Acta Neurobiol. Exp. 1970, 30: 263–277

EFFECT OF ABLATION OF AUDITORY AND "ASSOCIATIVE" CORTEX ON THE ORIENTING REFLEX

Radu ROGOZEA, Julia UNGHER and Viorica FLOREA-CIOCOIU

Institute of Neurology, RSR Academy, Bucharest, Romania

The present investigation was carried out as a further step in our attempt to establish the part played by various nervous structures and pathways in the orienting reflex and its habituation (Rogozea and Ungher 1965, 1966, 1968, Rogozea et al. 1969). We approached in this study the role played by the auditory and "associative" cortex.

Experiments reported in the literature assessing auditory discrimination before and after ablation of the auditory cortical areas, provide information on the nervous processes requiring the presence of the auditory cortex. These data have shown that bilateral ablation of the auditory cortex does not impair the discrimination of frequency (Butler et al. 1957, Meyer and Woolsey 1952), intensity (Raab and Ades 1946, Rosenzweig 1946) and onset of tone (Kryter and Ades 1943, Meyer and Woolsey 1952). Bilateral removal of the auditory cortex was followed, instead, by a severe impairment in localization of sound in space (Neff et al. 1956) and in discrimination of both the duration (Scharloch et al. 1965) and temporal patterns (Diamond and Neff 1957) of tone.

Sharpless and Jasper (1956) reported, with regard to the orienting reflex, that the specificity of habituation to the frequency parameter of the repetitive tone utilized is unaffected by bilateral ablation of the auditory cortex.

The above mentioned data suggested to us the study of some quantitative (behavioral and EEG) parameters able to reveal changes in the orienting reflex and its habituation following ablation of the auditory and "associative" cortex.

MATERIAL AND METHODS

The investigation was carried out on 24 adult cats in which the orienting behavior and the concomitant EEG response were studied after ablation of the auditory and "associative" cortex. Surgical preparation of cats was carried out aseptically under general anestesia (hexobardital sodium). Cortical areas were removed bilaterally, in two successive operations. In 11 of the 24 cats chronic electrodes were implanted in a third operation in the remaining neocortex (right and left posterior lateral gyrus), dorsal hippocampus and mesencephalic reticular formation, according to the stereotaxic atlas of Jasper and Ajmone-Marsan (1954). According to the type of cortical ablation performed, the animals were grouped as follows: (i) 6 with bilateral ablation of the auditory areas A I, A II and posterior ectosylvian, secondary somatosensory (S II) area and temporoinsular cortex (as described by Rose and Woolsey 1949, 1958, Tunturi 1945, and Desmedt and Mechelse 1959); (ii) 7 with bilateral ablation of the middle suprasylvian and anterior lateral gyri ("associative" areas described by Buser et al. 1959); (iii) 6 with simultaneous ablation of the auditory and "associative" cortical areas; (iv) 5 with ablation of the posterior suprasylvian gyrus and lateral two-thirds of the posterior lateral gyrus (that is of the auditorily dumb part of the cortex). These animals were used as controls.

The experiments proceeded in an electrically and acoustically insulated cage. The cats were awake and free moving, the experimenter watching them from outside. The behavioral investigations were carried out before and were repeated one month after bilateral removal of the cortex. In cats with chronic electrodes the EEG component of the orienting activity was investigated concomitantly with the behavioral one. After ablation, the behavioral data were compared with those obtained before ablation, each animal being thus its own control, and the EEG data, with those obtained in 10 intact animals submitted to the same tests.

The orienting reaction was elicited by repetitive auditory stimuli applied through a loudspeaker placed inside the cage at the height of animal's ears. One stimulus was "indifferent" (a tone at 1000 c/sec, 25 db, generated by an Orion set) and another "familiar" to the cat (appellative "pss-pss" obtained from a tape-recorder). The duration of the stimulus was 3 sec and the intertrial intervals, 6 sec. Maximal number of trials was 100 in one session. The behavioral and EEG responses were observed. In order to note the somatic orienting reactions, the stimuli were presented when the animal was turned back to the loudspeaker. The orienting reflex was considered habituated when it was absent in three successive trials. The quantitative estimation of habituation consisted, as seen in Fig. 1, in the numerical evaluation of trials. The same stimuli were used before and after removal of the cortex.

Besides the orienting reflex, both the spontaneous behavior and bioelectrical activity were observed before and after ablation of the cortical areas.

The EEG recordings were obtained with a 6-channel Officine Galileo poly-physiograph.

At the end of the experiments the animals were killed and their brains were studied both macroscopically, to check the extent of the lesions, and microscopically, with modified Nauta technique, to determine the preterminal degenerations.

RESULTS

Behavioral data

None of the four types of bilateral cortical ablation was followed by any motor disturbance or particular change in the animal's spontaneous behavior (we considered as "spontaneous" the animal's behavior in the absence of any stimuli applied by the experimenter).

After the damage of the auditory and "associative" cortex the orienting behavior elicited by repetitive application of the "indifferent" (tone) and "familiar" ("pss-pss") stimuli differed both in somatic response type and resistance to habituation from that recorded in control experiments. Thus, repetitive stimulation elicited mostly generalized somatic responses, starts, characterized by a short and intense muscular contraction involving particularly the musculature of the fore-limbs, neck, face and eyelids. The incidence of complex motor responses (consisting in postural fixation following the increase in the muscular tonus, and orienting of the head and the eyes toward the source of the stimulus) or of the local motor responses (pricking of the ears) was lower than in preoperative control tests. On the other hand, the habituation of the somatic orienting reaction was delayed after ablation, requiring more presentations of the stimulus than in control experiments (Fig. 1, I and II). During habituation, no progressively decreasing evolution of motor reaction intensity was noted, as in control experiments, but an oscillating one, very intense reaction following sometimes after less intense ones and vice versa.

