are calculated by subtracting mean percentage trials with a response to CS⁻ from mean percentage trials with a response to CS⁺. Positive scores denote a differential tendency to emit the response during CS⁺; negative scores show a tendency to emit the response during CS⁻. Data are pooled and calculated from observations made on the last session of differentiation and the last session of reversal.

peared to be accidental contacts incurred while scrabbling to push open the reinforcer-tray flap.

A record was also taken of the latency with which subjects entered the reinforcer tray following CS⁺ lever retraction (third column, Table 2). There were no statistically significant differences in these latencies among any of the groups.

DISCUSSION

The results of Experiment 1 indicate that in an autoshaping procedure (a) water-deprived rats goal-track (enter the food tray during CS⁺) with the same probability and at the same rate as food-deprived rats; (b) food-deprived rats exhibit differential sign-tracking (CS⁺ contact), whereas water-deprived rats do not, and (c) the nature of CS⁺-directed behavior depends on both the deprivation state and the type of reinforcer. Food-deprived subjects reinforced with a solid food pellet showed a differential tendency to orient towards, sniff, paw, mouth, and bite the CS⁺ lever, while food-deprived subjects reinforced with sucrose solution showed a differential tendency to orient towards, sniff, paw, and lick the lever. Water-deprived subjects primarily directed

orienting or sniffing movements toward the CS⁺ regardless of reinforcer type (sucrose or water).

First, the results from the food-deprived subjects are consistent with those of Davey, Phillips, and Cleland (1981) in indicating that the form of signal-centered behavior can be influenced by reinforcer type, even under a single motivational state. Moreover, those responses that were differentially determined by reinforcer type were similar to the responses required to consume the reinforcer. In the majority of our casual and systematic observations of the food-deprived subjects, rats consumed the liquid reinforcer by poking their heads into the food tray and licking up the milk, and the solid pellet was consumed by seizing it directly with the mouth and chewing it. Such evidence might be considered as consistent with a stimulus substitution account of signal-centered behavior.

Second, deprivation state also influenced aspects of signal-centered behavior. Although rate of goal-tracking and reinforcer-retrieval latencies were similar across all groups, the food-deprived subjects showed a significantly greater tendency to contact CS⁺ than the water-deprived subjects. Whereas food-deprived subjects generally engaged in vigorous

CS+ contact, water-deprived subjects clearly did not.

One reason for differences in CS+ approach and contact tendency between subjects under the two deprivation states could be related to the problem of equating deprivation—and hence motivation—under the two deprivation states. Although 23½-hr water deprivation may be sufficient to support goal-directed behavior at similar levels to the food-deprivation schedule, it may be insufficient to generate substantial signal-directed behavior. Experiment 2 investigates this possibility by comparing sign-tracking and goal-tracking under two different water deprivation levels.

EXPERIMENT 2

In a one-lever autoshaping procedure, this experiment investigates the behavior of rats under either a 23½-hr water-deprivation schedule (as used in Experiment 1) or a more severe 47½-hr water-deprivation schedule.

METHOD

Subjects

The subjects were seven male Hooded Lister rats approximately 90 days old at the outset of the experiment. All were experimentally naive.

Apparatus

The experimental chambers, programming and recording equipment, and observational apparatus were identical to those used in Experiment 1.

Procedure

Before magazine training the seven subjects were divided into two groups. One group of four subjects was put on a 23½-hr water-deprivation schedule (nominally Group 24-hr), where each subject was given only ½-hr access to water every 23½ hours. The remaining group of three subjects was put on a 47½-hr water deprivation schedule (nominally Group 48-hr) and was allowed ½-hr access to water every two days. Experimental sessions were conducted every 2 days, and subjects in Group 48-hr received their ½-hr access to water immediately after these sessions. Group 24-hr subjects also received their ½-hr access to water following experimental sessions and also at a similar time on the alternate days when

no sessions were conducted. All subjects had free food available in the home cage.

Magazine training. As in Experiment 1 all subjects received five sessions of magazine training in which .8-ml water deliveries were presented on a VT 100-sec schedule.

