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CORTICAL ORGANIZATION IN GUSTATION (MACACA MULATTA)

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THE EVIDENCE for a cortical representation of gustation in primates is meagre and inconsistent. In a recent publication, Patton (11) reviews the experiments implicating the parainsular opercular cortex near the foot of the central fissure. He agrees, however, that the experiments reviewed are inconclusive, especially with respect to the possible role of the Island of Reil. He does state that the evidence seems to vindicate Bornstein's (5, 6) rejection of the classical view which places the representation of taste in the temporal allocortex. However, such an interpretation fails to account for the finding that, following temporal lobectomy, monkeys show a marked change in dietary habits (8).¹

Several primate studies concerning these problems have been completed since Patton's review. No alteration of quinine acceptance thresholds follows extensive ablation of the lateral parieto-temporo-preoccipital cortex (2). Dissociation of the change in dietary habits from a change in quinine acceptance threshold has been reported in two series of experiments: Following temporal lobectomy or anteromedial temporal ablations a marked change in dietary habits from herbivorous to omnivorous is not accompanied by any marked change in acceptance threshold for quinine (2, 13). On the other hand, ablations in the neighborhood of the anterior insula do alter quinine acceptance thresholds although no change in dietary habits can be observed (13). This report deals with experiments designed to amplify the latter observation.

MATERIALS AND METHODS

Six immature rhesus monkeys were used. Pre- and postoperative determinations were made of their acceptance of various dilutions of quinine hydrochloride solution by the method described by Patton and Ruch (12). Data were plotted as preference threshold curves (10). Each plotted point for percent quinine solution of total fluid drunk represents the average values obtained in two separate tests for each concentration. Reliability of the method is shown by the distribution of the rejection thresholds in a total of ten normal monkeys as compared with those of Patton (Fig. 1).

Subpial ablations were made with a 19-gauge sucker after separation of the lips of the sylvian fissure by gentle dissection. One monkey received an ablation intended to be restricted to island cortex; in another the ablation was intended to include island cortex plus anterior supratemporal plane; a third monkey received an ablation intended to include

¹ Analysis of the relative importance of visual, tactile, and olfactory stimuli in determining food selection has not been systematically performed. However, it seems permissible to include observations on dietary habits in a discussion of taste, since gustatory stimuli must be used in food selection even if they are not the sole basis on which such selection is made.