It is noteworthy that the resistance to habituation depended upon two factors: (i) the nature of the stimulus applied, the resistance being more marked with the "indifferent" than with the "familiar" stimulus (Fig. 1, I and II), and (ii) the type of damage, the most striking abnormalities being produced by simultaneous bilateral ablation of the auditory (AI, AII, posterior ectosylvian, SII and temporoinsular) and "associative" (middle suprasylvian and anterior lateral) cortical areas, followed in decreasing order by those produced by ablation of the auditory cortex and, finally, by those noted after bilateral removal of the "associative" cortex (Fig. 1, IABC and IIABC). In addition, following these last three types of cortical ablation, besides the delay of habituation, the response could be disinhibited earlier by unexpected external stimuli and its re-habituation was delayed also.

Bilateral removal of the posterior suprasylvian and posterior lateral gyri did not induce any significant disturbances in the habituation process (Fig. 1, ID and IID).

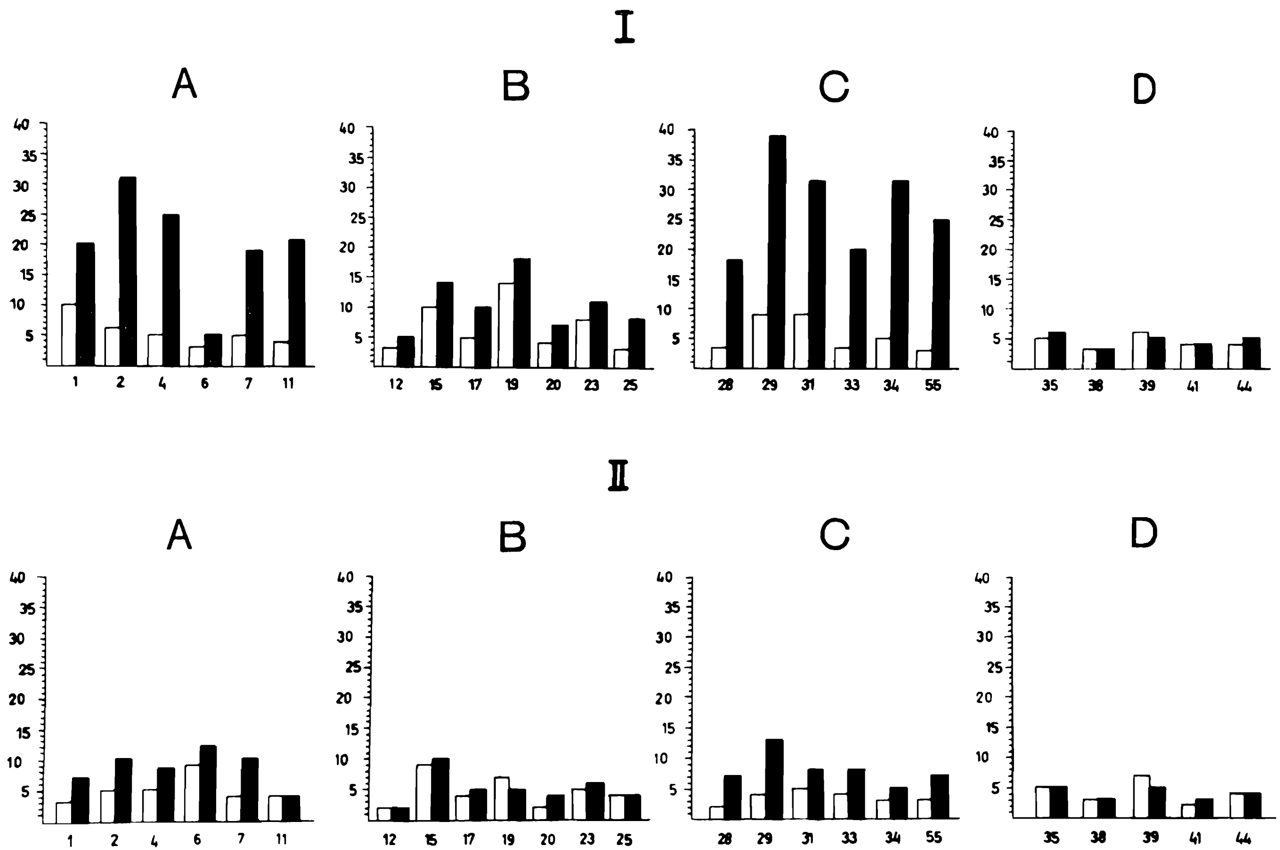

Fig. 1. Resistance to habituation (in trials) of the orienting behavior elicited by tone (I) and appellative "pss-pss" (II) before (white bars) and after (black bars) ablation of the cortex. A, Ablation of the auditory cortex; B, Ablation of "associative" cortex; C, Simultaneous ablation of auditory and "associative" cortex; D, Ablation of posterior suprasylvian and lateral two-thirds of the posterior lateral gyri. Ordinate: number of trials (repetitive applications of stimuli in one session); abscissa: the number of the cat.

