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Relation of Rotation to Egocentric and Allocentric Spatial Learning in the Rat

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CROWNE, D. P., P. A. TOKRUD AND P. BROWN. *Relation of rotation to egocentric and allocentric spatial learning in the rat.* PHARMACOL BIOCHEM BEHAV 43(4) 1151-1153, 1992.—In this experiment, we asked whether the relation between amphetamine-induced rotation and the learning and retention of left-right discrimination extends to allocentric spatial learning or is limited to egocentric spatial tasks. Rotation was established following injections of *d*-amphetamine sulfate, and rats were classified as nonrotators, midrotators, or strong rotators. Animals were successively trained on navigation in the Morris water maze (allocentric) and delayed spatial alternation in a water T-maze (egocentric). There were no rotation effects in water maze learning but rotators and nonrotators differed significantly in delayed spatial alternation learning but not relearning. Strong rotators learned more slowly than midrotators, clearly implying that rotational bias and directional learning are not linearly related. We show that it is egocentric spatial learning that is facilitated by a nigrostriatal dopamine asymmetry and extend the generality of the left-right discrimination findings.

Amphetamine Dopamine Rotation Spatial learning Left-right discrimination
Delayed spatial alternation

THERE is a strong relation, grounded in two experiments, between amphetamine-induced rotation and the learning and retention of left-right discrimination (11,12). Nonrotating rats are slow to learn this simple spatial problem and do not retain it. Rotation is the expression of a small hemispheric asymmetry in the nigrostriatal concentration of dopamine (5). Directional sense might have just such a neurochemical basis, and the importance of the finding is that it provides nice evidence in favor of a biochemical spatial mechanism.

The discrimination of left and right relies on internal cues; it is egocentric in contrast to allocentric spatial localization, which requires the use of external cues or landmarks. This is a distinction drawn by Semmes et al. (10) that has considerable support in studies of cortically damaged humans (2,10), monkeys (1,9), and, most recently, rats (4,7). In this experiment, we asked whether the relation between rotation and position discrimination is actually a more general one, extending to allocentric spatial learning, or is limited to tasks specifically requiring egocentric spatial orientation. We also sought to extend the left-right discrimination findings to more complex spatial learning. Rats were successively trained on two spatial tasks: navigation in the Morris water maze, entailing place localization by means of distal (allocentric) cues, and delayed spatial alternation in a water T-maze, an egocentric task considerably more difficult than left-right discrimination.

METHOD

Subjects

The experiment used 26 male Long-Evans hooded rats, between 392-457 g at the beginning of testing, obtained from a breeding colony at the University of Waterloo. They were housed in individual cages, provided lab chow and water ad lib and maintained on a 12 L : 12 D cycle with lights on at 10:30 a.m. Animals were handled daily for 1 week before the start of the experimental procedures. Testing was conducted with two cohorts, formed by random assignment. Two animals died between the water maze and delayed spatial alternation tasks and so the analyses are based upon an *N* of 24.

Procedure

Rotation. Rotation was tested in a cylindrical chamber (diameter = 25 cm, height = 25 cm), and there were three test sessions. The first two, 1 week apart, preceded the water maze and the last session was 1 month after water maze training concluded and 1 month before delayed spatial alternation training. Each session began with a 10-min habituation period, after which the animal was injected with *d*-amphetamine sulfate (1.0 mg/kg, IP). Rotation testing began 20 min later. Full 360° rotations completed within 5 s were counted for 20 min. Net rotations were calculated and summed for the three

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sessions. Animals were classified as nonrotators (1–16 net rotations, $M = 6.50$; $n = 6$), midrotators (22–48 net rotations, $M = 34.67$; $n = 9$), and strong rotators (53–138 net rotations, $M = 85.56$; $n = 9$). The criteria for grouping animal as rotators or nonrotators match those of previous studies (11,12). Rotational direction was also recorded in the rotators. Nine rats rotated left, nine right. Net rotations and rotational direction were not determined until the end of each spatial test; the experimenters thus had no knowledge of any animal's classification.

