Fig. 2. Shock-rate acceleration ratios for individual Ss and groups as a function of the punishment ratio.

punishment on avoidance responding requires parametric examination of avoidance schedule parameters as well as punishment schedules parameters.

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suppression. The data suggest that rats initially exposed to low ratios will show more suppression at higher ratios than will rats initially exposed to the higher ratios.

The effects on shock rate (Fig. 2) parallel those on response rate. FR values which produced response rate suppression also produced shock rate acceleration. This indicates that the effect of the punishment shocks was not to merely increase the efficiency of responding. Although there was a tendency for decreases in response rate to be greater than increases in shock rate, there are a few instances where substantial increases in shock rate are found without any noticeable decrease in response rate. This reflects a shift to a less efficient pattern of responding.

DISCUSSION

Punishment of avoidance results in an avoidance schedule in which the S-S parameter is kept constant while the R-S parameter at times becomes zero. Under such conditions, responding serves to increase the shock density of the situation. It is not surprising that responses subsequently become less probable or that the decrease in response probability is related to the degree to which responses increase shock density.

The responses which do not occur (i.e., are "suppressed" by the punishment contingency) are not randomly distributed. Both McIntire et al (1968) and Sandler et al (1966b) found that responses tended to occur in bursts following a shock. Such responses are commonly attributed to the escape training implicit or explicit in the early avoidance training and to a resultant eliciting property of the shock. Bursting, however, is inefficient, and in a ratio punishment situation, results in maximum increase in shock density. This suggests that

if the change in shock density effected by the punishment contingency were the only controlling factor, bursting should be eliminated rather than maintained or enhanced. One factor which might account for the maintenance of bursting is the use of short S-S intervals and long R-S intervals. While bursting is inefficient relative to evenly spaced responding at the same overall rate, a response during the S-S interval produces a greater and more immediate reduction in shock density than a response in the R-S interval.

This type of approach makes it clear that a meaningful statement of the effects of

Lesion effects on visual cliff performance in the rat¹

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centerboard capable of inducing descents in the other Ss.

Light- and dark-reared rats received ablations of the superior colliculus, striate cortex, or both areas, and were later tested on a visual cliff. No significant difference in side preference was recorded between groups. Significantly more "no-descents" were recorded for the group undergoing the combined lesions, despite the use of a

Depth discrimination, as indicated by visual-cliff performance, is present in many organisms at birth or within a short time thereafter (Walk & Gibson, 1961). Behavioral studies have indicated both innate and learned components to visual discrimination (e.g., Gibson & Walk, 1960), but little direct investigation has aimed at

Table 1
Summary of Performance on the Visual Cliff for All Groups

Operation	Rearing Light Conditions	N	Descent Preference		
			Deep	Shallow	No Descent
Superior Colliculus	DR	10	1	9	0
	LR	5	0	5	0
Striate Cortex	DR	10	0	10	0
	LR	5	0	5	0
Superior Colliculus and Striate Cortex	DR	20	1	4	15
	LR	10	1	1	8
Sham Operated	DR	10	1	8	1
	LR	5	0	5	0
Non-Operated	DR	10	0	9	1
	LR	5	0	5	0

identifying the neural mechanisms underlying depth discrimination. Many structures probably involved in this discrimination have been suggested.

The present study was designed to investigate the role of superior-colliculus and/or striate-cortex lesions in the visual-cliff performance of the rat.

SUBJECTS

A total of 90 naive Long-Evans hooded rats of both sexes were included in this study. There were 40 experimental and 20 control Ss, all of which had been dark-reared, in addition to 30 light-reared Ss. The light-reared animals were raised under normal laboratory lighting conditions.

APPARATUS

The visual cliff was constructed with a 3-in.-wide centerboard of eight parallel copper rods, suspended 3 in. above a 3 x 5 ft sheet of heavy glass. The glass was bordered by 8-in.-high boards painted flat gray. Under the glass were patterns of red and white ½-in.-sq checks. The pattern on the shallow side was flush with the underside of the glass, while the deep-side pattern was suspended at a point 18 in. beneath the glass. Diffuse overhead lighting illuminated the centerboard and the patterns. The Os viewed the cliff from behind screens located 8 ft from the cliff centerboard. The copper-red centerboard was connected to a scrambled electric shock source. Shock intensity could be continuously varied from 0 to 5.0 mA.