EEG data

After the cortical ablations the remaining cortex and the mesencephalic reticular formation did not exhibiting any conspicous changes

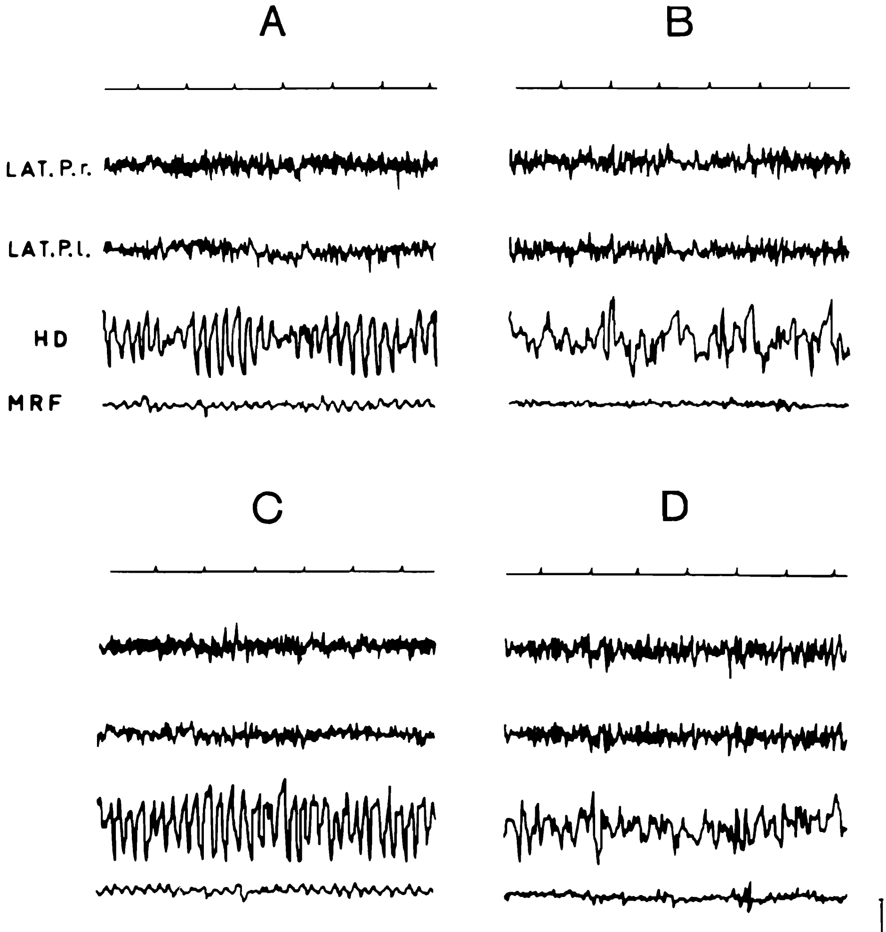

Fig. 2. Effect of cortical ablations on spontaneous EEG activity. A, Cat 11; recording 40 days after ablation of auditory cortex. B, Cat 17; recording 42 days after ablation of "associative" cortex. C, Cat 29; recording 35 days after ablation of auditory and "associative" cortex. D, Cat 39 (control); recording 51 days after ablation of posterior suprasylvian and the lateral two-thirds of the posterior lateral gyri. In this case the cortical recording electrodes had been implanted at the medial one-third level of the remaining posterior lateral gyrus. In this and subsequent figures: LAT.P.r., right posterior lateral gyrus; LAT.P.l., left posterior lateral gyrus; HD, dorsal hippocampus; MRF, mesencephalic reticular formation; S, stimulus. The figure under the stimulus indicates the number of its repetitive applications (trials). EmkG, electromechanogram. Bipolar recordings. Calibration: time in seconds on the first lead (in Fig. 3, 4 and 5 on the third lead). Amplitude: 50 μv.

in spontaneous bioelectrical activity. Besides, the dissociation between the faster cortical and the slower hippocampal rhythms was present in every damaged animal (Fig. 2). The only anomaly in spontaneous EEG activity consisted in a higher incidence of the synchronous 4–5 c/sec theta wave bursts in the dorsal hippocampus, especially following