Autoshaping. For the following 10 sessions, water delivery was paired with each of 25 insertions into the chamber of the left lever (CS+). The lever was present for 10 sec and was retracted at the moment of water delivery. On Session 10 of this phase, all subjects were video recorded and their behavior analyzed according to the response topographies outlined in Experiment 1.

RESULTS

Table 3 shows CS+ contacts, tray entries, and tray-entry latencies for the two groups. Whereas CS+ rates were relatively low for Group 24-hr ($.07 \pm .04$ contacts/trial) and stood at rates similar to those observed in water-deprived subjects in Experiment 1, CS+ contact rates for Group 48-hr were significantly higher ($1.40 \pm .50$ contacts/trial; $U = 0, p < .05$). There was no significant difference between the two groups on CS+ tray-entry rate ($U = 6, p > .05$) or reinforcer-retrieval latencies ($U = 5, p > .05$).

Figure 3 illustrates the response topography profiles for the two groups, and Table 4 shows the individual subject profiles within each group. The main points to indicate here are (a) Group 48-hr subjects sniffed more but oriented less towards the lever, and (b) Group

Table 3

Mean rate of CS+ contact/trial, CS+ tray entry/trial, and tray entry latency following CS+ in Experiment 2. Data are taken from the last three sessions.

Subject Number	Rate of CS+ Contacts	Rate of Tray Entry During CS+	Tray Entry Latency (secs)	Deprivation Group
R273	0.06	1.48	0.56	24 HR
R275	0.03	3.08	0.40	
R271	0.18	2.48	0.18	
R278	0.00	1.29	0.76	
MEAN	0.07	2.08	0.48	
±SEM	0.04	0.43	0.13	
R221	0.60	2.26	0.38	48 HR
R225	1.31	1.92	0.44	
R227	2.28	1.56	1.73	
MEAN	1.40	1.90	0.90	
±SEM	0.50	0.20	0.50	

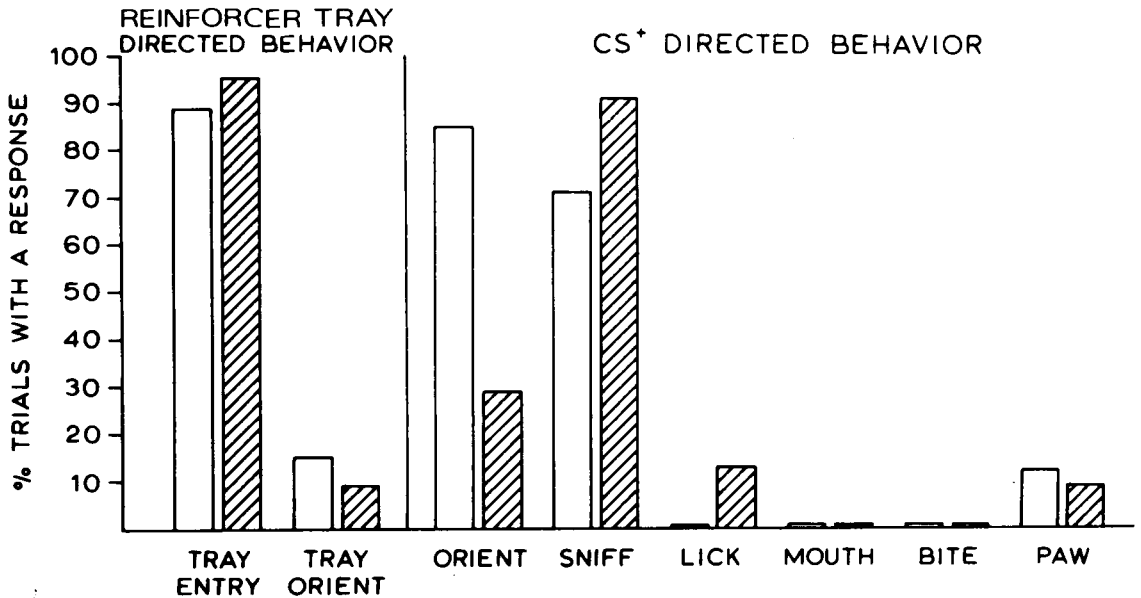


Fig. 3. Mean percentage trials with at least one occurrence of a particular response topography. Unfilled bars = 24-hr Group, hatched bars = 48-hr Group. Data are taken from the final session.