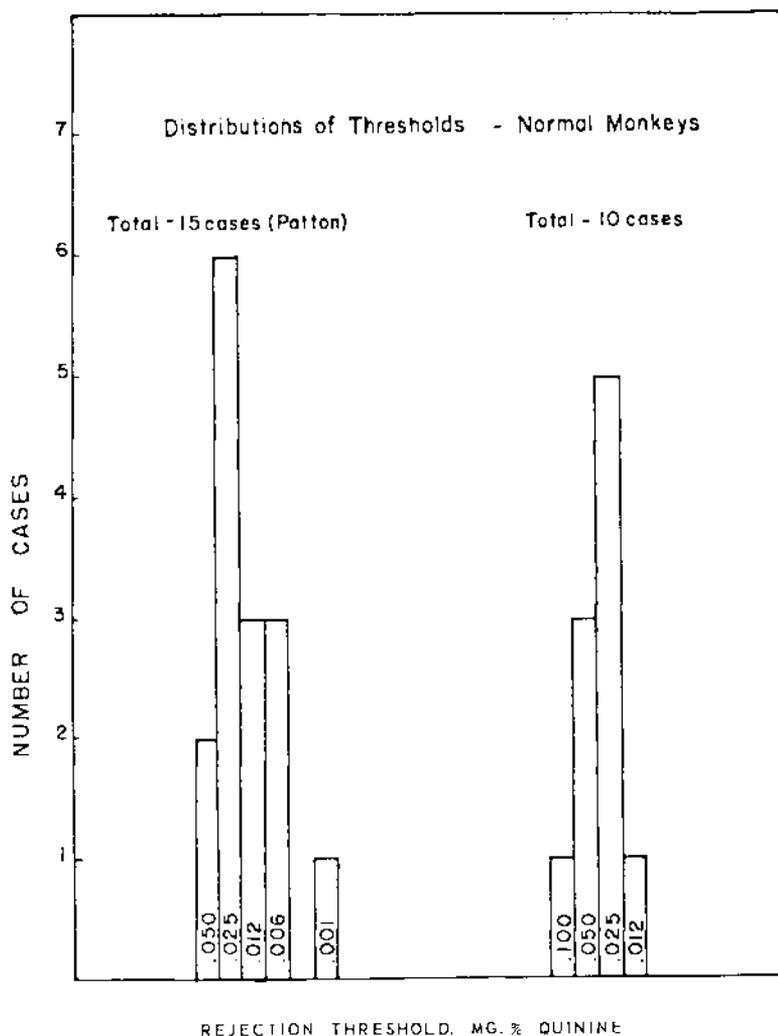


FIG. 1. Comparison of rejection thresholds for ten normal monkeys, represented on right, with those obtained by Patton (10), represented on left. Numbers in bars refer to concentration of solution of quinine hydrochloride.

only insula and operculum. The other three animals were given ablations including insular, opercular, and anterior supratemporal cortex. After completion of the testing program, all animals were sacrificed, their brains perfused with saline and formalin, fixed, dehydrated in alcohols, imbedded in celloidin and serially sectioned. Nissl preparations were made; from them the lesions were reconstructed and thalamic degeneration described. The lesion in one of the brains with the more extensive ablations was found to invade the internal capsule deeply; despite a severe ageusia, this animal is therefore not included in the report.

RESULTS

Lesions restricted to the cortex of the Island of Reil or to this cortex plus that of the anterior supratemporal plane resulted in no change of acceptance threshold to quinine (Figs. 2, 3). Partial ablations of island cortex and ante-

