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Short-Latency Auditory Projection to the Frontal Telencephalon of the Pigeon

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An auditory projection to the frontolateral telencephalon of birds, originally described by Iljitschew, is confirmed for the pigeon. Potentials evoked by acoustic stimuli were recorded from the neostriatum frontale closely surrounding the nucleus basalis, in anesthetized and awake subjects. The latency of these responses was short (5 to 8 ms) compared to that of responses recorded from the orthodox avian telencephalic auditory projection in the neostriatum caudale, field L (12 to 14 ms). The intensity and frequency sensitivities of the frontal auditory potentials, however, were similar to those of the area L responses. Clicks delivered to the auditory meati were more effective than the same stimuli directed at other parts of the head or beak. Ipsilateral and contralateral auditory stimuli were equally effective. Occlusion of the ear openings attenuated the responses; thick pasting of the remainder of the head or beak did not affect them. Trigeminal deafferentation similarly did not attenuate the frontal auditory potentials, but ablation of the cochleae totally abolished them. The hypothesis that the frontal auditory responses are due to an artifactual stimulation of trigeminal mechanoreceptors projecting to the nucleus basalis is thus rejected. The neural pathway subserving this projection and the functional role that it may play are discussed.

INTRODUCTION

In a series of papers starting in 1963 and on the basis of evoked potential studies, Iljitschew and collaborators described the functional properties of an auditory projection they located in the frontolateral forebrain of

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the pigeon (*Columba livia*), eagle (*Aquila rapax*), and sparrow (*Passer domesticus*) (17–20, 30). Similarly based on evoked potential evidence, Erulkar (10) however, described an auditory projection to the caudomedial telencephalon of the pigeon. Karten (22, 23), continuing the work begun by Wallenberg (40) and Boord (3), traced the auditory pathway of the pigeon from the nucleus mesencephalicus lateralis pars dorsalis (equivalent to the mammalian inferior colliculus) through the nucleus ovoidalis thalami (equivalent to the mammalian medial geniculate) to the telencephalon with degeneration techniques. He found a discrete projection only to the medial neostriatum caudale, coinciding with the cytoarchitectonic field L described by Rose (33). This projection corresponds closely with the anatomic locus given by Erulkar, and indeed several electrophysiological studies have since confirmed that this region is a major auditory center in birds [dove, *Streptopelia risoria* (2) starling, *Sturnus vulgaris* (27–29); zebra finch, *Taeniopygia guttata* (45); owl, *Tyto alba* (25)].

Nevertheless, in agreement with Iljitschew's evidence, Adamo and King (1) again described evoked auditory responses from the frontal forebrain of the pigeon. Harman and Phillips (14), besides confirming the presence of the field L auditory projection in the chicken (*Gallus gallus*), also found auditory evoked potentials in a frontolateral region of the telencephalon. Karten (23), failing to find an anatomical correlate for this latter electrophysiological finding, suggested that the responses were probably not auditory but somesthetic in nature. Karten based this conclusion on the fact that Naumov and Iljitschew (30) and Harman and Phillips (14) had located the evoked potentials in the neighborhood of the nucleus basalis telencephali. Previously Wallenberg (41) had established, in the pigeon, that the nucleus basalis is the termination of a direct ascending pathway, the tractus quintofrontalis, that originates from the main sensory nucleus of the trigeminal nerve in the medulla [see also Wallenberg (42) for crow, *Corvus corone*, and duck, *Anas platyrhynchos*]. Karten (23) surmised that the acoustic stimuli used by the various experimenters could have given rise to vibrations capable of activating trigeminal mechanoreceptors and that the potentials might, in fact, be nucleus basalis responses. Certainly the purported auditory potentials have a relatively short latency [pigeon: 6 to 8 ms (30), 5 to 8 ms (1); chicken, 6 to 12 ms (14)] compared to the field L potentials [pigeon, 12 to 15 ms (10), 14 to 20 ms (1); chicken, 14 to 16 ms (14)]. This would correspond with the fact that the quintofrontal tract bypasses the mesencephalic and thalamic synaptic relays characteristic of the orthodox auditory sensory pathway to area L. Indeed, by recording from the nucleus basalis in the pigeon, Witkovsky *et al.* (44) found a short-latency (2.7 ms) evoked potential elicited by electrical stimulation of the beak and also units that were activated by

tactile stimulation of the soft palate. However, those authors also located units in the neostriatum frontale, dorsal to the nucleus basalis responding to the acoustic stimuli. As did Karten (23) they argued that these units had been indirectly activated by mechanical stimulation of trigeminally innervated mechanoreceptors which are known in birds to respond to vibration in the lower audio-frequency range (37).

