

BRIEF REPORT

Behavioral Bias and Left-Right Response Differentiation
in the Rat

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To examine the proposition that lateral asymmetry facilitates left-right response differentiation in rats, we examined the relationships between the strengths of several behavioral biases and the scores on a learning task requiring left-right response differentiation. No support was found for a simple model positing a monotonic relationship between any behavioral bias and the learning scores. However, performance showed a U-shaped relationship to one behavioral bias. This finding conforms to a curvilinear model in which rats at either extreme of asymmetry are disadvantaged, at low degrees of asymmetry by a lack of navigational reference, and at high degrees by resultant strong position habits; moderately asymmetrical rats have neither disadvantage and are best able to use the asymmetry as a reference in processing left-right information. © 1989 Academic Press, Inc.

Corballis and Beale (1976) have proposed that an animal's ability to perform a left-right response differentiation—e.g., to give “a left response to one stimulus and a right response to another, when the stimuli themselves convey no extrinsic left-right information” (p. 38)—depends critically on the animal's own lateral asymmetry. It is argued that neural asymmetry provides an internal means by which left and right responses

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can be differentiated. A hypothetical animal with perfect bilateral symmetry, tested in a symmetrical environment, should therefore be incapable of distinguishing between its left and right responses. On the basis of this view of symmetry as impeding and asymmetry as facilitating, we might expect a monotonic relationship between degree of endogenous biological asymmetry and relative proficiency at distinguishing left from right: the greater the lateral asymmetry of the animal, the greater its ease at telling left from right. Recent evidence that degree of left-right confusion is inversely related to degree of functional hemispheric asymmetry in adult humans (Manga & Ballesteros, 1987) supports this view.

For the rat, Zimmerberg, Strumpf, and Glick (1978) reported findings similarly compatible with such a monotonic model. Individuals with strong amphetamine-elicited rotational biases, arguably reflective of endogenous asymmetries in the nigrostriatal pathways, both learned and relearned a consistently left or consistently right escape response in an electrified T maze in fewer trials than did rats without strong drug-elicited bias. Like Corballis and Beale, Zimmerberg et al. argue that an endogenous asymmetry can provide an internal reference by which left and right responses can be differentiated, in the absence of which the distinction between left and right responses would be difficult or impossible.

Reasoning that stable lateral behavioral biases must derive from cerebral asymmetry (cf. Glick & Shapiro, 1985), in the present work we assessed the relationship between scores on a left-right response-differentiation test and the strengths of lateral behavioral biases of 104 rats, the prediction being that strongly biased animals would master this left-right task faster than less biased ones.

Subjects were black-hooded Long-Evans rats of both sexes. They were trained to escape from a water-filled T maze at whose choice point the rat was required to turn left or right, depending on whether the inside walls of the maze were light (correct turn right) or dark (correct turn left). The water was 25 cm deep throughout and the maze walls extended 21 cm above the surface of the water. The runway of the maze was 60 cm long, and the cross-piece of the T was 80 cm long; an escape ramp at the end of the correct alley, but out of sight of the rat from the choice point, served as reinforcer. Water and room temperatures were kept at 25°C. A correction procedure was used, the animal being left to swim until it had reached the ramp. A correct response was recorded when the first turn at the choice point was in the correct direction and the rat reached the ramp without returning to the choice point. Over successive days, 25 quasi-randomly mixed trials per day were given (intertrial interval approx 3 min), until the criterion of 10 consecutive correct responses was reached; the number of trials taken to reach this criterion served as the measure of the animal's ability to tell left from right.

The observations of postural-motor bias derived from three tests which

had proved in these animals to be reliable across days: three measures derived from open-field behavior (initial turn upon release, initial direction of exploration, and an index ("wall-hugging ratio") of the rat's preference for locomoting with its left or right side adjacent to a wall); three derived from observations of a rat stepping down from a beam (direction(s) taken by head, forefeet, and back feet); and an index ("circling ratio") of the preference for leftward or rightward swimming in a rotatory swimming test (see Noonan & Axelrod, 1989). Each test was administered for 5 successive days, and for each rat on each measure, the strength of the bias independent of direction was computed by taking the absolute value of the difference between the directional score and the no-bias value for the mean across days (cf. Collins, 1985).