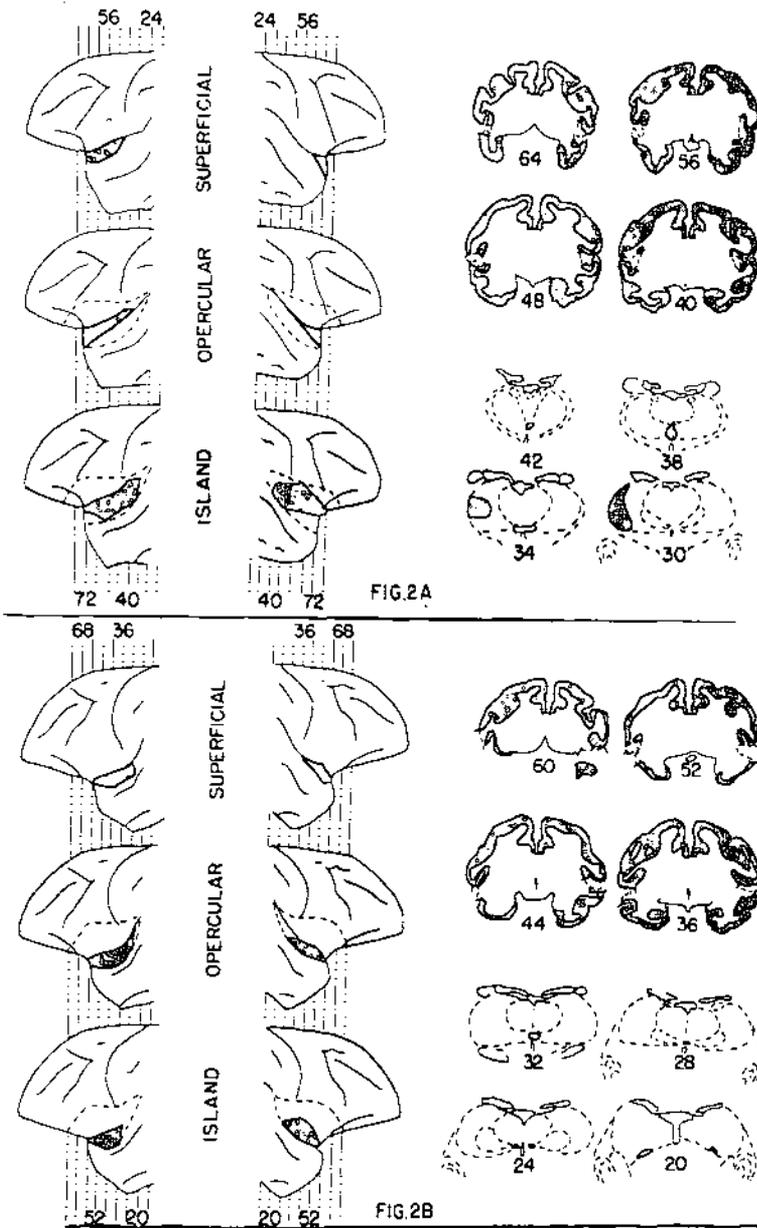


FIG. 2. A: Representation of brain of monkey with ablation of cortex of Island of Reil. Reconstruction of superficial lesion, involvement of operculum and supratemporal plane, and island appear on left. On right representative cross sections through lesion and through thalamus show depth of ablation and involvement of thalamic projections. Black indicates lesion on reconstruction; dashed lines, outline of island. Retrograde degeneration in thalamus is shown in black. On cross sections through lesion, cortex appears in black and lesion is indicated by dashes. Gustatory preference threshold curves for this animal shown in Fig. 3A. B: Representation of brain of monkey with ablation of cortex of Island of Reil and of anterior supratemporal plane. Reconstructions and representative cross sections as in A. Gustatory preference threshold curves for this animal shown in Fig. 3B.

rior supratemporal plane plus operculum resulted in marked (above 30 per cent acceptance at 0.05 g. per cent quinine hydrochloride solution) and prolonged (3-6 months) ageusia (Figs. 4, 5). An ablation which included portions of island and opercular cortex with only minimal invasion of the supratemporal plane resulted in a moderate (above 30 per cent acceptance at .0125 g. per cent quinine hydrochloride solution), though sustained (2 months) ageusia (Figs. 6, 7).

Retrograde degeneration was present in the n. medialis ventralis of the thalamus in all brains, thus linking the projection of this nucleus to the anterior portions of the Island of Reil.² In addition, retrograde degeneration in the n. ventralis posteromedialis (arcuate) was present in the brains of all animals which had shown an ageusia. This supports previous findings (7, 10, 18) that the projection of this nucleus terminates in the frontal operculum. Where anterior supratemporal plane had been resected, degeneration was found in the nucleus limitans of the medial pulvinar.

DISCUSSION

Ablations limited to the anterior portion of the Island of Reil and anterior supratemporal plane, or to the operculum (10), are insufficient to produce ageusia. Only combined removals of cortex from the anterior part of the island and operculum alter a monkey's quinine acceptance threshold. Extension of the lesion to involve additional cortex in the anterior supratemporal plane produces a marked and prolonged ageusia. It appears, therefore, that the "primary" cortical representation of taste includes this entire extent of anterior sylvian (opercular, insular, and supratemporal) cortex, with a gustatory "macula" focussed on the junction of the frontal operculum and the anterior insula.

In Patton's animals with opercular lesions, retrograde degeneration in the nucleus ventralis posteromedialis (arcuate) was massive (10). Thus failure of these animals to show ageusia suggests that destruction of this nucleus alone was not the cause of the ageusia reported by Blum *et al.* (3) in their thalamic taste studies. The present experiments implicate all nuclei located near the midline and surrounding (but not including) the n. centromedianum in gustatory mechanisms.

The "primary" representation of taste defined in this study can be compared to the striate cortex in vision. An animal's ability to perform visual discriminations remains intact if even a small portion of the geniculostriate system is functioning (17). In like manner, ageusia results only when extensive ablations are made of anterior sylvian cortex. As in vision, however, deficits in discrimination are produced by invasion of another cortical sys-

² This observation conflicts with that of previous reports which have placed this projection to (i) the anterior temporal (10) or (ii) the subcallosal cortex (11). The former finding can be explained by assuming that the projection from the thalamus to the island was interrupted by the anterior temporal ablation which, in order to include the amygdala, extended deep into the hemisphere. The latter finding is a discrepancy which must await further experiments for clarification.