Clear-cut evoked responses to weak acoustic stimuli in the frontal region of the forebrain were incidentally observed by one of us in connection with a study of the somesthetic forebrain projections in the pigeon (6). Their behavior did not agree well with the artifact hypothesis (Delius, unpublished observations). This motivated us to reexamine the issue.

METHODS AND RESULTS

The first phase of the study, carried out on 10 adult homing pigeons of local breed, was aimed at locating the focus of the forebrain potentials in question. The birds were anesthetized with Equithesin (intramuscular injection; initial dose, 0.25 ml/100 g body weight; supplementary doses, 0.08 ml/100 g) and placed on an electric heating blanket, while their gape was ventilated with a stream of air. The head was held in a holder as described by Karten and Hodos (24) but which was angled at 45° such that the ear–beak baseline was horizontal. This procedure gave better access to the frontal portions of the forebrain. Having opened the skull over the target area with a dental burr, a bipolar concentric electrode (0.2-mm diameter, active tips staggered by 0.5 mm) was lowered stepwise into the forebrain with a stereotaxic micromanipulator according to a systematic exploration grid. Potentials were amplified differentially with a passband of 10 to 100 Hz (occasionally 1000 Hz), and the animal was grounded via the earbars. Click stimuli (1-ms square wave pulses, repeated every 2 s) were delivered by a miniature earphone connected to the contralateral hollow earbar by a 10-cm length of polythene tubing. The responses were either averaged digitally ($N = 32$), displayed on an oscilloscope and photographed, graphed with a plotter, or superimposed ($N \approx 5$) on a storage oscilloscope and then photographed.

Maximal responses of as much as 150 μV but mostly between 50 and 100 μV peak-to-peak were recorded 3 to 4 mm below the dural surface at 3 to 4 mm anterior to the vertical meatal plane and 3 to 4 mm lateral to the midline plane. On the dorsal aspect of the brain this corresponds to a point just posterior to a major branching of the dorsal cerebral ophthalmic vein that runs in the vallecular groove (32). Responses of smaller amplitude could sometimes be recorded as much as 1 mm away from this main locus, but generally the active region appeared to be quite restricted. On a track yield-

