Posterior cortical lesion influences on successive discrimination reversal performance by rats

F. ROBERT TREICHLER and EDWARD J. CONLEY
Kent State University, Kent, Ohio

Groups of hooded rats sustained posterior cortical lesions before and after testing on a series of seven successive brightness-discrimination reversals. If damage had been inflicted before the test series, animals were always severely impaired on reversal tasks. If given reversal training as normals, about 70% of the animals performed nearly as proficiently postoperatively as they had originally. The 30% of the subjects that failed performed similarly to the animals that had sustained damage before testing. Impairments of successive discrimination reversal and the typical retention deficits of cortically damaged rats appeared to have similar capacities to be modified by preoperative training.

Although rats that have undergone removal of the posterior half of their cerebral cortex are deficient in the retention of a preoperatively learned luminous flux (brightness) discrimination, such animals are nearly as capable as normals when trained on simple acquisition of the usual brightness discrimination task (Horel, Bettinger, Royce, & Meyer, 1966). However, cortically lesioned animals have been shown to be different from normals when successive reversals of a brightness task are required. This property was first noted by Gonzalez, Roberts, and Bitterman (1964) when they discovered that, although initial acquisition of the brightness task was unimpaired, lesioned rats failed to improve over a series of reversals of this problem. Because the damaged areas in this study were more extensive than the usual "visual" lesion and were inflicted at early ages, the basis of the impairment was not entirely clear. Accordingly, Birch, Ferrier, and Cooper (1978) undertook a replication of this study; they used adult animals and restricted removals to areas 17, 18, and 18a. Their results showed that failure to improve on successive reversals of a simultaneous brightness discrimination was a characteristic associated with the typical posterior-visual lesion so long as the task involved spatial properties, that is, so long as the rat was required to go to different locations to make choices of discriminanda. A possible interpretation of all these results is that posterior-lesioned rats have multiple behavioral impairments that set them apart from nonlesioned animals. These impairments include both an inability to use prior-learned informa-

tion to support postlesion performance on a test of brightness retention and a failure to use the information that ordinarily supports improvement on successive brightness reversals.

The present investigation attempted to elucidate some properties of the successive reversal impairment and to compare these characteristics with those seen in more traditional "retention" tests. A specific concern was to evaluate whether or not successive discrimination reversal (SDR) training of intact rats might ameliorate the consequences of a subsequent posterior lesion when the rats were tested on a series of reversals administered postoperatively. Accordingly, in our first study we compared the SDR performance of groups of rats that either were lesioned and then trained or were given SDR training prior to lesion. The latter group was subsequently operated on, and its performance was compared with the two previous test outcomes.

METHOD

Fifty adult (80- to 120-day-old) male Long-Evans hooded rats served as subjects. During testing, these animals' weights were maintained at 85% of the average weight of a similarly aged, freely fed group. Aspirative subpial lesions were administered to animals under sodium pentobarbital anesthesia, and a 2-week recovery period was always provided between lesion and test. All subjects were sacrificed after their final tests, and their brains were examined histologically to verify extents of cortical damage and thalamic degeneration.

An apparatus similar in dimensions and light sources to the one used by Lashley (1935) allowed discrete-trial, simultaneous, two-choice discrimination training. This apparatus provided rear-illumination of two translucent doors with 281 nits for the bright alternative and .85 nits for the dim alternative at any simultaneous choice. These values were measured via a Macbeth illuminometer placed 5.8 cm from the lighted surfaces, the nearest point in the choice compartment where subjects could view both doors. A choice response was defined as contact with one of the two illuminated doors between the choice compartment and the goal-boxes. A correct choice was followed by the raising of the door to

The contributions of E. J. Conley were partially supported by NSF Undergraduate Research Participation Grant SPI-7826936. The authors also wish to acknowledge the assistance of Brian Dister in animal testing and surgery. Requests for reprints should be sent to F. Robert Treichler, Department of Psychology, Kent State University, Kent, Ohio 44242.

the goalbox, where one Noyes pellet was available. Correctional training procedures were used throughout testing, and positions of correct alternatives were determined by a systematically counter-balanced series. After a food pellet had been consumed, animals were trained to return to the start chamber via a side alley so that the trials would always be initiated by the opening of the door to the choice compartment and no handling between trials would be required.