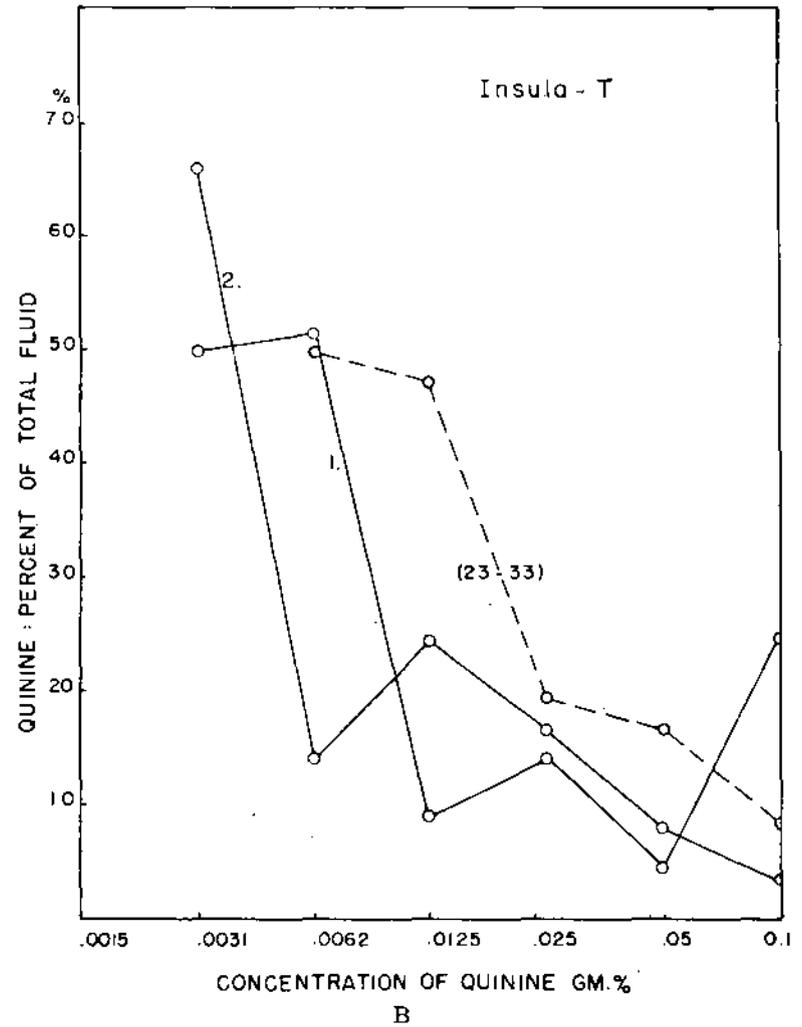
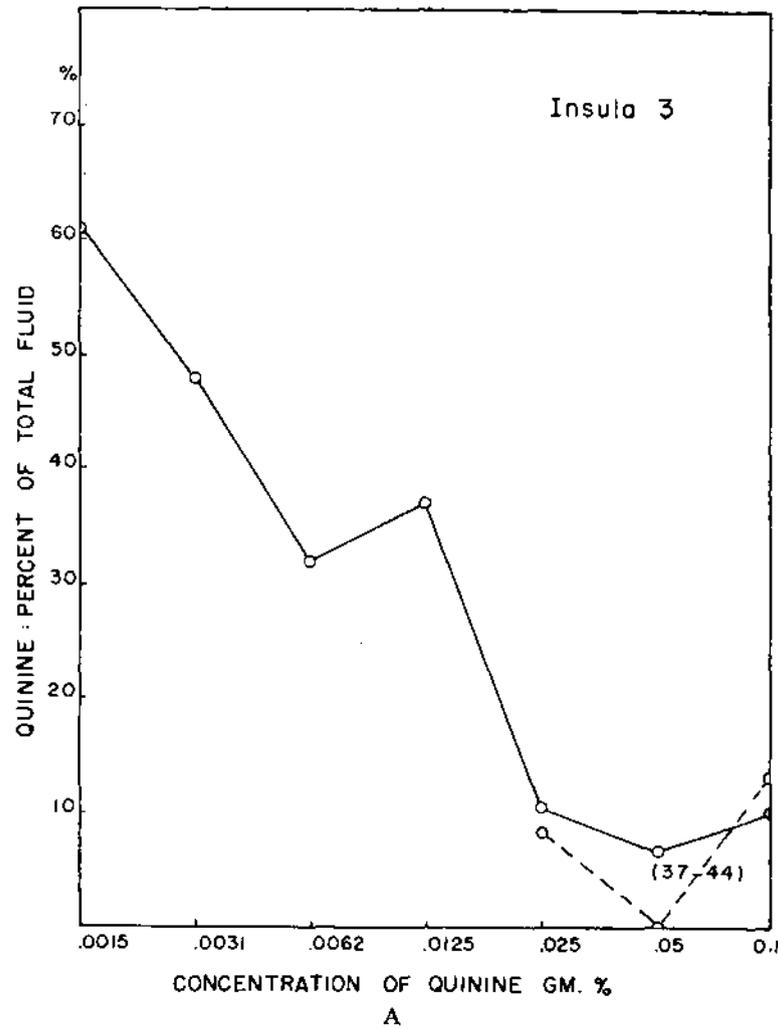


