Failure of Induced Asymmetries to Improve Left–Right Response Differentiation in the Rat

MICHAEL NOONAN
Department of Psychology
Canisius College, Buffalo

SEYMOUR AXELROD
Department of Psychiatry
State University of New York at Buffalo

ABSTRACT. Rats (and humans) appear to be able to distinguish between left and right by referring to an intrinsic asymmetry as a navigational aid; this suggests that experimentally induced asymmetries might also facilitate such a distinction. We assessed the effects of asymmetries produced by unilateral shaving, unilateral vibrissotomy, and asymmetrical cortical lesions on acquisition of a left–right response differentiation. None of the treatments improved performance relative to appropriate control treatments; the rats were evidently unable to use these induced asymmetries to form the lateral differentiation. The results are related to evidence provided in an earlier report (Noonan & Axelrod, 1989) that even some reliable intrinsic asymmetries cannot function as navigational aids.

SEVERAL LINES OF EVIDENCE, consistent with arguments presented by Corballis and Beale (1976), suggest that in both humans and rats a lateral asymmetry of the central nervous system (CNS) is a necessary condition for efficient distinction between left and right. For example, left–right discrimination in children increases monotonically with age from about 5 years to about 12 years (Belmont & Birch, 1963; Boone & Prescott, 1968), an increase that may be attributable to a parallel development of hemispheric specialization. Boone (1965) also suggested that left–right discrimination in children improves *pari passu* with the development of stable handedness (and of whatever brain asymmetry underlies handedness), although there is evidence (Belmont & Birch, 1963) that the establishment of stable handedness lags behind lateral discrimination of personal body parts.

Another example derives from a tachistoscopic study requiring judgments of the congruence between the direction of tilt of a "T" figure and an accompanying verbal label; Manga and Ballesteros (1987) found a right-visual-field advantage with a group of adult human subjects who had reported that they rarely or never experienced difficulty in identifying left or right, but found no interfield difference with subjects who had reported that they frequently or always experienced such difficulty. Manga and Ballasteros attributed the Field × Group interaction to the presence in the first group and absence in the second of lateralization in the CNS of the functions tapped by the task.

Most rats injected with *d*-amphetamine display pronounced and reliable biases toward circling either to the left or to the right (Jerussi & Glick, 1976); in some rats,the bias is slight or absent. The direction chosen by biased animals has been linked to an intrinsic asymmetry in the nigro-striatal dopaminergic system (Glick & Shapiro, 1985). Zimmerberg, Strumpf, and Glick (1978) found that strongly biased rats had better acquisition and retention scores than unbiased rats on a task requiring consistently unilateral responses in a T-maze. Zimmerberg et al. (see also Glick, Zimmerberg, & Jerussi, 1977) likened the nigro-striatal asymmetry presumably underlying the directional bias to a navigational instrument: Just as reference to a magnetic compass enables the determination of north and south, so reference to the lateral asymmetry allows the rat to distinguish between left and right.

Corballis and Beale (1976, pp. 149 ff) reviewed evidence that left–right discrimination by children can be facilitated by a variety of procedures that induce perceptual–motor asymmetries. We report here on three attempts to improve rats' proficiency in acquiring a left–right response differentiation by inducing pronounced asymmetries, thus providing them with a strong basis for reference. In the first two experiments, the somesthetic states of the animals were made strikingly asymmetrical on the assumption that the induced asymmetries would result in corresponding central asymmetries; in the third experiment, CNS asymmetries were produced directly by aspiration of cortical tissue.

Subjects and Lateral Response-Differentiation Task

Subjects were adult black-hooded Long-Evans rats of both sexes. In all three studies, rats were trained to escape from a water-filled T-maze. At the 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, 80-cm long; an escape ramp at the end of the correct alley, but out of sight from the choice-point, served as the reinforcer. Water and room temperature 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 approximately 3 min), until the criterion of 10 consecutive correct responses was reached; the number of trials taken to reach this criterion was the dependent variable in all three experiments.

Experiment 1: Short-Term Lateral Depilation

Reasoning that the central somesthetic representation in a rat whose body has been deprived of hair on one side must be decidedly asymmetrical, and that the rat could use the asymmetry to distinguish between left and right, we used an electric clipper to remove all the hair from the entire left or right body half (including all hair and vibrissae on the head, trunk, and legs of that side) of 18 rats. As controls, 18 other rats were clipped on their dorsal or ventral body halves. The rats were then housed together in a large, environmentally enriched community cage for 3 days, after which they were moved into individual cages. Water-maze training began on the 4th day after clipping.