Place navigation. Animals were trained in standard place navigation in a circular tank containing a submerged and hidden escape platform. The tank, 120 cm diameter and 57 cm high, was made of blue swimming-pool liner fastened to a metal frame. It was filled daily to a height of 38 cm with 20°C water made opaque with 2 l milk powder. The platform was clear Plexiglas, 17 cm diameter and 37 cm high; it was placed in a quadrant of the pool arbitrarily designated as NW, NE, SE, or SW. There was a rich variety of extramaze cues in the room: a large shelving unit at arbitrary east, the colony rack and the experimenter to the south, door to the northwest, and wall shelves to the west. Illumination was overhead fluorescent. There were 4 days of training, four trials per day. In each trial, animals were lowered into the pool facing the wall at arbitrary N, E, S, or W locations. Individual rats were randomly assigned one of these target quadrant locations to start. Subsequent trials began from different, randomly determined compass points. Trials had a maximum duration of 120 s after which the animal was removed from the pool and returned to its home cage. When rats found the platform, they remained for 5 s before removal to their cages. Two days of reversal followed with the platform relocated to the opposite quadrant. Learning was expressed by three measures: latency to find the platform, heading error, and quadrant entries. The last was a ratio of target to nontarget entries:

$$\frac{\text{Target} - \text{nontarget}}{\text{Target} + \text{Nontarget}}$$

Individual water maze performance was not known to the experimenter who tested the animals on delayed spatial alternation.

Delayed spatial alternation. Training in spatial alternation was carried out in a T-maze suspended in the pool. The maze was constructed of milk-white Plexiglas. The runway was 72.5 cm long and the arms 48.5 cm; the width was 15.5 cm. At the end of each arm was a 17.5-cm goalbox that, like the ticks on the capital letter T, extended parallel to the runway, preventing a view of the escape platform. The platform, of clear Plexiglas, was at water level, 34 cm. The walls of the T-maze were 24 cm high, 17.5 cm above and 6.5 cm below the surface of the water. The pool was filled daily with 20°C clear water, circulated by an air pump and rubber hose to eliminate the possibility of odor trails.

On the first of 20 daily trials, animals were placed in the water at the start of the runway and given one correct trial. Thereafter, the location of the platform alternated. However, a correction procedure was followed so that the platform was not relocated until a correct choice was made. On each trial, after rats had found and climbed on the platform they remained there for 5 s and were then returned to their home cages. Each animal completed its 20 trials in succession with an intertrial interval closely approximating 15 s. At criterion (90% correct), there was a 48-h interval followed by relearning that continued until 90% correct was again reached. Learning and relearning were expressed by the number of errors to criterion.

RESULTS

As a first step, we examined the reliability of amphetamine-induced rotation. The correlation of net rotations in the first two test sessions 1 week apart was 0.63. Totaled net rotations from these 2 weeks correlated 0.68 with rotations in the third session 5 weeks later. These coefficients are significant at 0.001. They are slightly higher than values previously reported and extend the time interval between test sessions (6). The Spearman rank order correlation of the rotation and rotational direction classifications was 0.76, $p < 0.001$.

Next, the three rotational groups were compared in place navigation by analyses of variance (ANOVAs) of latency, heading error, and quadrant entry ratio. None of these yielded a significant rotational group main effect or group × trial blocks interaction. Learning occurred, however, for on each measure the effect of trial blocks was significant at 0.001 or beyond: latency, $F(5, 105) = 38.29$; heading error, $F(5, 105) = 4.78$; quadrant entry ratio, $F(5, 105) = 16.88$.

A similar ANOVA on errors to criterion in delayed spatial alternation resulted in a significant group × learning/retention interaction, $F(2, 21) = 3.46$, $p = 0.05$. Newman-Keuls individual comparisons ($\alpha = 0.05$) of alternation learning showed the nonrotators to differ reliably from both rotator groups and the two rotator groups to differ from each other. No group differences appeared in retention. The analysis was repeated with the rotator groups combined, and a similar picture emerged. There was again a groups × learning/retention interaction, $F(1, 22) = 6.16$, $p = 0.02$. The simple main effect of rotators vs. nonrotators in learning was significant, $F(1, 22) = 6.31$, $p = 0.02$. These delayed spatial alternation findings are shown in Fig. 1.

This same sequence of ANOVAs was repeated with nonrotators, left rotators, and right rotators. None of the water maze main effects or interactions involving rotational direction reached significance. There was a significant interaction in the delayed spatial alternation analysis, $F(2, 21) = 3.38$, $p = 0.05$. The individual comparisons revealed that both left

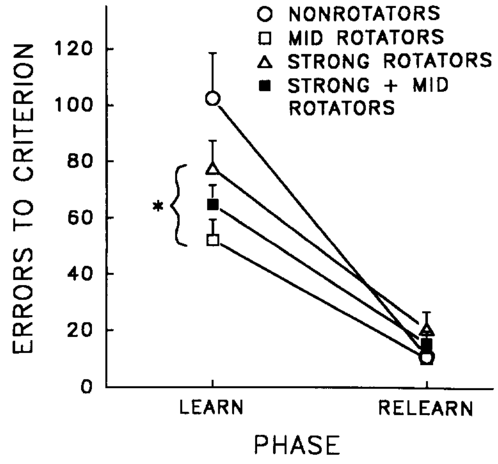

FIG. 1. Delayed spatial alternation learning and relearning by rotators and nonrotators. Mean ± SEM errors to criterion are shown. *Significant difference from nonrotators.

and right rotators learned in fewer trials than nonrotators but did not differ from each other. The groups did not differ in retention.