48-hr subjects also showed some CS⁺-directed licking (two out of three subjects), whereas no CS⁺-directed licking was observed in the 24-hr group.

DISCUSSION

These results suggest that whereas goal-directed behavior (i.e., goal-tracking and reinforcer-retrieval latency) may have reached an asymptote with water deprivation levels of 23½ hours or less, signal-directed behavior can be facilitated by increases in deprivation be-

yond this level. Hence, the failure to observe substantial CS⁺ contact in water-deprived subjects in Experiment 1 may be a result of inadequate deprivation. Nevertheless, even with water deprivation as severe as 47½ hours, signal-directed behavior in Group 48-hr still did not display the vigor exhibited by Groups F/P and F/S in Experiment 1. Increased deprivation from 23½ to 47½ hours appeared to substitute orienting reactions with active exploratory "sniffing" responses, and the increase in CS⁺ contact rate was mainly a result of nose

Table 4

Percentage trials with at least one occurrence of a particular response topography in Experiment 2. Data are taken from the final session.

Subjects	Food Tray Directed Activities		CS Directed Activities						Group
	Tray Entry	Tray Orient	Orient	Sniff	Lick	Mouth	Bite	Paw	
R273	95	10	90	90	0	0	0	0	24 HR
R275	95	0	80	35	0	0	0	0	
R271	100	15	80	70	0	0	0	0	
R278	65	35	90	90	0	5	0	55	
MEAN	88.8	15.0	85.0	71.3	0.0	1.3	0.0	13.8	
±SEM	8.0	7.4	2.9	13.0	0.0	1.3	0.0	13.8	
R221	100	0	24	96	0	0	0	4	48 HR
R225	100	8	16	88	20	0	0	4	
R227	88	20	40	88	16	0	0	16	
MEAN	96.0	9.3	26.7	90.7	12.0	0.0	0.0	8.0	
±SEM	4.0	5.8	7.0	2.7	6.1	0.0	0.0	4.0	

contacts with the lever. Only a small percentage of trials exhibited the oral and manual responses characteristic of Groups F/P and F/S in Experiment 1, but those oral responses that did occur (licking) were consistent with the finding in Experiment 1 that oral responses differentially emitted to CS⁺ were characteristic of UCS consummatory behavior.

Despite the obvious problems involved in comparing deprivation levels across motivational states, it does seem curious that such severe water deprivation is necessary in the rat to incur reasonable levels of CS contact—especially when relatively mild states of food deprivation can induce high CS contact rates (e.g., Boakes, 1977). The reasons why CS-contact behavior is difficult to obtain with water reinforcement are unclear; however, a number of possibilities suggest themselves: (a) In accordance with the conditional release account of signal-centered behavior, CS-UCS episodes may “conditionally release” behavior systems related generally to the reinforced motivational state. Thus, autoshaping with food and water reinforcers may release quite different CS-directed responses, which in the case of water reinforcement might be inappropriate for CS contact; (b) schedule parameters suitable for producing vigorous CS-directed behavior with food reinforcement may be inappropriate for generating sign-tracking with water reinforcement. This possibility awaits parametric studies manipulating CS and inter-trial interval (ITI) durations; and (c) vigorous CS contact might be unique to food reinforcement, not because CS-food episodes release CS-directed behavior systems, but because hunger or sizable body-weight reductions have unique arousal properties that are manifest in increased exploratory behavior and facilitated orienting responses (e.g., Bolles & Petrinovich, 1956; Konorski, 1967). Experiment 3 investigates some aspects of the last possibility by manipulating combinations of deprivation states and reinforcers.