FIG. 3. A, B: Gustatory preference threshold curves for monkeys with island and island plus supratemporal ablations respectively (Fig. 2A, B). Solid lines indicate preoperative determinations; broken lines, postoperative determinations. Numbers indicate days postoperative.

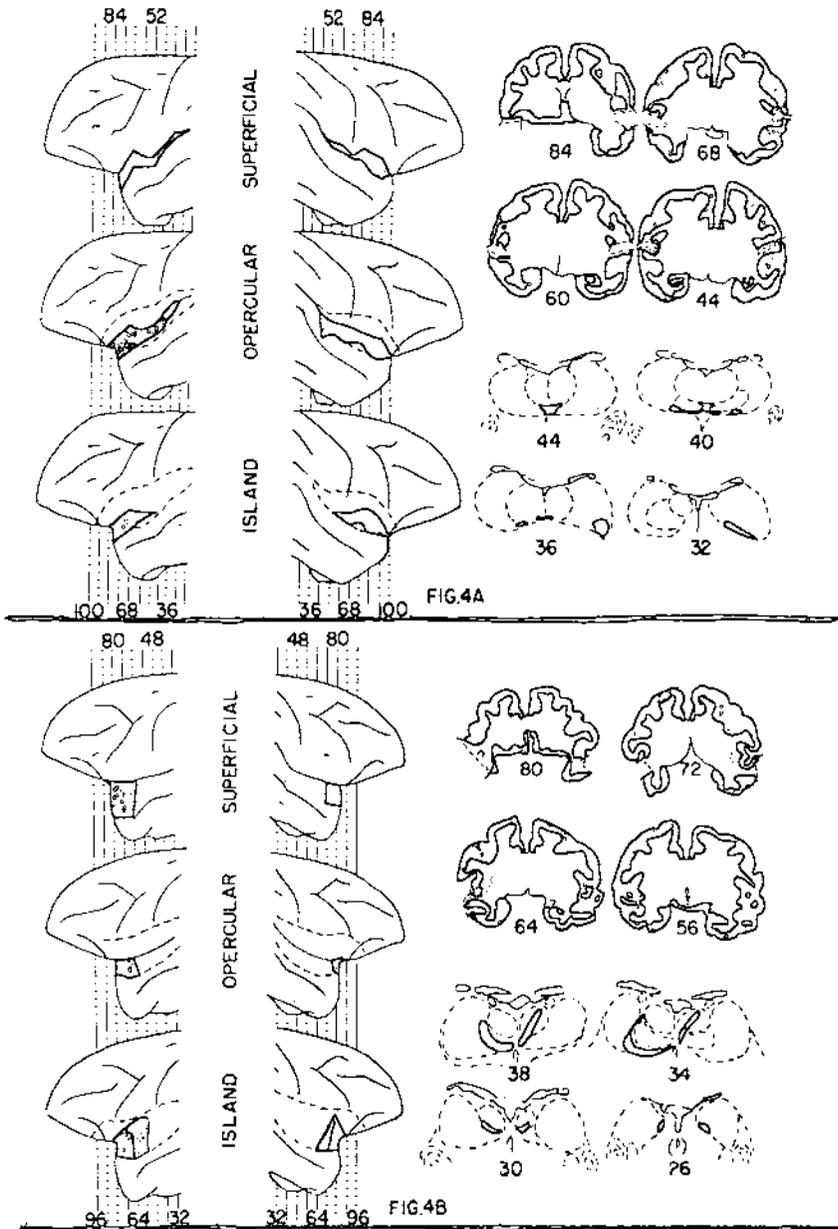


FIG. 4. A, B: Representation of brains of monkeys with extensive ablations of opercular, island and supratemporal cortex. Reconstructions and representative cross sections indicated as in Fig. 2. Gustatory preference threshold curves for these animals appear in Fig. 5A and B respectively.