DISCUSSION

Rotating and nonrotating animals were equally proficient in learning the location of the submerged platform by each of the commonly used measures. This report thus differs slightly from Camp et al. (3), who reported that rotating rats had a small heading error advantage in reversal learning in the water maze. But, while an asymmetry in nigrostriatal dopamine is of little benefit in place learning guided by extrapersonal cues it is critical in the learning of tasks that require the discrimination of left and right. Nonrotating rats are disadvantaged in simple left–right discrimination, and we now show that they learn delayed spatial alternation only with difficulty. Indeed, nonrotating rats made nearly 40% more errors in reaching criterion than rotators. We did not, however, find that nonrotators were impaired in relearning after the 48-h interval. Perhaps the absence of a rotator–nonrotator relearning difference reflects the considerable memory requirement of delayed spatial alternation and the many trials required to learn it. It is thus unlike left–right discrimination, which may be acquired in 10–20 trials and not retained by animals lacking the basis to distinguish direction.

Although better than nonrotators, animals with a strong rotational bias acquired spatial alternation more slowly than midrotators, a finding that suggests a U-shaped relation. There is precedent for this in the recent report (8) that rats with a strong turning bias took longer to learn a conditional left–right discrimination than moderately biased animals and resembled animals with little or no directional bias. If, as seems likely, these behavioral biases reflect an endogenous asymmetry, we can readily account for this result and ours. Animals lacking the lateral (nigrostriatal) asymmetry simply do not have the neurochemical basis to distinguish left and right and must depend upon other less effective mechanisms. Strongly biased animals are too ready to follow the bias, in particular in the early and middle stages of learning, failing to alternate or to use the conditional cue.

Our findings emphasize the distinction between allocentric and egocentric spatial learning and extend the generality of a neural basis for the discrimination of left and right.

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REFERENCES

1. Brody, B. A.; Pribram, K. A. The role of frontal and parietal cortex in cognitive processing tests of spatial and sequence functions. Brain 101:607–633; 1978.
2. Butters, N.; Soeldner, C.; Fedio, P. Comparison of parietal and frontal lobe spatial deficits in man: Extrapersonal vs personal (egocentric) space. Percept. Motor Skills 34:27–34; 1972.
3. Camp, D. M.; Therrien, B. A.; Robinson, T. E. Spatial learning ability is related to an endogenous asymmetry in the nigrostriatal dopamine system in rats. Soc. Neurosci. Abstr. 7:455; 1981.
4. Crowne, D. P.; Novotny, M. F.; Maier, S. E.; Vitols, R. The effects of unilateral parietal lesions on spatial localization in the rat. Behav. Neurosci. (in press).
5. Glick, S. D.; Shapiro, R. M. Functional and neurochemical mechanisms of cerebral lateralization in rats. In: Glick, S. D., ed. Cerebral lateralization in nonhuman species. Orlando, FL: Academic Press; 1985:157–183.
6. Jerussi, T. P.; Glick, S. D. Drug-induced rotation in rats without lesions: Behavioral and neurochemical indices of a normal asymmetry in nigrostriatal function. Psychopharmacology (Berl.) 47: 249–260; 1976.
7. Kesner, R. P.; Farnsworth, G.; DiMattia, B. V. Double dissociation of egocentric and allocentric space following medial prefrontal and parietal cortex lesions in the rat. Behav. Neurosci. 103: 956–961; 1989.
8. Noonan, M.; Axelrod, S. Behavioral bias and left–right response differentiation in the rat. Behav. Neural Biol. 52:406–410; 1989.
9. Pohl, W. Dissociation of spatial discrimination deficits following frontal and parietal lesions in monkeys. J. Comp. Physiol. Psychol. 82:227–239; 1973
10. Semmes, J.; Weinstein, S.; Ghent, L.; Teuber, H.-L. Correlates of impaired orientation in personal and extrapersonal space. Brain 86:747–772; 1963.
11. Willar, C. D.; Crowne, D. P. Circling, hemispheric asymmetry, and left–right discrimination. Brain Res. 500:405–407; 1989.
12. Zimmerberg, B.; Strumpf, A. J.; Glick, S. D. Cerebral asymmetry and left–right discrimination. Brain Res. 140:194–196; 1978.