An additional behavioral bias was assessed during the water-maze testing itself. In the acquisition of this task, some rats develop position habits, showing more or less marked preferences for turns in one direction. Other rats, by contrast, show little evidence of such a bias, tending to emit left and right responses in roughly equal proportions. The strength of this "turning ratio" was computed as the absolute difference between 0.5 and the quotient of right-response trials to total trials. This water-maze bias proved to be unrelated in direction or strength to the open-field, step-down, and rotatory-swimming biases. Because the lateral choices made by the animal during this training are doubtless influenced by the reinforcement it receives on the first (and subsequent) trial(s), we would not advocate this measure as an appropriate assessment of an endogenous *directional* bias of the animal. Nevertheless, it did provide for a direct assessment of the *strength* of bias shown during task acquisition.

The expectation of a monotonic relationship between behavioral bias and left-right learning scores was unconfirmed. For all indices of behavioral bias, the Pearson correlations with the water-maze scores were close to zero and nonsignificant (see Table 1).

An alternative account can be advanced, however, which preserves the argument that perfect lateral symmetry should make the distinction between left and right impossible, but which questions the assumption that a steadily increasing degree of asymmetry would prove to be increasingly advantageous. Several neural asymmetries have been documented in rats (Glick, 1985, *passim*). The degree of asymmetry in a population of rats may center on a moderate, and optimal, level, with some individuals possessing more or less asymmetry than the optimum. It would still be expected that individuals at the lower extreme of asymmetry (i.e., those with relatively symmetrical neurobehavioral systems) would do poorly at left-right response differentiation, because they lack a sufficiently strong internal left-right reference. But at the high end of the range of endogenous asymmetry, too strong a resultant behavioral

TABLE 1
Relationships between Left-Right Response-Differentiation Scores and Strengths of Behavioral Lateral Biases

| Behavioral bias | Monotonic model Pearson <i>r</i> | Curvilinear model <i>F</i> (quadratic) |
|-------------------------------------|-------------------------------------|---|
| Open-field test | | |
| Initial turn | -.066 | 1.989 |
| Initial direction | -.142 | 1.128 |
| Wall-hugging ratio | .030 | 0.103 |
| Step-down test | | |
| Direction of head | .044 | 0.849 |
| Direction of forefeet | -.071 | 0.940 |
| Direction of back feet | -.082 | 0.632 |
| Rotatory-swimming test | | |
| Circling ratio | -.065 | 0.321 |
| Left-right response differentiation | | |
| Turning ratio | -.004 | 5.103* |

* $df = 1, 101$; $p = .026$.

bias would also prove to be disadvantageous for an animal faced with the water-maze task presented here, requiring as it does equal readiness to respond leftward or rightward. A moderate degree of bias would both provide an internal "navigational" reference and allow for the necessary readiness to emit either a left or a right response. Thus a U-shaped relationship would be predicted between response differentiation and strength of lateral bias (cf. Glick, Zimmerberg, & Jerussi, 1977).

We therefore applied multiple-regression analysis to determine whether the water-maze scores were significantly related to the square of each of the aforementioned indices of bias strength (i.e., whether the function relating the learning scores to the bias had a significant quadratic component). The answers were for the most part negative (Table 1). However, the analysis involving the bias derived from the water-maze behavior itself revealed the quadratic component to be both significant ($p = .026$) and of the predicted form, moderate degrees of bias being associated with lower trials-to-criterion scores than either low or high degrees of bias. Evidently, moderately biased rats made reference to the bias shown during this task—or to its underlying neural substrate—and suffered neither from too weak an internal reference nor from too strong a tendency to turn unidirectionally.

That moderately biased rats were better at acquiring the left-right response differentiation than rats which during acquisition emitted left and right responses closer to a 50:50 proportion, despite the fact that the task required the ultimate achievement of responses mixed in just such a proportion, clearly suggests that at least some asymmetries can

be usefully consulted by an animal processing left-right information. Future research should focus on what characterizes a consultable asymmetry and on the mechanism of consultation itself.

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