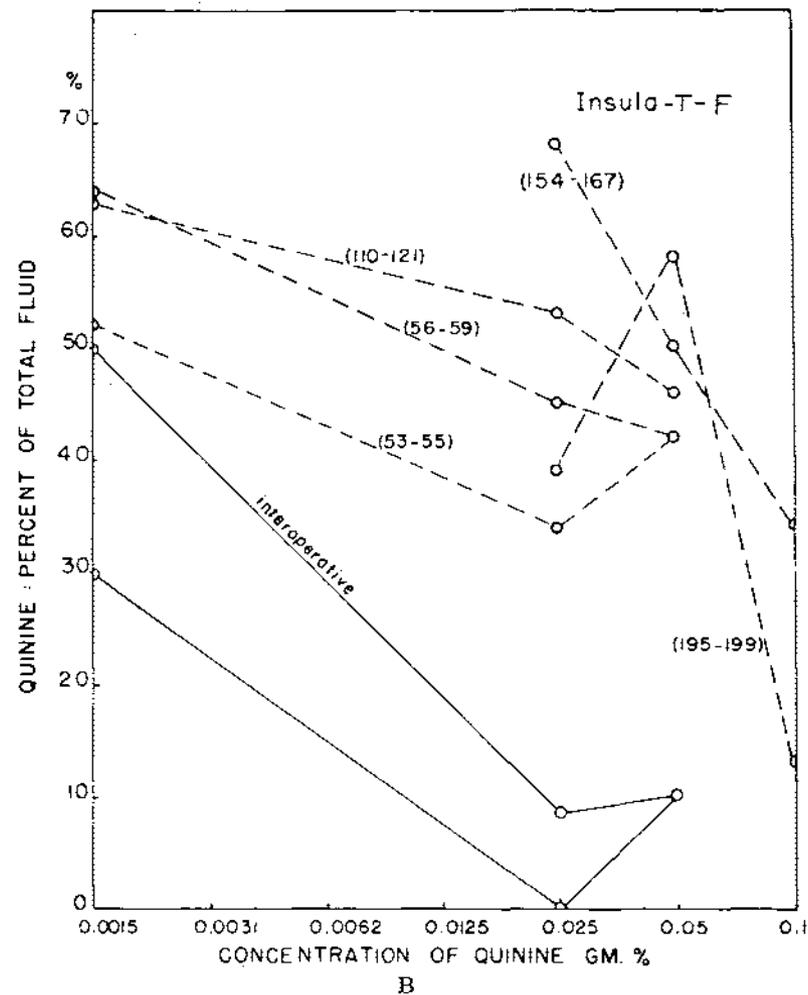
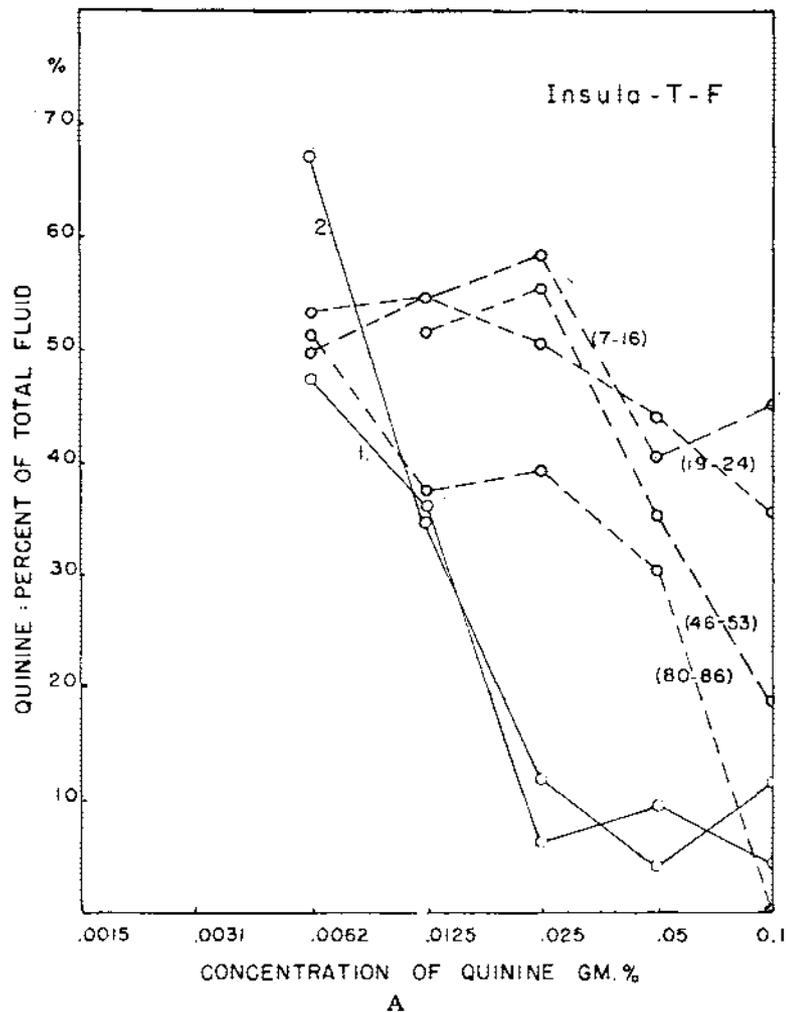