EXPERIMENT 3

In a series of early studies comparing food and water reinforcement, Petrinovich and Bolles (1954) found that water-reinforced rats learned a position habit more quickly than food-deprived rats, whereas food-deprived rats mastered a response alternation task more rap-

idly than water-deprived rats. In a later study, however, Bolles and Petrinovich (1956) found that this differential effect of reinforcer type was not a difference in the motivational state or the nature of the reinforcer per se but in overall deprivation level. They discovered that response alternation was generated in rats suffering reduced body weight regardless of the reinforcer, whereas those whose body weight was normal did not exhibit a tendency to alternate. Thus, rats who were both thirsty and hungry readily learned alternation behavior using a water reinforcer. In the autoshaping procedure used in the present series of experiments, hungry rats that both sign-track and goal-track do so by rapidly switching from lever to food tray a number of times during a single trial; they may do this because their reduced body weight facilitates alternation. Furthermore, since water and food deprivation are not truly independent and water deprivation is normally accompanied by loss of body weight, the production of increased levels of CS contact with increased water deprivation in Experiment 2 may be mediated by the effect of this manipulation on body weight rather than by the increased need for water per se.

METHOD

Subjects

The subjects were eight male Hooded Lister rats, all of whom had participated as water-deprived subjects in Experiment 1.

Apparatus

The experimental chambers and programming and recording equipment were identical to those used in Experiment 1.

Procedure

All subjects had previously received autoshaping training using the two-lever procedure in Experiment 1. At the beginning of Experiment 3, the animals remained in their Groups W/S and W/W and both groups were 23½-hr water deprived. Experiment 3 consisted of three phases.

Phase 1 (Thirsty). Group W/S received 10 sessions of differential autoshaping in which the CS⁺ lever preceded delivery of .8 ml of 20% sucrose solution. The CS⁻ lever was inserted independently into the chamber for the same duration and with the same frequency as CS⁺. ITI (100 sec) and CS durations (10 sec)

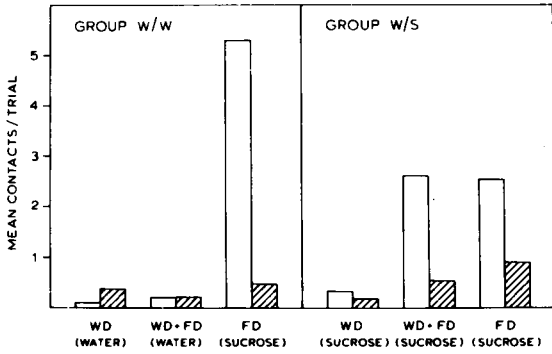


Fig. 4. Mean contacts/trial to CS+ (unfilled bars) and CS- (hatched bars) for both groups at the end of each phase of Experiment 3. WD = water deprivation, FD = food deprivation. In brackets beneath each deprivation state is the type of reinforcer used in that phase of the experiment. Data are means taken from the last three sessions of each phase.

were identical to those used in Experiment 1. Group W/W received 10 sessions of identical training except that CS+ was paired with delivery of .8 ml water. A session lasted for 25 CS+ presentations.

Phase 2 (Hungry/Thirsty). Both Groups W/W and W/S were given a further 10 sessions on the differential autoshaping procedure with the reinforcer type they received in Phase 1. However, during Phase 2 both groups were maintained on their 23½-hr water-deprivation schedule and also made hungry by be-

ing subjected to a food-deprivation schedule that reduced their weight to 80% of their body weight measured at the end of Phase 1.

Phase 3 (Hungry). For the final 10 sessions all subjects were taken off the water-deprivation schedule and given free access to water in the home cages. However, they were all maintained at 80% body weight. During this final phase all subjects were given 20% sucrose solution as the reinforcer.

RESULTS

Figure 4 shows CS+ and CS- contact rates for both groups at the end of each phase of the experiment, and Table 5 displays the data for individual subjects. At the end of Phase 1 neither Group W/W nor W/S was contacting CS+ more frequently than CS-. This result is consistent with the performance of these water-deprived subjects in Experiment 1. However, at the end of Phase 2, during which both groups were made thirsty and hungry, all subjects in Group W/S showed differential responding to CS+ ($T = 0, p < .05$), while subjects in Group W/W did not ($T = 2, p > .05$). Similarly, rate of CS+ contact in Group W/S was significantly higher than that in Group W/W ($U = 0, p < 0.5$), whereas rate of CS- contact did not differ between groups ($U = 3.5, p > .05$). At the end of Phase 3, where all subjects received autoshaping training with a food reinforcer under food-deprivation conditions alone, both groups showed differential contact rates to CS+ ($T = 0, p < .02$). There was no difference in contact rate between groups at the end of this phase ($U = 7, p > .05$).