Pretraining procedures entailed familiarization with the apparatus and learning to traverse it for rewards administered both in the goalboxes and in the startbox upon return. In formal testing, differentially illuminated doors were inserted between the choice compartment and the goalboxes, and no rewards were given in the startbox. Test sessions provided 30 trials per day, and sessions were continued until a subject had achieved a criterion of 18 correct of 20 consecutive trials or had failed to meet that criterion in 17 days (510 trials). After original learning, reinforcement contingencies were reversed until criterion was once again met; this procedure was continued through seven more reversals. Testing was terminated if an animal had failed to meet criterion in 17 days. Because Parker and Treichler (1973) have demonstrated that posterior cortical lesions may produce more severe impairments when rats are required to select the dimmer, rather than the brighter, of two alternatives as the correct choice in a brightness task, the present study compared performance on a reversal series that began with either the brighter or dimmer alternative designated as being correct.

Sixteen rats underwent surgery prior to testing. After the 2-week recovery period, they were tested on an SDR series that began with a task that required choosing either the brighter or the dimmer door (8 subjects per group). Thirty-four rats began their SDR series as normals (18 to the bright door and 16 to the dim) and then received lesions after having met criterion on the seventh reversal. Following the recovery period, these subjects were tested on an SDR series like the one in which they had performed as normals. Subjects were assigned to conditions in an unbiased fashion, and squads of approximately 6 animals (both originally lesioned and originally normal) were under test during the same calendar periods.

RESULTS

The primary dependent variable in this study was the number of trials required to attain a criterion of 18 correct of 20 consecutive responses. Although these scores did show substantial variability among subjects, all animals tested as normals met this criterion in less than 510 trials. Table 1 presents median scores for subjects tested under the various conditions of the present experiment. Original SDR testing of lesioned and normal subjects revealed severe impairment with the lesion and no overlap in performance of these two groups. In confirmation of Parker and Treichler (1973), original learning that required a "dim" choice by lesioned animals was significantly more difficult than training that entailed choosing the bright (Mann-Whitney $U = 4$, $p = .001$).

Reference to Table 1 also shows that original SDR training as normals yielded animals that were less severely affected by the lesion than were their naive counterparts. Comparison of the B and C sections of Table 1 shows much greater communality than does the comparison of Sections A and C (similarly lesioned subjects). It must be emphasized, however, that such similarities are not intended to suggest that

the lesions had no influence on SDR learning in subjects trained preoperatively. Rather, it should be noted that about 28% (9 of 32) of the trained-then-lesioned subjects failed to achieve criterion within the training limits of a reversal test (510 trials), and these failures were usually on the first reversal (in 7 of 9 cases). When Wilcoxon comparisons of normal and postoperative SDR performance of the animals that had received the test series both as intact animals and as operates were made, it was found that significantly fewer trials ($p < .01$) were required for original acquisition than were required on the first postlesion test. This was true for animals trained to go to either the brighter or the dimmer alternative. Similar Wilcoxon comparisons of normal and postoperative performance conducted at all (first through seventh) reversals for the subjects that did attain performance criteria in all postoperative testing showed no significant differences ($p > .05$) at any serial reversal for either the bright- or dim-going task. Thus, it appeared that the combination of lesion and prior training yielded some impairment of initial postoperative performance relative to original learning, and there was a subset of animals that were deficient in meeting the requirements of the reversal component in these tests. However, the majority of subjects were capable of meeting the performance criterion in a series of reversals in about the same number of trials that had been necessary when they were tested on this series as normals.

Mann-Whitney comparisons between the performance of originally lesioned and that of lesioned-after-learning groups yielded significant differences ($p < .05$) at every reversal for groups that began on a dim-going task and every reversal except for the first one for the group that began with a bright-going task.