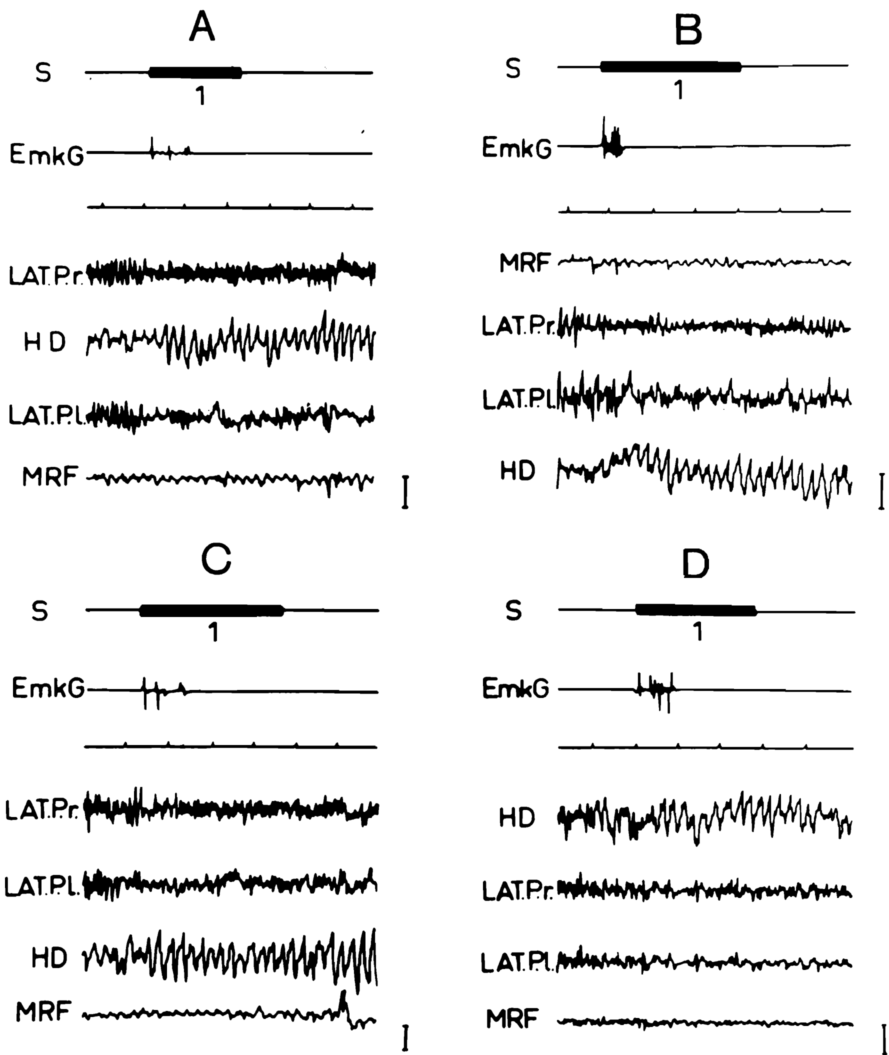

Fig. 3. The arousal reaction elicited by appellative "pss-pss" after cortical ablations. A, Cat 4 with ablation of auditory cortex. B, Cat 23 with ablation of "associative" cortex. C, Cat 31 with ablation of auditory and "associative" cortex. D, Cat 44 with ablation of the posterior suprasylvian and of the lateral two-thirds of the posterior lateral gyri.

simultaneous ablation of the auditory and "associative" cortex or following ablation of the auditory cortex alone (Fig. 2AC).

As in control recordings, the EEG component of the orienting reflex to the repetitive stimuli utilized was, with all ablation types, an arousal response consisting in low-voltage fast activity in the rest of the cortex and high-voltage slow (4–5 c/sec, 150 μv) theta activity in the dorsal hippocampus (Fig. 3).

The EEG tracings from animals with the first three types of the cortical ablations did, however, show a delay in EEG habituation which overlapped the delay of habituation of the somatic component of the

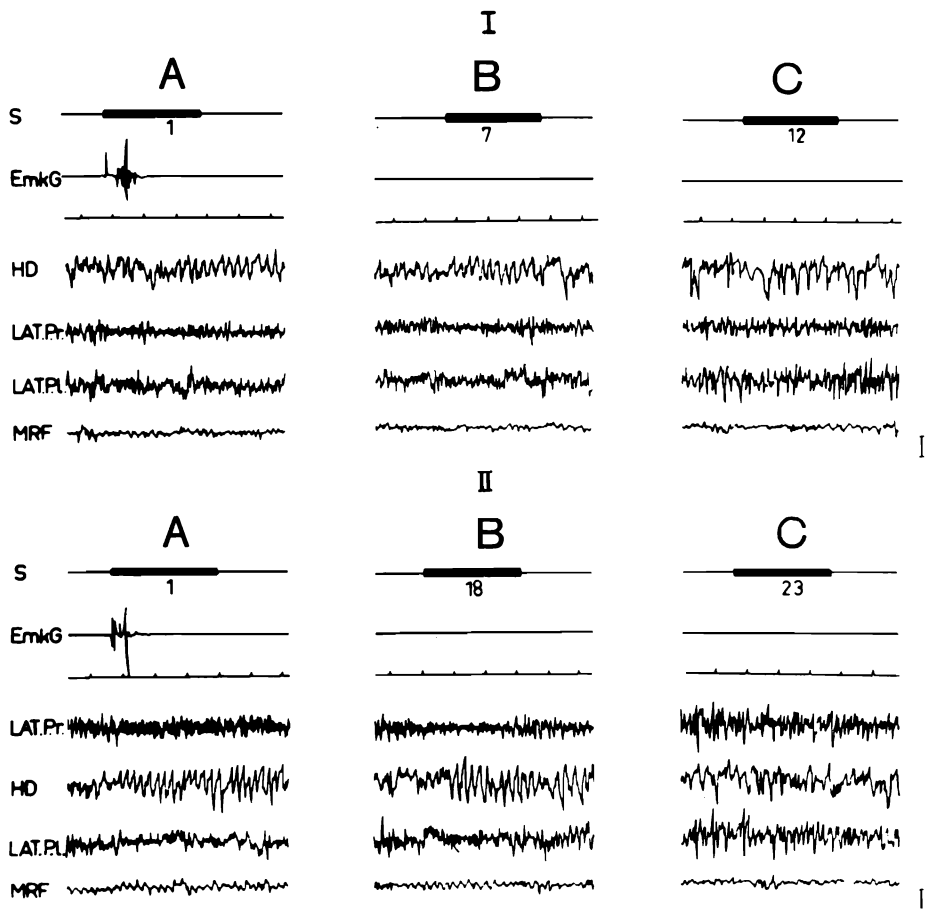

Fig. 4. Effect of cortical ablation on habituation of arousal reaction elicited by appellative "pss-pss". I, Intact cat (control). II, Cat 29 after ablation of auditory and "associative" cortex. A, Somatic and EEG orienting reaction at first application of stimulus; B, Habituation of motor reaction with persistence of arousal reaction; C, Full habituation of orienting reflex.

