Effects of subcallosal lesions on "hypothesis" behavior in rats[1]

PHILLIP C. GREEN AND CHARLES F. LEVINTHAL
UNIVERSITY OF CINCINNATI

In studying effects of subcallosal lesions in juvenile and adult rats on a simple learning task, Ss ran a multiple-path maze, each path differing in length and position, but all leading to the goal box. Relative to Cs, Es in both age groups (1) failed to learn a preference for the shortest path to the to the goal; (2) showed greater activity; and (3) showed fewer "balks." Juvenile Es generally showed fewer lesion effects than adults.

Krechevsky (1933) used the term "hypothesis" to designate behavior wherein an organism consistently uses a particular cue or response over other alternatives available to it. He showed that normal rats tend to use many hypotheses to run a maze having several alternative routes to the goal. The effect of small cortical lesions was to reduce the number of hypotheses employed, while rats with more extensive cortical lesions tended to perseverate, i.e., adopt a single hypothesis and stay with it.

Work on effects of subcortical lesions on maze performance in the rat has indicated that while lesions of thalamus or pretectal nuclei appear to have little effect (Ghiselli & Brown, 1938), some limbic structures do appear to influence maze learning. Thomas et al (1959) found that septal lesions, sufficient to make rats irritable, produced significantly more errors on a Lashley III maze. Also, studies by Thomas & Otis (1958) and by Kaada et al (1961) have involved the hippocampus in impairment of maze learning.

In the present study, an attempt has been made to explain deficits in maze behavior under the term *disinhibition*, used by Kaada et al (1961) and McCleary (1961). The latter, working with subcallosal lesions in cats, first described these lesions as producing impairment in development of fear-motivated passive avoidance, while having little effect on active avoidance. Recently, McNew & Thompson (1966) have noted deficits in both active and passive avoidance with lesions of septum and hippocampus, again using aversive stimulation as the relevant motivator. To our knowledge, however, no one has tested the disinhibition concept using a non-aversive performance measure like the "hypothesis" maze response.

In accord with the disinhibition hypothesis, which emphasizes the S's inability to inhibit ongoing movement, it was expected that, relative to controls, rats lesioned as adults would show (1) fewer entrances into the first-encountered path of a three-path maze even though it is shortest, alternative paths become successively longer, and all lead to the goal box; (2) a significant increase in activity since extirpation of both cortical and subcortical structures have typically shown increased rather than decreased levels; (3) longer running latencies, if Hypothesis 2 holds true; (4) fewer balks, i.e., a tendency to leave the start box more readily; and (5) minimal differences in start box latencies. Finally, another variable of interest in this study—age of lesion—led to the expectation, based on findings in other species (Kling, 1962; Green & Kling, 1966), that (6) early-lesioned rats should show less behavioral change than later-lesioned rats.

Procedure

The apparatus used in this study was a three-unit multiple-U maze. For each trial, S could locate the goal box by first entering a common path connecting the alternative goal paths and then selecting one of these to gain access to another common path and then to the goal box. Mild homogeneous illumination was provided by fluorescent fixtures mounted below a milk-plastic floor.

Juveniles were lesioned between 15 and 25 days postpartum; adults were lesioned at 90 to 120 days of age. Bilateral anterior subcallosal lesions were made stereotaxically using No. 26 insulated Nichrome wire, bared about 1 mm from the tip, and were produced with a Grass lesion-maker at maximum setting for 30 sec. All Ss began testing at the same age (mean =199 days). Prior to initiating a drive state, all Ss were given one 5-min. habituation trial in the maze. They were then placed on 24-hr. water deprivation and run through the maze again using a forced-choice technique in which baffles occluded the two alternative paths, forcing S to sample all paths equally. Finally, baffles were removed and each S was given 50 free-choice trials in the maze. Recorded were start-box-exit and maze-running latencies, path choices, retrace behavior, and balks (failure to leave the start box within 60 sec.).

Subsequent histological examination indicated that lesions in both groups were relatively symmetrical and comparable in size, with maximum damage concentrated in an area immediately ventral to the rostrum of the corpus callosum.

Results

An analysis of data representing initial path entries by Ss in each treatment group indicated a significant lesion effect, as seen in Fig. 1. Based on a disinhibition interpretation, the "path" hypothesis appeared tenable. Because Path 2 was entered seldom only Paths 1 and 3 were evaluated. Response trends were similar in