FIG. 5. A, B: Gustatory preference threshold curves for animals with extensive ablations of cortex of island, operculum and anterior supratemporal plane (Fig. 4A, B). Solid lines indicate preoperative determinations; broken lines, postoperative determinations. Numbers indicate days postoperative.

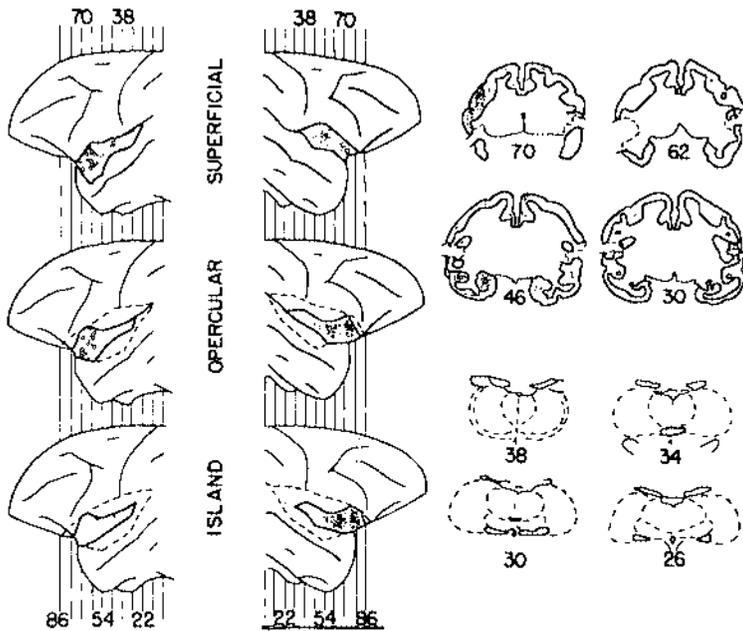


FIG. 6. Representation of brain of monkey with ablation of opercular and island cortex. Reconstructions and representative cross sections indicated as in Fig. 2. Stippled area in reconstruction indicates undercutting lesion which presumably extensively interrupts fibers from operculum and island. Gustatory preference threshold curve for this animal shown in Fig. 7.

tem. For visual processes it has been shown that ablation of the inferior occipitotemporal cortex without invasion of the geniculostriate system produces deficits in performance and learning of a variety of visual discriminations without concomitant field defects (1, 2, 4, 9, 14). It is likely that, for gustatory processes, the dissociation of change in dietary habits and change in quinine acceptance thresholds has a similar basis. Thus, anteromedial temporal cortex serves gustatory discriminative mechanisms (2, 13) while anterior sylvian (opercular, insular, and anterior supratemporal) cortex serves more "primary" gustatory functions.

SUMMARY

1. Pre- and postoperative determinations of acceptance threshold for quinine hydrochloride solution were made in six immature monkeys.