orienting response (Fig. 4, IABC and IIABC). The nature of the stimulus and the type of cortical ablation affected the habituation of the EEG arousal response in the same way as they affected the somatic response habituation. Thus, on the one hand, the most marked resistance to habituation was noted with the "indifferent" stimulus (Fig. 5, IABC and IIABC) and, on the other, the most marked abnormalities of habi-

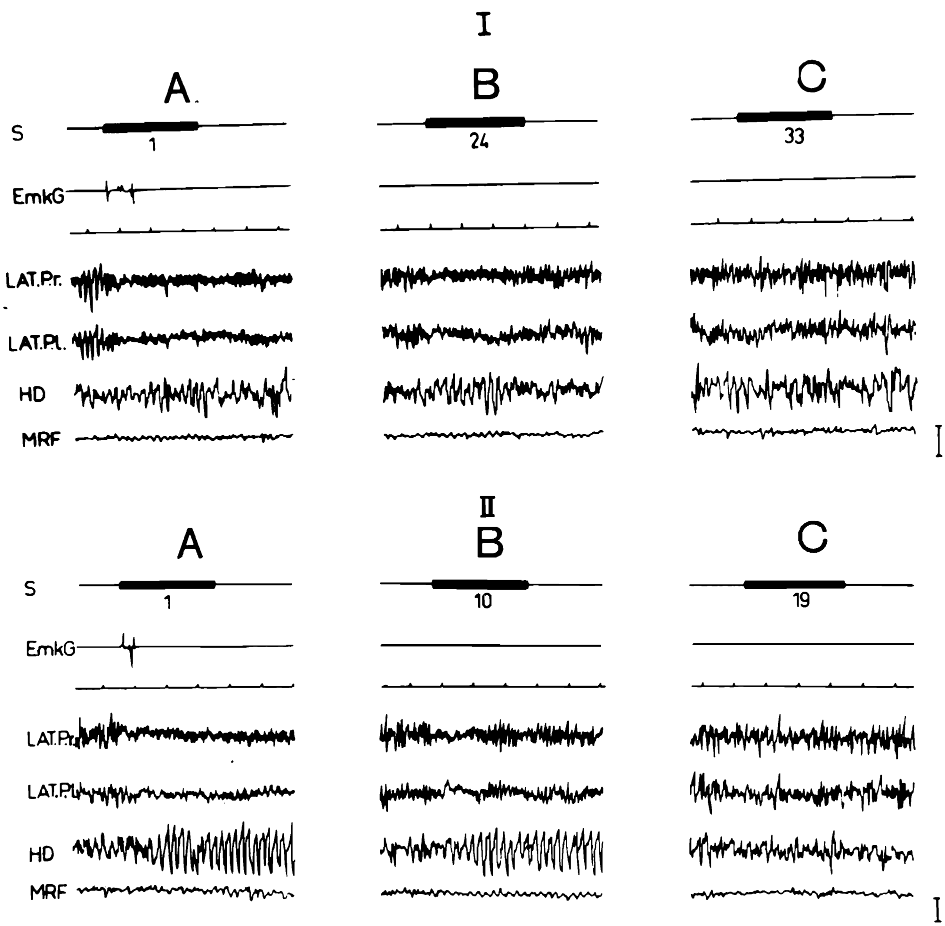

Fig. 5. The arousal reaction after cortical ablation, as a function of the nature of the repetitive stimulus. Cat 31 with ablation of auditory and "associative" cortex. I. Arousal elicited by tone. II. Arousal elicited by "pss-pss". A, Motor and EEG orienting reaction at first application of stimulus; B, Habituation of motor reaction with persistence of arousal reaction; C, Full habituation of orienting reflex. During the arousal to "pss-pss" a more distinct and persistent hippocampal theta rhythm is found. Note earlier habituation of arousal reaction to the "familiar" stimulus than to the tone.

tuation appeared after simultaneous ablation of the auditory and "associative" cortex, followed in decremental order by those noted after ablation of the auditory and, lastly, after ablation of the "associative" areas. The EEG findings showed also that after the above mentioned three types of cortical ablation, the hippocampal theta rhythm was more distinct and persistent during the arousal reaction to the "familiar" than during that to the "indifferent" stimulus (Fig. 5, IABC and IIABC).

There were no such bioelectrical alterations after bilateral ablation of the posterior suprasylvian and the posterior lateral gyri.

As to the sequential order in which the two components of the orienting reflex were extinguished after the cortical ablations, the first was the somatic and the second the arousal response, as in control experiments.

Anatomical data

The correlation of macroscopic data on the extent of the lesions with the microscopic data obtained on modified Nauta preparations, enabled us to establish that: (i) ablation of the auditory cortex (AI, AII, posterior ectosylvian, SII and temporoinsular areas) was associated with preterminal degenerations in the medial geniculate body (more in its pars principalis and less in its pars magnocellularis), inferior colliculus and, less, in the superior colliculus and in the posterior nuclear group of the thalamus; (ii) ablation of the "associative" cortex (the middle suprasylvian and the anterior lateral areas) was associated with degenerations involving the pulvinar, thalamic reticular and lateralis posterior nuclei, the mesencephalic tegmentum and, less, the caudate nucleus, lateral geniculate body and superior colliculus; (iii) ablation of both the auditory and "associative" cortex was accompanied by overlapping of the degenerations described in (i) and (ii); (iv) finally, in animals with ablations of the posterior suprasylvian and posterior lateral gyri, degenerations were noted in the pulvinar and lateralis posterior nucleus.

