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MASS FUNCTION AND EQUIPOTENTIALITY: A REANALYSIS OF LASHLEY'S RETENTION DATA

ROGER K. THOMAS, JR.[1]

University of Georgia

Summary.—Detailed analyses of "subgroups" of *S*s, defined by lesion size and locus, for Lashley's (1929) retention data suggested that parietal neo-cortical damage resulted in deficits that were relatively independent of total lesion size. It was suggested that Lashley's retention data provided questionable support for the principles of equipotentiality and mass function as he presented them and he did not include enough *S*s to assess the validity of these principles for measures of acquisition following brain damage.

The history of explanations of cerebral cortical functioning shows that opinions about this process have alternated between a position which held that specific functions are localized in specific cortical areas and a position which held that the cortex functions as a unit or mass [see Boring (1950, Chapters 3 and 4; Krech, 1962) for detailed historical accounts]. Perhaps the best known statement of the "mass function" position was Lashley's (1929) which held that the amount of cortex removed was the determinant of behavioral deficit and not the place in the cortex from which tissue was removed. A corollary to the principle of mass function, also suggested by Lashley, was the principle of "equipotentiality." Equipotentiality held that one area of the cortex might take over the function of another if one area were destroyed; this was said to be particularly applicable to the association areas.

Lashley's principles of mass function and equipotentiality (1929) have been disputed in certain contexts (see Morgan, 1951, pp. 777-779); however, a recent authority summarized the current view of these principles as follows:

> While some recent reports take exception to these principles, Lashley's conclusions still hold for the effects of cortical lesions on alley-maze performance of rats (Chow, 1967, p. 707).

The present work reexamined some of Lashley's data (1929) which were important in the derivation of the principles of "mass function" and "equipotentiality." Specifically, the data reexamined were the error scores in retention of the Lashley III maze and the locus of the lesions in the rats from whom the error scores were determined. It will be helpful first to review Lashley's training procedures.

> Rats were trained in Maze III. . . . After adaptation in the food compartment, they were given 1 trial on the first day of training and 5 trials per day thereafter until a record of 10 consecutive errorless trials (criterion of learning) was obtained. With the com-

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pletion of these trials, training was discontinued for 10 days; then retention tests (preliminary retention tests) were given. These consisted of retraining with 5 trials per day until the criterion of learning was again attained. The animals were then immediately subjected to operation. Ten days after operation, retraining was carried out as before, training being continued until 10 consecutive errorless trials were obtained, or until 150 trials had been given . . . (Lashley, 1929, p. 89).

The quantitative data in question here may be seen in Lashley's Table XIV (1929, pp. 92-93), and the lesion diagrams may be seen in the appendix of the same text, Plates V through VII. Lashley's general conclusion about these data was:

In evaluating these data, it must first be noted from Table XIV that no case with less than 10 per cent of the entire cortex destroyed shows any significant loss of the habit, whatever the locus of the lesion, and that serious disturbance of the habit is rare in any case with less than 15 per cent destruction (Lashley, 1929, p. 95).

While Lashley gave himself some leeway with regard to the 15% figure, this figure has nevertheless become a "rule of thumb" for lesion sizes necessary to affect retention of the Maze III. For example, Rosner (1953) did a general study of maze retention as a function of neocortical lesions which included a replication of Lashley's work described above. Rosner explicitly agreed with Lashley's conclusion about "mass action" and the 15% minimal lesion; however, the smallest lesion in his replication of Lashley's work was 17.9%.

Statistical comparisons of the pre- and postoperative errors in retention for various "subgroups" (as determined by this investigator) according to lesion size gave the following results: (a) *Ss* with lesions ranging in size from 4.5 to 4.9% (Nos. 60—64, Lashley's Table XIV) did not differ significantly on the pre- and postoperative retention measures. (b) *Ss* with lesions ranging from 6.1 to 8.7% (Nos. 65—69) differed significantly on the pre- and postoperative tests (Mann-Whitney U^2, $p = .004$); however, the greater deficit was seen on the preoperative test (this is not surprising because *Ss* might have benefited from the additional experience of the preoperative retention test). (c) *Ss* with lesions ranging from 9.7 to 11.0% (Nos. 70—74) had significantly more errors on the postoperative retention test (Mann-Whitney U, $p = .008$). (d) *Ss* with lesions ranging from 11.6 to 14.9% (Nos. 75—87) had significantly more errors postoperatively (Mann-Whitney U, $p < .002$).