To determine the histological results, surface plots of the extent of damaged cortical tissue were constructed from each subject's perfused brain on standard Lashley diagrams. These plots were then overlaid by a transparent grid comprising 1-mm squares, and a score based on the number of squares that contained damaged tissue (at least half) was recorded for each animal. Scores for the group that underwent cortical removal before SDR training and the group that underwent cortical removal after SDR training were compared via a Mann-Whitney test, and no reliable difference ($U = 325$, $z = 1.46$, $p > .05$) in the extent of cortical damage was noted between these groups. Similar comparisons of the lesion-extent scores for the group initially trained to choose the brighter alternative and the group initially trained to choose the dimmer one within each training condition also showed no significant differences. One further Mann-Whitney comparison was conducted using the scores derived from the cortical plots. Among those subjects that received their cortical damage

Table 1
Median Trials-to-Criterion (18 Correct of 20 Consecutive Trials) Scores on Successive Reversals
When Lesioned Before Training, Normal, or Lesioned After Training

Reversal	A. Lesioned			B. Normal			C. Lesioned After Training as Normal					
	To BA (n = 8)		MTC to DA (n = 8)	MTC to BA (n = 18)	MTC to DA (n = 16)		To BA†			To DA		
	MTC	NR					MTC	NC	M	MTC	NC	M
OL	93		258	67	72		172	16		139	16	
1	510*	3		128	131		180	13	242	192	12	286
2	510*	2		143	138		168	12	182	134	11	236
3	510*	1		146	106		134	12	235	144	11	220
4				118	111		144	12	206	136	11	162
5				75	99		152	12	210	89	11	156
6				114	74		111	12	150	138	11	204
7				99	90		80	12	146	119	11	155

Note—OL = original learning; BA = brighter alternative, DA = dimmer alternative. MTC = median trials to criterion; NR = number of subjects attaining reversal; NC = number of subjects attaining criterion on indicated task, M = median that includes subjects failing to attain criterion (scored as 510). *Failed to meet criterion. †Two subjects died.

after training as a normal, a comparison of lesion extent was made between the 9 animals that failed to complete postoperative reversal testing and the 23 animals that did complete this testing. No significant differences ($U = 118$, $z = 1.30$, $p > .05$) were observed between these subgroups, and it appeared that the differences in behavioral outcomes were not attributable to systematic differences in the extent of area affected by surgical intervention.

Areas of retrograde thalamic degeneration were also recorded for each subject, and these included both the lateral geniculate and the nucleus lateralis pars posterior. Patterns of degeneration consistent with those noted by Parker and Treichler (1973) were observed, but no systematic differences between groups with different training conditions or behavioral outcomes were revealed in either the extents or locations of degeneration.

DISCUSSION

The results provide reasonable support for the view that information from SDR training can influence performance on a similar task presented after an intervening lesion. One contribution of information retained from the preoperatively learned task was to improve postlesion performance on a reversal series relative to performance shown by rats that had sustained their damage before SDR training. These outcomes are in some accord with views expressed by LeVere, Davis, and Gonder (1979) regarding the utilization of preoperatively learned information and serve to support their contention that the lesioned rat's behavior is not independent of previous experience.

A possible interpretation of the present results is that they may represent an extension of the class of outcome reported by LeVere and Morlock (1973). These investigators provided brightness discrimination training to either a bright or a dim alter-

native, then administered lesions to their subjects, and then compared the performance of groups given either a retention or a reversal of their original task. In accord with many previous demonstrations, retention of the preoperative task was impaired, but the reversal performance to either alternative also required the extensive retraining characteristic of reversal by intact animals. Such an outcome suggested that the lesion, while effective in influencing retention, did not do so by eliminating preoperatively acquired information. Similarly, the present experiment may be viewed as providing a situation in which preoperatively learned information was maintained and, rather than impairing postoperative performance as in LeVere and Morlock's reversal situation, the stored information served to enhance subsequent SDR performance.

Potential bases for enhanced postoperative performance after original SDR training are not revealed by the present study. However, a subsequent test undertaken in our laboratory and a recent report by Gray and Meyer (1981) do allow some speculation about this issue. We gave 15 additional animals brightness training in our situation (all to the brighter door) and then lesioned and measured them on a retention test. They showed the usual relationship between original learning and postoperative relearning; that is, they required about the same number of trials to attain criterion postoperatively as they did when initially trained as intact animals. These subjects were then administered a series of reversals and, although 13 of the 15 attained criterion on the first reversal, they did not meet the criterion of 18-of-20 correct on subsequent reversals. Specifically, 6 of the 13 remaining animals did not meet criterion on the second reversal, 6 others failed at the third reversal, and the 1 remaining subject failed at its attempt on the fourth reversal. Although this performance was not quite as poor as that seen in our initially lesioned subjects, it seemed evident that one preoperative

acquisition did not have the same ameliorating effect on reversal tests that was provided by training on the SDR series. Perhaps the "protection" provided by original SDR training is a simple overlearning effect. Although Lashley (1921) reported that brightness losses were not reduced by overtraining in acquisition, Gray and Meyer (1981) have recently noted about a 50% reduction in the number of postoperative trials to criterion on a bright-going task when they gave about four times the usual number of original training trials. In our seven-reversal original-learning sequence, there appears to have been a substantial opportunity for overlearning, and it is certainly evident that just one brightness acquisition was not sufficient to eliminate the impairment of SDR performance.