As an illustration of the various types of ablation performed, the respective lesions and the secondary preterminal degenerations are reconstituted in Fig. 6.

DISCUSSION

Assessment by the quantitative method of the rapidity of habituation of the behavioral and EEG component of the orienting reflex elicited by repetitive auditory stimuli showed that ablation of the auditory and

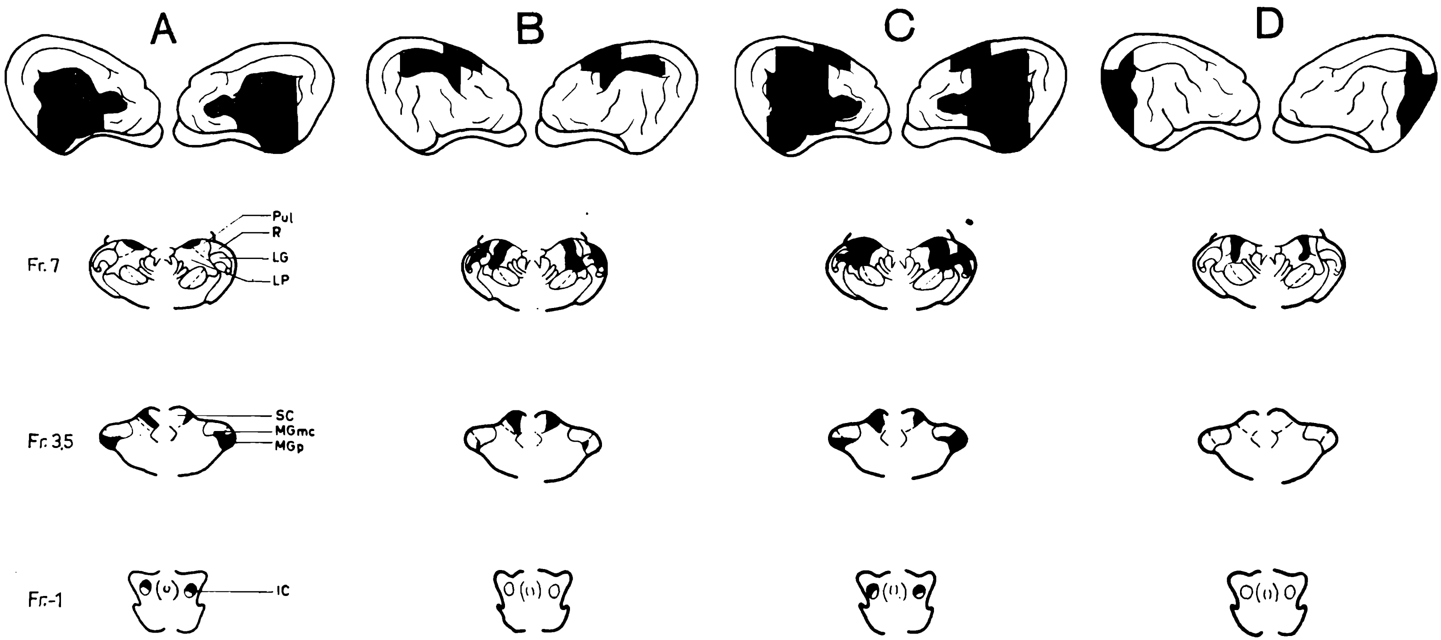

Fig. 6. Reconstitution of the four types of cortical lesions and the secondary preterminal degenerations. A, Cat 7 with bilateral ablation of auditory cortex. B, Cat 23 with bilateral ablation of "associative" cortex. C, Cat 29 with bilateral ablation of auditory and "associative" cortex. D, Cat 41 with bilateral ablation of posterior suprasylvian and of lateral two-thirds of posterior lateral gyri. Fr, frontal level at which sections were carried out. Pul, pulvinar. R, thalamic reticular nucleus. GL, lateral geniculate body. LP, lateralis posterior nucleus. SC, superior colliculus. MGmc, medial geniculate body (magnocellular division). MGp, medial geniculate body (principal division). IC, inferior colliculus.

"associative" cortical areas disturbs the rate at which this process develops, inducing a delay. The possibility that some cortical ablations induce disturbances in resistance to habituation was noted also by Dreher and Żernicki (1969) on another experimental model. Sharpless and Jasper (1956), who showed that ablation of the auditory cortex leaves unaffected the specificity of habituation to the sound frequency utilized, failed to note postoperative alterations in the arousal response extinction rate, because their method did not allow quantitative investigation of this process.

Once it has been established that the cortical ablations induce a delay in the orienting response habituation process, three questions arise to which we shall attempt to provide an answer on the basis of our data: (i) which of the cortical areas studied plays the most important role in the control of the orienting reflex; (ii) suppression of which pathways and central mechanisms underlies these postoperative disturbances; (iii) what accounts for the different degrees of resistance to habituation as a function of the nature of the repetitive stimulus employed.

With regard to the first question, our data suggest that the auditory cortical areas (AI, AII, posterior ectosylvian, SII and temporoinsular) exert the most important control over the orienting reaction, as the most marked delays in its habituation process were induced, in of severity order, by bilateral and simultaneous ablation of the auditory and "associative", auditory and, finally, "associative" cortex. These observations are in agreement with the data reported by Rasmussen (1955, 1960) and Desmedt (1960) with regard to auditory cortex control of the ascending acoustic pathways. From our data it also appears that, although participating in the auditory input control, the "associative" (middle suprasylvian and anterior lateral) areas play, however, a less important role than that played by the auditory ones.

