

Brief Communication

An equipotential function of the cerebral cortex

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Rats were prepared with serial injuries to the neocortex. Their postoperative performance of a learned task, when measured after each procedure, confirmed two predictions from a quantitative theory that the neocortex is equipotentially involved in remembering of memories.

The mammalian neocortex is a highly differentiated organ. Its various subregions have been shown to be involved in the performance of different kinds of functions. However, the study we describe in this report completes what we believe to be a proof of the existence of an equipotential function of the cortex in remembering (Cloud, D. R. Meyer, & P. M. Meyer, 1982; P. M. Meyer & D. R. Meyer, 1982).

The study assessed the performances, by rats, of a brightness-discrimination problem. Male Long-Evans hooded rats, 3 months of age, were used. The animals were first trained, with shock avoidance as the motive, to exit from a choice compartment by selecting a white door instead of a black door. Then they were prepared, by the pia-stripping method, with an injury to a posterior quadrant of the cortex, that is, of all of the cortex that lies posterior to bregma and between the rhinal and the longitudinal fissures. Then, after 12 days' recovery from surgery, they were given retraining on the problem and, after having reached the preoperative criterion of performance, were subjected to second-stage injuries that destroyed both anterior quadrants of the cortex. Then they were retrained on the problem once again; after completion of that final phase, their brains were removed and reconstructed through the use of Nissl methods. The behavioral, surgical, and histological procedures were described in detail in D. R. Meyer and P. M. Meyer (1977).

The question was whether we could accurately predict the number of trials the subjects would require to relearn and re-learn the problem. We have previously observed that if trained with our procedures, a rat with an injury to a quadrant of the cortex will relearn the problem in 8.5 ± 1 mean trials. It does not matter whether the injury is anterior or posterior, even though the problem is a

visual task and a posterior injury destroys the zones of termination of the visual projections (Hughes, 1977; D. R. Meyer & P. M. Meyer, 1977).

We also have observed that, with only one exception, animals with first-stage two-quadrant injuries relearn the problem in 17 ± 2 trials. That is twice the cost of a one-quadrant injury to the cortex, and suggests that impairments of performance of the problem are governed by a law of mass action. We have found that that law describes the impairments of bilateral anterior preparations, of subjects with either left- or right-sided hemidecortications and of subjects with an injury to one posterior quadrant and the contralateral anterior quadrant (Cloud et al., 1982; Hata, Diaz, Gibson, Jacobs, P. M. Meyer, & D. R. Meyer, 1980).

The exception to the law is that rats that are prepared with first-stage ablations of both posterior quadrants require 25 trials, instead of 17, to relearn the problem after surgery (Gray & D. R. Meyer, 1981). We have argued that the difference of 8 mean trials is the regionally specific cost of an injury that destroys or completes the destruction of the posterior cortex. We also have argued that the rest of the cost, that is, of 17 mean trials, is due to an impairment of a function that is shared by all subsectors of the cortex.

We have found that the two hypothetical impairments can be dissociated, because the main impairment will not reappear after second-stage injuries to the cortex. For example, if a rat with a one-quadrant injury is given retraining on the problem and is re-retrained after having been subjected to a second-stage injury to the cortex, it will re-learn the problem essentially at once if it still has one posterior quadrant (Cloud et al., 1982; Glendenning, 1972). However, if its second-stage injury completes the destruction of both posterior quadrants, the animal will re-learn the problem in 8 mean trials (Cloud et al., 1982; Gray & D. R. Meyer, 1981). We believe that the regionally specific impairment is due to a loss of form vision (Horel, Bettinger, Royce, & D. R. Meyer, 1966; Lavond & Dewberry, 1980; Lavond, Hata, Gray, Geckler, P. M. Meyer, & D. R. Meyer, 1978), but will stress

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once again that the cost of that impairment is small when compared with the nonspecific costs of injuries to the posterior cortex.