PROCEDURE

Experimental animals were raised in total darkness from within 4 h of birth until they were 30 days old. At that time, each S was randomly assigned to one of the following groups: (1) superior-colliculus ablated, (2) striate-cortex ablated, (3) superior-colliculus and striate-cortex ablated, (4) sham operated, or (5) nonoperated. Thirty-day-old light-reared animals were also randomly assigned to the same treatment groups. All Ss, except for the nonoperated groups,

were lightly anesthetized with sodium pentobarbital in subdued red-light conditions and treated as determined by their group assignment. Ablations were bilateral and by way of visually guided subpial aspiration. Individual operations required less than 20 min each.

Postoperative recovery was allowed for 10 days in individual cages under the same light conditions in which the Ss were raised (i.e., either normal laboratory light or darkness). At 40 days of age, each experimental and control animal was tested on the visual cliff for side preference. Each animal was exposed to light in his home cage, placed on the floor for 10 min prior to testing. Testing consisted of observing each S after its being placed, facing longitudinally, on the center of the centerboard. Test sessions lasted for 6 min or until the S descended. A descent was recorded when the S had removed all four feet from the centerboard. Facial whiskers were cut prior to testing. Os were not aware of the rearing or operation history of the rats at the time of the test.

The first 3 min of the test session were observed without the delivery of shock. During the second 3 min, gradually increasing intensities of shock were delivered until the S "moved about" the centerboard. At that movement-eliciting intensity, increases were discontinued, and the rat was observed until the test session was concluded. A "no descent" was recorded for Ss not leaving the centerboard during the 6-min test session. Descents to the deep or shallow side were recorded as they occurred, with the test session terminating at that time.

RESULTS

Table 1 summarizes the data. Performance differences of ablated animals as compared to control Ss are not significant ($p > .05$), with the exception of the light- and dark-reared Ss with both superior-colliculus and striate-cortex ablations. The Ss receiving the combined operation showed a significant ($p < .001$) tendency not to descend, i.e., most of the Ss

with combined ablations, regardless of rearing condition, remained on the centerboard throughout the test session. Operated animals included in these results were those in which the ablation was restricted to the prescribed area and 90% complete, or greater, as determined by histological analysis.

DISCUSSION

Statements concerning the individual importance of the superior colliculus or the striate cortex in basic visual tasks are not supported by the results of this study. To affirm that the critical innate mechanism of depth perception is functionally located in either the cortex or the superior colliculus is not allowed by the results. Rather, a statement of the importance of the integrity of either one or the other of these areas for normal visual-cliff performance is required. The apparent behavioral normality of all groups (except for the combined-lesion group) indicates that visual-cliff performance is not noticeably impaired by rearing conditions and/or ablation of either the striate cortex or the superior colliculus of the rat; however, abnormal cliff behavior results from the simultaneous ablation of both these neural structures, regardless of rearing condition.

Of procedural significance are the relatively few no-descents recorded for all but the combined-operations groups. Earlier studies (e.g., Walk & Gibson, 1961) have reported difficulties in obtaining results without the processing of large numbers of Ss due to an inability to induce choice behavior in immature Ss. Although several methods of forcing choice behavior have reportedly had some success (e.g., icetrays), the procedure used in this study seems maximally effective.

From the results, it can be concluded that dark-reared rats, at 40 days of age, discriminate depth on a visual cliff at the first opportunity. Further, visual-cortex or superior-colliculus lesions do not, by themselves, interfere with depth discrimination in either light- or dark-reared rats. Concurrent and simultaneous lesions of both these neural areas resulted in a functional "blindness" on the visual cliff in that Ss refrained from emitting choice behavior, i.e., they did not descend from the centerboard, even under conditions that induced descents from normal and other operated rats.

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