Table 5

Mean contacts/trial to CS+ and CS- for both groups at the end of each phase of Experiment 3. Data are means from the last three sessions of each phase. (W = water reinforcer; S = sucrose reinforcer; WD = water deprived; FD = food deprived)

Experimental Group	Mean Contacts/Trial for Each Subject				Experimental Group ± Means Sem	
	R213	R194	R214	R193		
WD/W	CS+	0.34	0.10	0.08	0.00	0.13 0.08
	CS-	0.34	0.15	0.90	0.08	0.37 0.19
WD + FD/W	CS+	0.29	0.15	0.00	0.36	0.20 0.08
	CS-	0.12	0.42	0.03	0.30	0.22 0.09
FD/S	CS+	0.30	6.97	13.23	0.56	5.27 3.07
	CS-	0.20	0.68	0.68	0.17	0.43 0.15
		R191	R192	R189	R190	
WD/S	CS+	0.71	0.60	0.00	0.08	0.35 0.18
	CS-	0.42	0.12	0.02	0.18	0.19 0.09
WD + FD/S	CS+	4.75	0.67	4.98	0.38	2.70 1.25
	CS-	1.14	0.42	0.17	0.33	0.52 0.22
FD/S	CS+	5.46	1.03	3.69	0.32	2.63 1.19
	CS-	1.52	0.18	1.76	0.06	0.88 0.44

Table 6 shows the individual tray-entry data during CS+ and CS- at the end of each phase of Experiment 3. Group W/W exhibited a higher tray-entry rate during CS+ and CS- for all three phases of the experiment ($T = 0, p < .05$) and for Group W/S mean tray-entry rate during CS+ was higher than that during CS- for Phases 1 and 3 ($T = 0, p < .05$).

Finally, there was no statistical difference between Groups W/W and W/S in rate of CS+ tray entry throughout all phases of the experiment ($U = 5, 7, 3; p > .05$ in all cases).

DISCUSSION

To summarize the results of Experiment 3: (a) subjects that were simultaneously food and water deprived and given a water reinforcer

Table 6

Mean tray entries/trial during CS⁺ and CS⁻ for both groups at the end of each phase of Experiment 3. Data are means for the last three sessions of each phase. (W = water reinforcer; S = sucrose reinforcer; WD = water deprived; FD = food deprived)

Experimental Group	Mean Tray Entries/Trial For Each Subject				Experimental Group Means \pm Sem		
	R213	R194	R214	R193			
WD/W	CS ⁺	2.44	2.45	1.32	0.81	1.76	0.41
	CS ⁻	1.32	1.65	0.55	0.79	1.08	0.25
WD + FD/W	CS ⁺	2.21	1.60	1.39	1.34	1.64	0.20
	CS ⁻	0.48	1.17	0.65	0.93	0.81	0.15
FD/S	CS ⁺	3.58	1.89	2.20	3.01	2.67	0.38
	CS ⁻	1.70	1.62	1.57	1.02	1.48	0.15
		R191	R192	R189	R190		
WD/S	CS ⁺	0.01	0.53	2.69	0.92	1.04	0.58
	CS ⁻	0.0	0.46	1.02	0.85	0.58	0.23
WD + FD/S	CS ⁺	2.31	1.79	0.77	0.70	1.39	0.39
	CS ⁻	3.09	1.12	1.55	0.44	1.55	0.56
FD/S	CS ⁺	1.86	3.04	0.38	0.59	1.47	0.62
	CS ⁻	1.67	0.52	0.20	0.58	0.74	0.32

failed to exhibit differential CS⁺ contact, whereas subjects that were simultaneously food and water deprived but given a food reinforcer *did* acquire differential sign-tracking; (b) all subjects demonstrated their ability to acquire differential sign-tracking when given a food reinforcer under conditions of food reinforcement, and (c) neither deprivation state, combination of deprivation states, nor reinforcer type had any significant effect on rate of tray entry during CS⁺.