However, it is important to emphasize that the lesion is not without harmful consequence to subjects that are trained on SDR prior to infliction of cortical damage. The need for significantly larger numbers of trials to reach criterion on the first postoperative task than on original learning is a pattern of results different from that typically observed when only a single acquisition precedes the lesion. Under this latter circumstance, as noted previously, approximately the same number of trials are required to attain criterion both pre- and postoperatively. Thus, it appears that prior SDR training and the lesion combine to yield an impairment on the first postoperative test, but when required to do subsequent serial reversals, most animals that have undergone training as normals are more adept than naive visually decorticate subjects. The appearance of relatively poor performance on the first postoperative test might be viewed as a simple consequence of reversal from the seventh test in the preoperative series. However, we have tested several animals (three or four in each direction) in a sequence in which their initial postlesion task was the same as the last one in the preoperative series, and their performance was not significantly different from that observed in our animals that had reversed for the initial postoperative task.

One other facet of the performance of the group that underwent lesioning after SDR training merits comment. Note that there was no differential effect of cortical removal on the initial performance of bright- or dim-going tasks as there was in animals

that received damage prior to such training. This finding can be interpreted as providing further support for LeVere et al.'s (1979) view of lesioned animals' nonindependence from information gained prior to undergoing brain damage. In the present situation it is suggested that information about general task requirements such as choosing a dimmer alternative may serve as an influential determinant of postoperative performance.

An overview of the present experimental outcomes suggests that the impairment of rats with posterior cortical lesions on the SDR task is a reliable and fairly general phenomenon. However, we conclude that, because of the sensitivity of this performance to modulation by the same factors that influence simple retention and reversal tasks, successive reversal impairments need not be considered an additional and distinctive consequence of cortical damage.

REFERENCES

- BIRCH, M. P., FERRIER, R. J., & COOPER, R. M. Reversal set formation in the visually decorticate rat. *Journal of Comparative and Physiological Psychology*, 1978, **92**, 1050-1061.
- GONZALEZ, R. C., ROBERTS, W. A., & BITTERMAN, M. E. Learning in adult rats with extensive cortical lesions made in infancy. *American Journal of Psychology*, 1964, **77**, 547-562.
- GRAY, T. S., & MEYER, D. R. Effects of mixed training and overtraining on recoveries from amnesias in rats with visual cortical ablations. *Physiological Psychology*, 1981, **9**, 54-62.
- HOREL, J. A., BETTINGER, L. A., ROYCE, G. J., & MEYER, D. R. Role of neocortex in learning and relearning of two visual habits by the rat. *Journal of Comparative and Physiological Psychology*, 1966, **61**, 66-78.
- LASHLEY, K. S. Studies of cerebral function in learning: II. The effects of long-continued practice upon cerebral localization. *Journal of Comparative Psychology*, 1921, **1**, 453-468.
- LASHLEY, K. S. The mechanisms of vision: XIII. Nervous structures concerned in the acquisition and retention of habits based on reactions to light. *Comparative Psychology Monographs*, 1935, **11**, 43-79.
- LEVERE, T. E., DAVIS, N., & GONDER, L. Recovery of function after brain damage: Toward understanding the deficit. *Physiological Psychology*, 1979, **7**, 317-326.
- LEVERE, T. E., & MORLOCK, G. W. Nature of visual recovery following posterior neocortical ablation in the hooded rat. *Journal of Comparative and Physiological Psychology*, 1973, **83**, 62-67.
- PARKER, T. D., & TREICHLER, F. R. The influence of restricted posterior neocortical ablation on brightness preference and brightness discrimination performance of rats. *Physiology & Behavior*, 1973, **10**, 473-478.

(Manuscript received April 14, 1982;
revision accepted for publication June 15, 1982.)