Now we shall state our predictions from the theory of the outcomes of the present study. The animals' first-stage injuries destroyed a posterior quadrant of the cortex, and hence, we expected them to relearn the problem in 8.5 mean trials. Their second-stage injuries were bilateral anterior ablations, and hence, since they were left with one posterior quadrant, we expected them to re-learn in 2-3 trials. Effectively, the latter is a zero score, for 2-3 trials is what would be expected had the rats been retrained after first-stage injuries and then re-retrained as a test of forgetting without having undergone the second-stage surgical procedures (Glendenning, 1972).

Were the two predictions accurate? We found that the five rats of the study relearned the problem in 7.4 ± 2.3 mean trials. They re-learned the problem in $3.4 \pm .5$ mean trials. Hence, both predictions were confirmed within about 1 mean trial, even though the methods of the investigation involved five successive procedures that required about 4 weeks to execute. Histological evaluations showed that the extent of neocortical damage and dorsal thalamic degeneration was comparable to that of previous investigations (Hata et al., 1980; Howarth, D. R. Meyer, & P. M. Meyer, 1979).

Figure 1 compares the study's final result with those of similar investigations. Groups in which unilateral injuries were performed were balanced with respect to laterality. In Group A of the present study, the animals were

trained (TR), prepared with a first-stage ablation (shown in black), retrained following recovery from surgery (RT), prepared with a second-stage ablation (shown in black, with the first-stage ablation shown in cross-hatch), and finally tested for ultimate performance of the problem. The procedural description is followed by the theoretic mean score for the group (TS), and then by the rounded observed mean score for the group (OS). The standard errors for the latter scores are not included, but were typically about 10% of the mean observed score.

The findings for Groups A ($n=5$), B ($n=19$), C ($n=12$), and D ($n=19$), which were all trained as normals and then retrained between operations that spared at least one posterior quadrant, were essentially the same regardless of the scopes and loci of the first operations (Cloud et al., 1982; D. R. Meyer & P. M. Meyer, 1977). Their scores were also within 2 trials of the TS obtained from Group E ($n=14$), which were not subjected to a second operation and provided a control for forgetting of the problem over time (Glendenning, 1972). Hence, for such subjects, the second operations had a trivial effect upon performance.

The findings for Groups F ($n=7$), G ($n=6$), H ($n=14$), and I ($n=6$) were also approximately the same. However, the second operations for those subjects completed the bilateral destruction of the posterior cortex, and hence they required about 8 mean trials to recover from their posteriorly specific impairments (Cloud et al., 1982; D. R. Meyer & P. M. Meyer, 1977). The Group F result is particularly striking, for the animals required only 7 mean