The fact that the cortical ablations performed did not prevent the occurrence of the orienting reflex and that only its aspect and, particularly, its habituation rate were affected, suggests that the postoperative abnormalities are due to a disturbance of the corticofugal system which controls the auditory afferent impulses, and not to a primary disorder in the afferent pathways.

In order to answer the second question, i.e. which corticofugal pathways are involved in the appearance of the habituation disturbances after ablation, we compared the behavioral and EEG data with the anatomic findings. We could thus establish that the marked habituation abnormalities, following removal of the auditory areas, coexisted with preterminal degenerations especially in the relay nuclei of the auditory pathways, namely in the medial geniculate body and inferior colliculus.

The less severe disturbances of habituation, secondary to removal of the "associative" cortex, coexisted with degenerations in the thalamic reticular nucleus and posterior nuclear group, in the mesencephalic tegment and in some relay nuclei of the visual pathways. Finally, the overlapping of such degenerations, in the case of simultaneous ablation of the auditory and "associative" cortex, induced the most severe disturbances in habituation, whereas the degenerations confined to the thalamic posterior nuclear group, following removal of the posterior suprasylvian and posterior lateral gyri, did not disturb the habituation of the orienting reaction. Our anatomic data, which confirm the observations of Rasmussen (1955, 1960), Desmedt (1960) and Kusama et al. (1966), supported by our behavioral and EEG data, suggest that the auditory cortical areas participate more than the "associative" cortex in the control of the orienting reaction, through their own system of corticofugal fibres terminating in the relay nuclei of the ascendent auditory pathways (including the cochlear nuclei, as shown by Rasmussen 1958). The marked resistance to habituation, concomitant with the preterminal degenerations in the relay nuclei, following ablation of auditory areas, is an argument favoring this view. Besides, the inhibitory cortical influence exerted at the relay nuclei level on the repetitive auditory messages may be demonstrated electrophysiologically also, by activation of this corticofugal system (Desmedt, 1960).

Even though the "associative" cortical areas control the orienting reflex less than the auditory cortex, they participate, however, in the centrifugal mechanism of regulation of the auditory afferent impulses. But, unlike the specific corticofugal system of the auditory cortex, the centrifugal projections of the "associative" areas are mediated by the thalamic reticular formation, the mesencephalon and the posterior nuclear group of the thalamus, as shown in our case by the postoperative degenerations. Presumably, this corticofugal system comprises descending pathways with numerous synapses. The ability of this corticofugal system to control the reactivity of some subcortical relays as above mentioned, was demonstrated through electrophysiological methods by Niemer and Jimenes-Castellanos (1950), Kreindler and Crighel (1967), etc. Its suppression, following ablation of the "associative" areas, induces the habituation delay. Suppression of both centrifugal systems by simultaneous bilateral ablations of the auditory and "associative" cortex will, naturally, be followed by the most severe disturbances in habituation.

The fact that the cortical ablations did not prevent the habituation of the orienting reflex and that their only effect was an habituation delay, suggests that the mechanisms of control of this reaction are more complex and include more nervous structures. We insist upon this point only to emphasize the participation of hippocampus in this complex control mechanism. As we have pointed out elsewhere (Rogozea and Ungher 1968), hippocampus can account for the different degrees of resistance to habituation as a function of the repetitive stimulus nature. The auditory messages with important affective significance, viz. the appellative "pss-pss", seem to be controlled especially by hippocampus. After cortical ablation the resistance to habituation of the orienting reflex was more moderate to the "familiar" than to the "indifferent" stimulus. Concomitantly, the hippocampal arousal (theta rhythm) was more distinct and persistent to the appellative "pss-pss" than to the "indifferent" stimulus. These data suggest the participation of hippocampus in the control of auditory messages with affective significance and the tendency of this structure to compensate for the postoperative absence of corticofugal inhibitory influences. However, it is not impossible that this compensating tendency of the hippocampus should involve a wider sphere of afferent impulses, which would account for the increased incidence of the spontaneous theta rhythm.

SUMMARY

1. The orienting reflex elicited by "familiar" and "indifferent" stimuli was behaviorally and electroencephalographically investigated in 24 cats before and after bilateral ablation of auditory cortex (first group), "associative" cortex (second group), simultaneous ablation of both auditory and "associative" cortex (third group), and bilateral ablation of posterior suprasylvian gyrus and lateral two-thirds of the posterior lateral gyrus (fourth group). Anatomical investigations on the preterminal degenerations induced by ablations were also performed.

2. Ablation of auditory and "associative" cortex induced a decrease in the incidence of targeting responses (directionary responses toward the stimulus) and an increase in the frequency of the start responses. This ablation induced also a delay in habituation of the orienting reflex.

3. The severity of the delay depended upon the type of cortical ablation. The most marked resistance to habituation was induced, in decremental order, by ablation of (i) both auditory and "associative" cortex, (ii) auditory, and finally (iii) "associative" cortex. It comes out that the most important part in the control of the reaction is played by the auditory and less by the "associative" cortex.

4. The marked resistance to habituation coexists, after ablation of auditory areas, with preterminal degenerations especially in the medial geniculate body and inferior colliculus, and after ablation of "associa-

tive" areas with degenerations in the thalamic reticular nucleus, posterior nuclear group, mesencephalic tegmentum and in some relay of the visual pathways. The data suggest that postoperative habituation disturbances are related to the suppression of the corticofugal control exerted upon the mentioned subcortical structures.