Results

Contrary to our hypothesis, the rats with induced lateral asymmetries (left or right side clipped) did not learn the left–right response differentiation significantly faster (M trials to criterion $\pm$ SEM = 50.6 $\pm$ 3.8) than the rats with the dorsal or ventral treatments (M = 44.8 $\pm$ 3.5).

Experiment 2: Long-Term Lateral Vibrissotomy

Steiner, Huston, and Morgan (1986) found evidence suggesting that 10 days of daily unilateral shaving of the mystacial vibrissae in rats produced an asymmetrical CNS effect resembling denervation supersensitivity. Reasoning that the induction of such an effect ought to facilitate the distinction between

left and right responses, we formed two groups of rats. One group comprised 19 animals whose mystacial vibrissae (on one side or the other) were cut close to the skin thrice weekly over a period of 75 days. Twenty rats served as controls, having either the dorsal or ventral half of their vibrissae repeatedly cut bilaterally. After the 75th day, the whisker-trimming continued as the rats proceeded through water-maze testing.

Results

The findings again failed to support the hypothesized relationship between induced lateral asymmetry and acquisition of left–right response differentiation. The combined left- and right-trimmed subjects averaged 66.0 ± 5.7 trials to criterion, which was not significantly different from the mean of the combined dorsal- and ventral-trimmed animals, 62.8 ± 5.1.

Experiment 3: Symmetrical and Asymmetrical Neocortical Ablations

We compared the left–right response-differentiation scores of rats given asymmetrical cortical lesions with the scores of control rats given symmetrical lesions. With the anesthetized rat placed in a stereotaxic apparatus for stability, the cortex was exposed, and aspiration lesions (approx. 10 mm²) were made in the cortex in one of the following four configurations: bilateral anterior ($n = 8$); bilateral posterior ($n = 8$); right anterior, left posterior ($n = 7$); right posterior, left anterior ($n = 7$). The anterior lesions were placed 2 mm posterior to the coronal cranial suture, and the posterior lesions were placed 2 mm anterior to the lambdoidal suture; all lesions were placed 5 mm lateral to the sagittal suture. In a fifth group, ($n = 8$), the cortex was exposed, but no lesions were made. Maze training began 27 to 30 days later.

Results

Unsurprisingly, the group comprising all animals with cortical lesions required more trials to reach criterion (72.6 ± 3.0) than the group without lesions (58.5 ± 5.8), $p < .02$, one-tailed t test. But the hypothesis that asymmetrical lesions would confer an advantage when compared with symmetrical ones was not confirmed: The combined groups with asymmetrical lesions did not require fewer trials (73.6 ± 4.4) than those with symmetrical lesions (71.8 ± 4.2).

Discussion

Four explanations for the failure of the induced asymmetries to facilitate left–right response differentiation suggest themselves.

1. The assumption that left–right response differentiation can only be accomplished by reference to an asymmetry carried by the subject may be incorrect, although the arguments provided by Corballis and Beale (1976) appear to make the assumption inescapable.

2. We have elsewhere proposed that rats as a group are centered on an optimal degree of asymmetry (Noonan & Axelrod, 1989); the additional asymmetries we produced here might therefore have disrupted the rats' processing of the information provided by their intrinsic "navigational instruments". If this was the case, then the control groups might have been expected to perform better than the experimental groups. Although in all three experiments, the trials-to-criterion means of the control groups were in fact lower than those of the experimental groups, the differences were slight and would not have been statistically significant, even with one-tailed tests.

3. Our manipulations were performed on adult rats. It is possible that, had the asymmetries been introduced at an earlier age, they might have been more readily integrated into the animals' navigational experience, and therefore might have become consultable navigational aids.

4. It seems most reasonable to conclude that not every central asymmetry, whether induced or intrinsic, can function as a navigational aid, and that the induced asymmetries were simply not ones that could be referred to by the rats; an unconsultable compass is of no use in distinguishing north from south. If the only central asymmetries rats can refer to when making lateral discriminations are in a restricted group of structures, then only manipulations that affect those structures ought to influence such discriminations. The implication would be that our manipulations did not affect the relevant structure(s).

Consistent with the interpretation that only a subset of possible asymmetries are available for directional orientation is our earlier finding (Noonan & Axelrod, 1989) that learning scores on the left–right response-differentiation task used here were (nonmonotonically) related to the strength of position habits exhibited during acquisition, but not to the strengths of reliable lateral biases in open-field, step-down, or rotatory-swimming tests. The intrinsic CNS asymmetries underlying those biases were, like those induced in the present experiments, not available for consultation in making the left–right discrimination in the water maze. A programmatic set of investigations aimed at specifying which intrinsic and induced asymmetries can provide a usable reference, and which cannot, would go a long way toward elucidating the mechanisms of lateral discrimination.

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