These data suggest that the appearance of signal-directed behavior is not simply a function of reduced body weight producing elevated states of arousal that facilitate CS contact, nor does it support the supposition that food deprivation might facilitate alternation between CS and food-tray locations (cf. Bolles & Petrinovich, 1956). Furthermore, food deprivation alone is not sufficient to generate contact with a reinforced CS. This seems to suggest that the motivational factor that produces strong CS⁺-directed responding under conditions of food deprivation is food reinforcement or food delivery itself.

GENERAL DISCUSSION

This series of experiments has found that (1) even under a single motivational state (food

deprivation) the nature of signal-centered behavior can be determined by type of reinforcer (i.e., liquid or solid); (2) although water reinforcement produces less signal contact than food reinforcement, this can be facilitated with more severe water-deprivation levels; and (3) high CS-contact rates using food reinforcement are not simply a product of reduced body weight facilitating CS contact.

The first finding is clearly consistent with stimulus substitution or surrogation accounts of signal-centered behavior. The differential effects of reinforcer type appeared to induce the rats to behave towards the CS⁺ lever as though it were the oral stimulus of solid or liquid food. This result is consistent with the findings of Jenkins and Moore (1973) on the form of autoshaped key pecking in pigeons to food and water reinforcers, and also with the results of Hull (1977), who found that the topography of instrumental lever pressing in rats resembled the response necessary for consuming the reinforcer (1977, Experiment 4). However, if a conditioned-release view is to account for the results of Experiment 1, it must postulate differing responses capable of release by differing reinforcer types, even under a single motivational system such as food deprivation. This could be achieved by suggesting that oral cues that identify food as either solid or liquid may elicit fixed patterns of appropriate consummatory behavior. The CS then comes to elicit these consummatory activities through its association with these oral cues (cf. Williams, 1981).

At first glance, the findings from Experiments 1 and 3, that identical reinforcers (i.e., sucrose) produce differing conditioned response topographies depending on the deprivation state (food vs. water deprivation), seem to be contrary to predictions from stimulus-substitution theory. Presumably this account would suggest that signal-directed behavior should be determined primarily by the nature of the activity required to consume the reinforcer rather than by deprivation state. Nevertheless, a stimulus-substitution interpretation could be salvaged if deprivation state were found to influence the unconditioned response (UCR) topography—a possibility that we have not systematically investigated. This possibility could even be extended to cover the results of Experiment 2: Level of deprivation might also influence UCR topography such that high de-

privation levels produce UCRs which when conditioned are more conducive to CS contact than lower deprivation levels.

Finally, this study adds another factor to the list of variables known to influence signal-directed response topography. It was already known that topography could be influenced by (a) the nature of the CS (Timberlake, in press; Timberlake & Grant, 1975), (b) the nature of the reinforcers from differing motivational states (Jenkins & Moore, 1973; Wasserman et al., 1975), (c) devaluation of the reinforcer used to generate sign-tracking (Cleland & Davey, in press), and (d) food satiation (Cleland & Davey, in press); it now appears that topography can be influenced by the nature of the reinforcer even when this is varied within a single motivational state. Although most of these facts can be reconciled with a stimulus-substitution account of signal-centered behavior, it is clear that stimulus substitution cannot provide a full account of signal-directed response topography. In particular, it is clear that the nature of the CS as well as the nature of the UCR can influence conditioned-response topography (cf. Dickinson & Mackintosh, 1978). In the light of these findings, it might be more valuable to attempt to integrate those data that specifically support stimulus-substitution accounts into a more precisely formulated conditioned-release view of autoshaping (cf. Cleland & Davey, in press; Timberlake, in press), the latter being an account that can accommodate interactions between the nature of the CS and CR topography. In the long term, this would seem a more fruitful heuristic approach than purely designing studies to test the relative applicability of both stimulus-substitution and conditioned-release accounts of signal-centered behavior.

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