It might be reasonable then to conclude that the minimal lesion which may have a significant effect on retention of the Lashley III maze is 9.7%, not the 15% minimum often cited; this in itself does not seriously question the mass

[2]The question may be raised whether the observations in question are independent and, therefore, whether the Mann-Whitney U test is appropriate. The writer's decision regarding the independence of the observations was based on (a) lack of significant correlation between the pre- and postoperative error scores ($r_s = 0.035$) and (b) satisfaction that Walker and Lev's criterion that "two observations are considered to be independent when information about one of them provides no clue whatever as to the other" (Walker & Lev, 1953, p. 14) has been met.

function principle but merely reduces the mass required; however, a further analysis which takes into account the location of the lesions suggests different conclusions.

The animals with lesions ranging from 9.7 to 11.0% (Nos. 70—74, see Plate VI) had lesions entirely confined to the parieto-occipital region of the neocortex, suggesting that this area might not be equipotential with others. Other investigators who have used rats, cortical lesions, and mazes have provided evidence which suggested that the rat's parieto-occipital neocortex may be special in maze behavior (Krechevsky, 1935; Forgays, 1952; Thomas, 1966). In view of this possibility, the animals with lesions ranging from 11.6 to 14.9% (Plates VI and VII) were divided into a group identified as having parieto-occipital involvement (Animals No. 76, 77, 79, 81, 83) and a group with minimal or no parieto-occipital involvement (Nos. 75, 80, 84, 87); four *S*s were difficult to place in the above groups so they were placed in a questionable group (Nos. 78, 82, 85, 86). These four questionable *S*s had parietal involvement, but in conjunction with the frontal or temporal cortical areas rather than the occipital. Statistical analyses for three subgroups (Mann-Whitney *U*s) showed that the group with parieto-occipital damage had significantly more errors postoperatively ($p < .016$), and the questionable group (with parietal + frontal or parietal + temporal damage) had significantly more errors postoperatively ($p = .014$). However, the group with minimal or no parieto-occipital damage did not differ significantly on preoperative and postoperative retention error scores ($U = 6.5$).

It appears that parietal involvement had a significant effect on maze retention that was independent of lesion size. One qualification to the present conclusion must be given. The rats with lesions ranging from 4.5 to 4.9% (Nos. 60—64) which showed no behavioral deficit had lesions in the parieto-occipital area, so something of a mass effect must be operating. Unfortunately for the present analysis, the lesions of the animals ranging from 6.1 to 8.7% were mainly outside the parieto-occipital area.

Lashley's data included animals with large neocortical lesions (as much as 31% damage) that made few errors postoperatively. However, he included a composite diagram of these animals (his Fig. 22, p. 94) which indicates that the parietal region considered in the Forgays (1952), Krech (1935) and Thomas (1966) studies was spared from much damage. Lashley did not overlook this spared common area but dismissed its significance by stating "these regions escaped destruction in many cases that lost the habit." It should be noted, however, that loss of habit following destruction of areas other than the parietal does not preclude the parietal area's being more significant to the maze habit than other areas. The point of the present analysis is that the parietal area appears not to be equipotential for the maze habit, and it is suggested that a certain amount of damage in this area is significantly related to the disruption of maze retention

whereas much more damage appears to be necessary for other areas of the brain to disrupt retention.

Lashley did not deny localization of function for man or rat, as a more detailed examination of his works makes clear (see Beach, Hebb, Morgan, & Nissen, 1960; Hebb, 1963), and his sophistication and leadership in neuropsychology were unsurpassed. However, he apparently did believe that the principles of mass function and equipotentiality were valid for acquisition and retention of complex alley mazes by the rat. The present work suggests that these historically important neurological principles received questionable support in Lashley's retention data (1929), and his data on acquisition did not include a sufficiently large number of *S*s and lesion sizes to permit a detailed reanalysis such as that done for the retention data. Apparently, Lashley derived the principles of mass function and equipotentiality as applied to maze retention from the more obvious trends in the data rather than the differences that finer statistical analysis yields (it should be noted, however, that Lashley did not have available to him the statistical techniques, particularly non-parametric, that are available today).

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