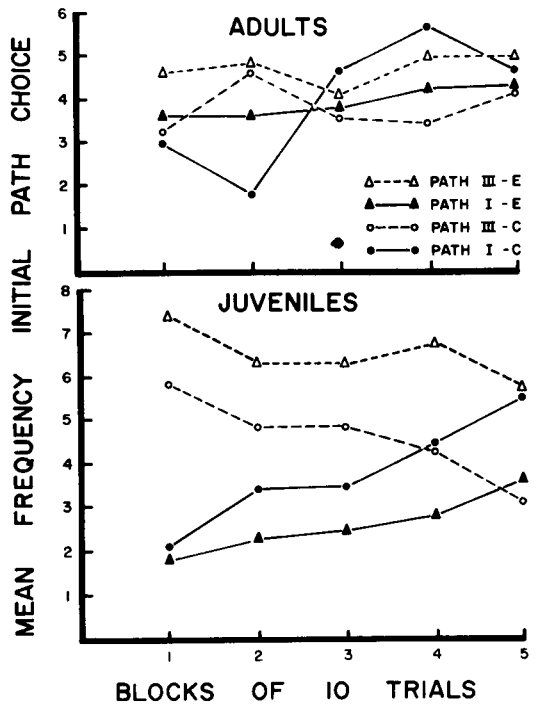

Fig. 1. Analysis of first path entered by adults and juveniles during maze running trials.

both age groups but most clearly observed in the juveniles. Both Es and Cs began testing with an initial preference for Path 3. This had been anticipated since, although Path 3 was the longest, it was spatially also the most continuous path to the goal. In both C groups, additional maze exposures produced shifts in preference from Path 3 to Path 1 (the shortest path, but also requiring an abrupt motor adjustment at the choice point) by Trial 30 of the fifty-trial series. Es, however, showed no reversal maintaining a consistent preference for Path 3 throughout testing. Es in both age groups selected this path more frequently than their respective Cs, with mean differences between Es and Cs for path preference significant beyond the .02 level of confidence (Mann-Whitney U test). Paradoxically, adult Es chose Path 1 more frequently than their Cs for the first 30 trials but reversed and Cs maintained this preference thereafter.

The hypothesis of increased activity for adult Es but not for juvenile Es, relative to Cs, was only partly upheld. On the activity measures (start box and maze-running latencies, retraces), no differences were found on start-box-exit behavior between Es and Cs, a finding which was emphasized even more when "balk" latencies were abstracted from the data. Therefore, it is evident that no initial bias between operates and non-operates was introduced by using a start box in this situation. Significant differences ($p \leq .04$, Friedman test) were found between Es and Cs in both age groups on the maze-running and retrace measures. Es tended to run faster but also make more retrace responses than Cs.

Of interest was the observation that, on maze-running time, means for adult Es and Cs showed a significant initial difference, postoperatively ($p < .02$, Mann-Whitney U test), and then converged continuously until by the final block of trials, group differences lacked significance. Conversely, the juvenile Es and Cs started at almost the same level and diverged until by the final block of trials they were noticeably divergent. However, since none of the differences reached significance, these data can only suggest an age difference produced by the lesion.

Finally, analyses for both age groups indicated that the hypothesis of fewer balks was substantially supported. Adult Es showed significantly fewer balks than Cs on at least half of the trials, while juvenile Es were consistently lower than Cs in balk frequencies throughout testing ($p \leq .01$, Friedman test). The same trends of curve convergence for adults and divergence for juveniles over trials occurred on this measure.

Conclusion

This tentative evaluation suggests that the hypothesis of "disinhibition" is tenable in this situation and may be invoked as a more physiologically-based phenomenon to supplant the older "hypothesis" concept of Krechevsky.

References

Ghiselli, E. E., & Brown, C. Subcortical mechanisms in learning: VII. The effect of cerebral injury upon the relative distribution of errors in a spatial maze. *J. comp. Psychol.*, 1938, 26, 301-309.

Green, P. C., & Kling, A. Effects of amygdalectomy on affective behavior in juvenile and adult macaque monkeys. *Proc. Amer. Psychol. Assoc.*, 1966, 93-94.

Kaada, B. R., Rasmussen, E. W., & Kviem, O. Effects of hippocampal lesions on maze learning and retention. *Exp. Neurol.*, 1961, 3, 333-335.

Kling, A. Amygdalectomy in the kitten. *Science*, 1962, 137, 429-430.

Krechevsky, I. Hereditary nature of "hypotheses." *J. comp. Psychol.*, 1933, 16, 99-116.

McCleary, R. A. Response specificity in the behavioral effects of limbic system lesions in the cat. *J. comp. physiol. Psychol.*, 1961, 54, 605-613.

McNew, J. J., & Thompson, R. Role of the limbic system in active and passive avoidance conditioning in the rat. *J. comp. physiol. Psychol.*, 1966, 61, 173-180.

Thomas, G. J., Moore, R. Y., Harvey, J. A., & Hunt, H. F. Relations between the behavioral syndrome produced by lesions in the septal region of the forebrain and maze learning in the rat. *J. comp. physiol. Psychol.*, 1959, 52, 527-532.

Thomas, G. J., & Otis, L. S. Effects of rhinencephalic lesions on conditioning of avoidance responses in the rat. *J. comp. physiol. Psychol.*, 1958, 51, 130-134.

Note

1. This research was supported by RD funds allocated to the Department of Psychology by the Graduate School of the University of Cincinnati.