2. The surgical procedure consisted of ablation of the cortex of the anterior part of the Island of Reil, the operculum, and the anterior supratemporal plane. Three animals received extensive though incomplete ablations involving all these loci; three other monkeys received more restricted lesions limited to the anterior portion of the island, island plus supratemporal or, island plus opercular cortex, respectively.

3. Only the more extensive ablations of opercular, island and supratemporal cortex resulted in ageusia. Some lowering of acceptance threshold, however, followed ablation of opercular plus island cortex, but no such low-

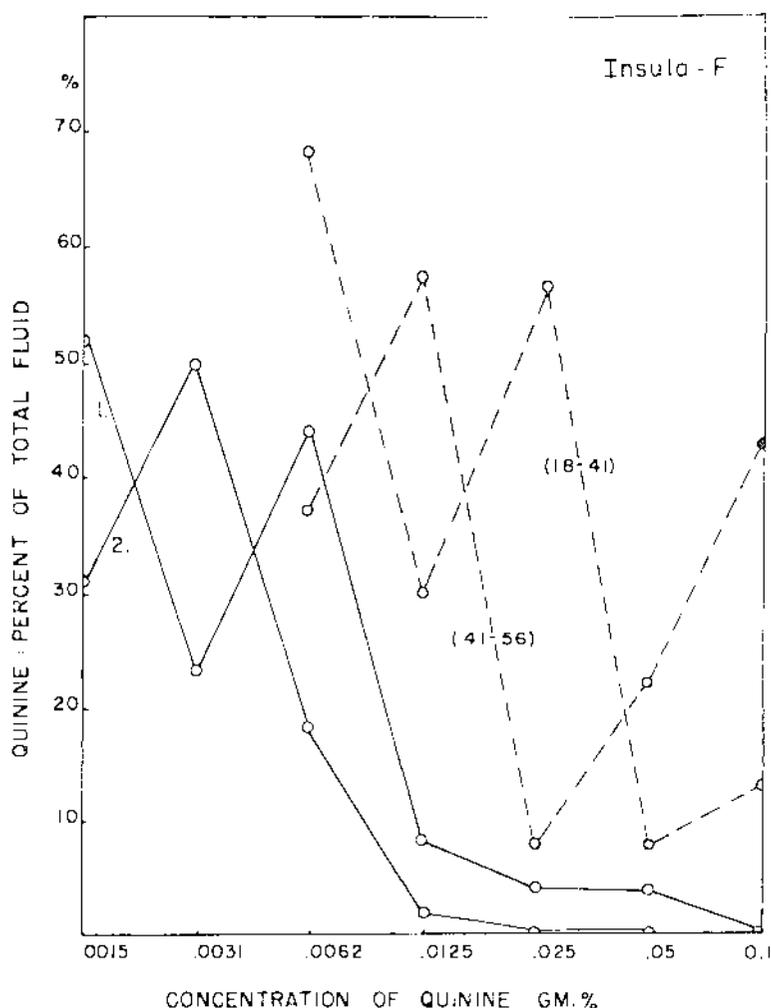


FIG. 7. Gustatory preference threshold curve for animal with ablation of insular and opercular cortex (Fig. 6). See legends for Figs. 3 and 5 for explanation.

ering followed ablation restricted either to island or to island plus anterior supratemporal plane.

4. These data, added to those obtained by Patton, can be made understandable by using an analogy to cerebral mechanisms in vision. As for vision, total incapacity results only from the most extensive involvement of the "primary" projection system. For gustation, therefore, it may be inferred that the "primary" cortical representation includes the cortex of the operculum, insula, and anterior supratemporal plane. As in vision, however, a cortical "macula" may be present. For gustation, this "macula" seems to be focussed on the junction of the frontal operculum and the anterior insula.

5. Continuing the analogy to vision, certain discrepancies in previous interpretations can be resolved. In vision, a dissociation of mechanisms of

discrimination performance from those of "field" have been demonstrated. The former depend on the integrity of the inferior occipitotemporal cortex, the latter on that of the "primary" projection (striate) cortex. In a similar manner a dissociation between dietary habits (food discrimination) and quinine acceptance threshold has been established in gustation. Thus anteromedial temporal cortex appears to be implicated in gustatory discriminations; anterior sylvian (opercular, insular, and anterior supratemporal) cortex in more "primary" gustatory functions.

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