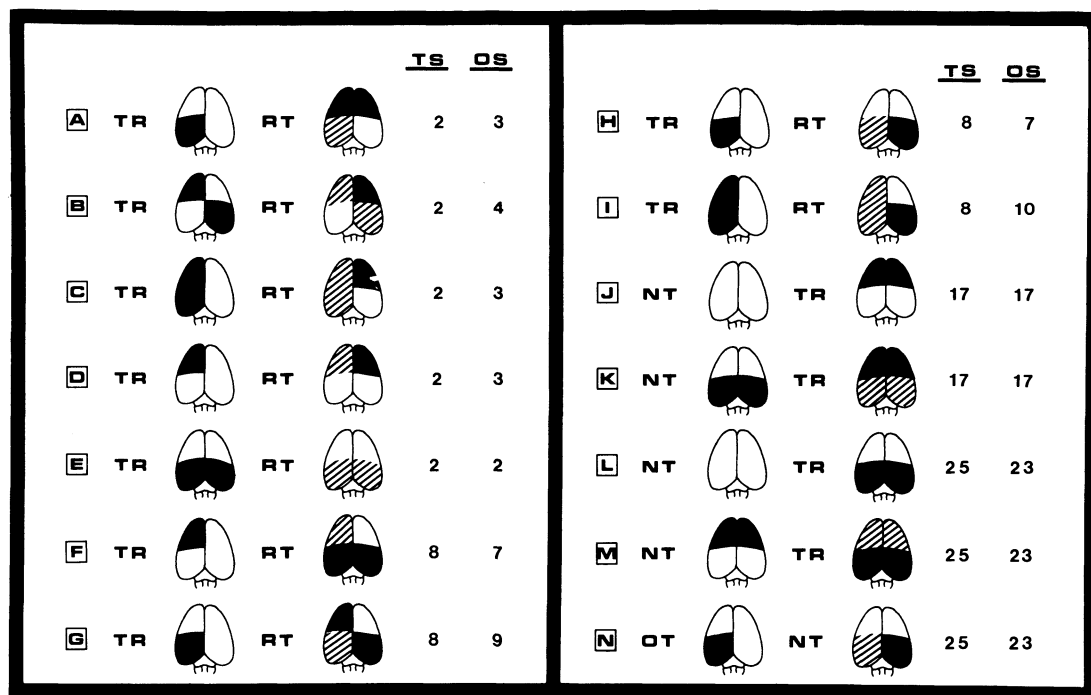


Figure 1. A comparison of the study's final result (Group A) with those of other studies in which similar procedures were employed. TS = theoretic mean score; OS = observed mean score; TR = training; RT = retraining; NT = no training; OT = overtraining.

trials instead of the 25 trials that it takes a first-stage bilateral posterior preparation to relearn the problem after surgery. The difference of approximately 17 trials is what would be expected from our theory on the grounds that the retraining following an injury to any quadrant of the cortex will protect an animal from any further cost of an injury to the equipotential mechanism. Moreover, and importantly, the savings were observed even though a first-stage anterior injury has no histologically detectable effect upon the visual pathways to the cortex (Hata et al., 1980).

The findings for Groups J (n=21), K (n=22), L (n=14), and M (n=68) show that if preoperative training is omitted (NT), the cost of a second-stage injury to the cortex is the same as the cost of a first-stage injury of the same scope and placement (Hata et al., 1980; Howarth et al., 1979; D. R. Meyer & P. M. Meyer, 1977). Hence, interoperative training on the problem conveys no protection of ultimate performance unless it is given to a subject with a memory to remember. The finding for Group N (n=15) shows that the effects of training both before and between the operations are not merely due to overtraining, for preoperative overtraining (OT) of a normal subject conveys no protection unless the subjects are also trained between operations (Glendenning, 1972).

We believe that the findings completely satisfy the requirements for a proof of the existence of a function that the cortex performs as a whole. Thus, we have shown that impairments of the function can be dissociated from a regionally specific deficit, and when that is done, that the effects of ablations of various scopes and placements are in very close concordance with predictions from the law of mass action. Also, we have shown that within broad limits, any kind of injury to the neocortex will permit the induction of recoveries from impairments of the function. And third, we have shown that the recoveries are jointly contingent upon retraining and the presence of a previous injury, which suggests that the function of the holistic system is retrieval of stored information.

We believe that our conclusions are significant because they suggest a partial basis for Hughlings Jackson's (1873) law of momentum. Neurologists have long been puzzled by the fact that slowly growing lesions of the cerebral cortex will often fail to yield presenting symptoms until the injuries are astonishingly large. There are, of course, exceptions to the rule: Thus, a very small somatomotor lesion is likely to be noticed at once. But lesions that produce impairments of remembering can easily be missed by the patient, for they tend to come and go and hence can be

confused with episodes of normal forgetting. We suggest that the impermanence of such impairments is due to compensations for impairments of cortical retrieval, and that memories, once recalled, remain accessible despite further growth of the lesion. But memories that are not recalled will not be protected, and hence a time will come when it will be apparent to the patient that he has a serious problem. When that will happen will depend, in part, upon the life-style of the individual, for a person who operates with very few memories will be the most vulnerable and soon will discover that the ones he has not used have been lost.

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