5. The resistance to habituation also depends upon the nature of the repetitive stimulus, the disturbances being less marked in case of a stimulus "familiar" to the animal. The concomitant presence of a hippocampal arousal, more evident during the reaction to this stimulus, supports the view that hippocampus participates in the control of auditory messages with affective significance, this participation partly compensating the abolished cortical control.

REFERENCES

BUSER, P., BORENSTEIN, P. and BRUNER, J. 1959. Etude des systèmes "associatifs" visuels et auditifs chez le chat anesthésié au chloralose. Electroenceph. Clin. Neurophsiol. 11: 305–324.

BUTLER, R. A., DIAMOND, I. T. and NEFF, W. D. 1957. Role of auditory cortex in discrimination of changes in frequency. J. Neurophysiol. 20: 108–120.

DESMEDT, J.E. and MECHELSE, K. 1959. Mise en évidence d'une quatrième aire de projection acoustique dans l'écorce cérébrale du Chat. J. Physiol. (Paris) 51: 448–449.

DESMEDT, J. E. 1960. Neurophysiological mechanisms controlling acoustic input. *In* G. L. Rasmussen and W. F. Windle (ed.), Neural mechanisms of the auditory and vestibular systems, Charles C Thomas, Springfield, p. 152–164.

DIAMOND, I. T. and NEFF, W. D. 1957. Ablation of temporal cortex and discrimination of auditory patterns. J. Neurophysiol. 20: 300–315.

DREHER, B. and ŻERNICKI, B. 1969. Studies on the visual fixation reflex. III. The effects of frontal lesions in the cat. Acta Biol. Exp. 29: 153–173.

JASPER, H. H. and AJMONE-MARSAN, C. 1954. A stereotaxic atlas of the diencephalon of the cat. Nat. Res. Council of Canada, Ottawa.

KREINDLER, A. and CRIGHEL, E. 1967. Reactivity changes in pulvinar-lateralis posterior complex induced by excitability alterations of primary and association neocortical areas. Rev. Roum. Neurol. 4: 297–302.

KRYTER, K. D. and ADES, H. W. 1943. Studies on the function of the higher acoustic nervous centers in the cat. Amer. J. Psychol. 56: 501–536.

KUSAMA, T., OTANI, K. and KAWANA, E. 1966. Projections of the motor, somatic sensory, auditory and visual cortices in cats. Progr. Brain Res. 21: 292–322.

MEYER, D. R. and WOOLSEY, C. N. 1952. Effects of localized cortical destruction on auditory discriminative conditioning in cat. J. Neurophysiol. 15: 149–162.

NEFF, W. D., FISHER, J. F., DIAMOND, I. T. and YELA, M. 1956. Role of auditory cortex in discrimination requiring localization of sound in space. J. Neurophysiol. 19: 500—512.

NIEMER, W. T. and JIMENEZ-CASTELLANOS, J. 1950. Cortico-thalamic connections in the cat as revealed by "physiological neurography". J. Comp. Neurol., 93: 101–103.

RAAB, D. H. and ADES, H. W. 1946. Cortical and midbrain mediation of a conditioned discrimination of acoustic intensities. Amer. J. Psychol. 59: 59–83.

RASMUSSEN, G. L. 1955. Descending or "feed-back" connections of auditory system of the cat. Am. H. Physiol. 183: 653.

RASMUSSEN, G. L. 1958. Anatomical discussion of neural mechanisms in audition by Galambos R. Laryngoscope 68: 404–406.

RASMUSSEN, G. L. 1960. Discussion of central mechanisms of the auditory system. *In* G. L. Rasmussen and W. F. Windle (ed.), Neural mechanisms of the auditory and vestibular systems, Charles C Thomas, Springfield, p. 217–223.

ROGOZEA, R. and UNGHER, J. 1965. Alterations of the orienting reaction induced by experimental convulsive seizures. Bol. Inst. Estud. Med. Biol. (Mexico) 23: 213–232.

ROGOZEA, R. and UNGHER, J. 1966. The orienting reflex of the cat during ontogenetic development. Bol. Inst. Estud. Med. Biol. (Mexico) 24: 53–65.

ROGOZEA, R. and UNGHER, J. 1968. Changes in orienting activity of cat induced by chronic hippocampal lesions. Exp. Neurol. 21: 176–186.

ROGOZEA, R., UNGHER, J. and FLOREA-CIOCOIU, V. 1969. The influence of GAMMA-aminobutyric acid intrahippocampally administered on the orienting reflex. Electroenceph. Clin. Neurophysiol. 27: 162–168.

ROSE, J. E. and WOOLSEY, C. N. 1949. The relations of thalamic connections, cellular structure and evocable electrical activity in the auditory region of the cat. J. Comp. Neurol. 91: 441–466.

ROSE, J. E. and WOOLSEY, C. N. 1958. Cortical connections and functional organization of the thalamic auditory system of the cat. *In* H. F. Harlow and C. N. Woolsey (ed.), Biological and biochemical bases of behavior, Univ. Wisconsin Press, Madison. p. 127–150.

ROSENZWEIG, M. R. 1946. Discrimination of auditory intensities in the cat. Amer. J. Psychol. 59: 127–136.

SCHARLOCH, D. P., NEFF, W. D. and STROMINGER, N. L. 1965. Discrimination of tone duration after bilateral ablation of cortical auditory areas. J. Neurophysiol. 28: 673–681.

SHARPLESS, S. and JASPER, H. 1956. Habituation of the arousal reaction. Brain 79: 655–680.

TUNTURI, A. R. 1945. Further afferent connections to the acoustic cortex of the dog. Amer. J. Physiol. 144: 389–394.

Received 19 November 1969