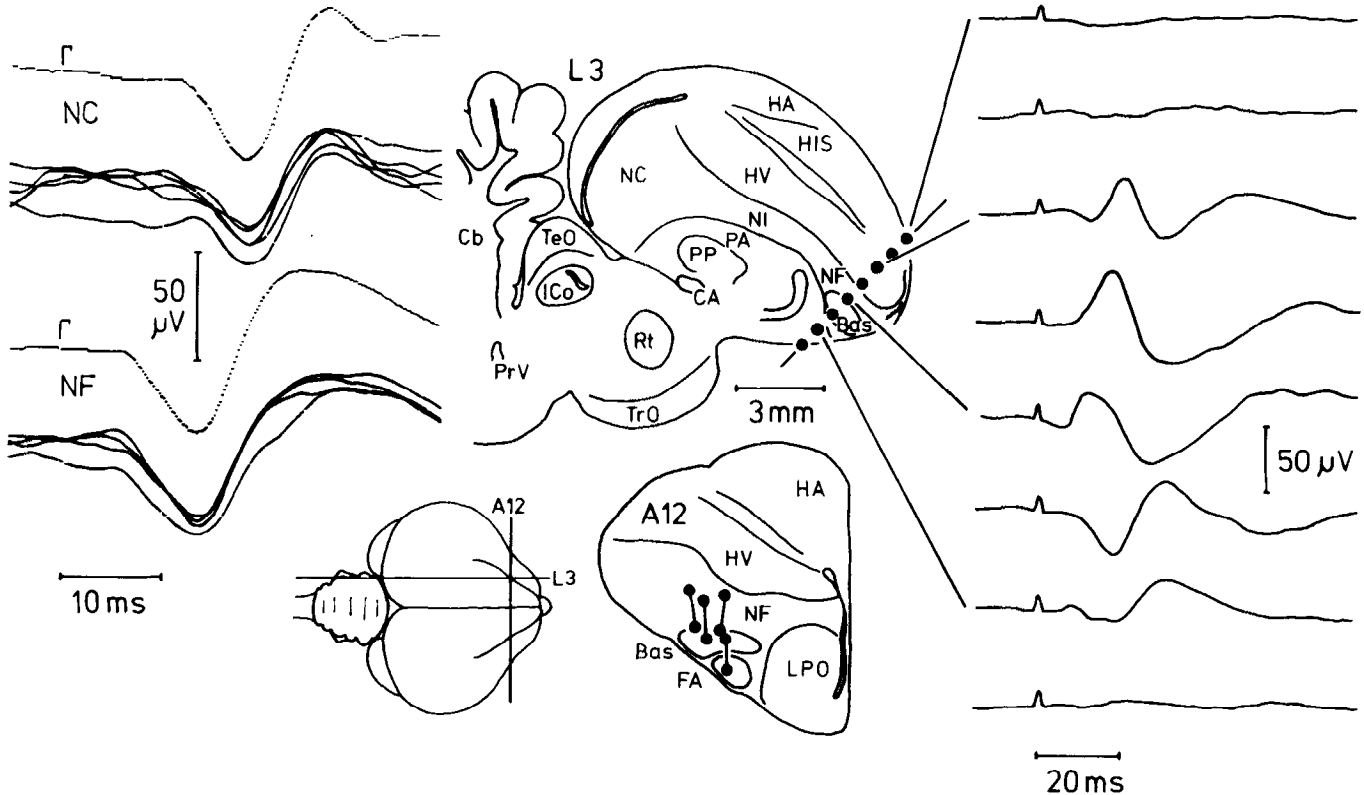

FIG. 1. Auditory evoked potentials from the pigeon forebrain. Right—averaged click-evoked potentials recorded during a penetration of the frontolateral forebrain with a bipolar electrode. The electrode positions were reconstructed from lesion-marked histological sections. Left—click-evoked potentials (with superimposed stimulus artifacts) simultaneously recorded from the neostriatum caudale (NC), field L, and from the neostriatum frontale (NF) close to the nucleus basalis (Bas). Below—locations of four bipolar electrode tips marked with lesions. The implanted electrodes all yielded large-amplitude potentials. Drawings of brain sections and abbreviations based on the Karten and Hodos (24) atlas. The approximate plane of the sections is indicated on a dorsal view of the pigeon brain.

ing maximum amplitude potentials it was usual to observe a polarity reversal as the electrode was advanced in depth, the potential being often markedly reduced at the exact reversal point. This indicates that the two electrode tips were then equipotential relative to the source of the evoked activity (Fig. 1).

In the remaining evoked potential experiments, electrodes were implanted chronically in nine birds, and recordings were made in the awake state. The operative procedure was similar to that described above. Bipolar electrodes were constructed from two insulated stainless-steel wires (0.1-mm diameter), situated side by side and with exposed tips staggered 1 mm apart. Such electrodes were cemented in place when a maximal evoked potential was recorded under anesthesia during the surgery. A bare loop of stainless-steel wire placed under the scalp served as an indifferent electrode. The electrodes terminated in a miniature connector that was also cemented to the skull with dental acrylic. Several days after the operation the bird was restrained in a cloth jacket and placed on a foam rubber cradle placed on a heavy stone table. The amplifier input leads were plugged into the connector on the bird's head. Acoustic stimuli were delivered either by a loudspeaker on a remote support or by a hand-held earphone. The recording procedure was the same as described above.

In the awake bird, the amplitudes of the potentials were about 30 to 50% larger in amplitude than in the anesthetized bird. The latency from the onset of the click at the subject's ear to the first inflection of the response was, however, unaffected and lasted 5 to 8 ms. This latency is almost twice as fast as that characterizing the auditory potentials recorded from field L under identical stimulation and recording conditions. Clicks at threshold intensity for a human observer of normal hearing (approximately 3 dB above a 70-dB SPL white noise background) reliably yielded small amplitude frontal forebrain potentials upon averaging. The amplitude augmented with increasing click intensity until the observer labeled them as loud ($\approx$10 dB above background); very loud clicks ($\approx$20 dB above background) did not yield any further amplitude gain (Fig. 2). The intensity sensitivity was comparable to that of the field L projection as ascertained in the doubly implanted subject mentioned above.

Iljitschew (17) obtained a tuning curve for the evoked potentials from the frontal forebrain area. In an anechoic soundproof chamber he presented tone bursts of a trapezoidal waveform envelope and of varying sound intensity to awake, chronically implanted subjects. He found the best frequency to be about 3 kHz. Measurements for the present study with similar stimuli indicated that the most effective frequencies lay between 2 and 5 kHz even though it was not possible to determine the precise optimum. The sensitivity was reduced markedly for the lower frequencies, as low as

100 Hz (Fig. 2). The evoked potentials in response to clicks showed an amplitude decrement at repetition rates above 2/s. At about 16/s the peak-to-peak amplitude decreased to nearly one-third of the maximum. Note that only the main component and the late slow wave were involved and that the shortest-latency, small-amplitude component, possibly reflecting presynaptic activity, was hardly affected (Fig. 2).

The earphone-probe opening, which delivered the clicks, was placed directly over or within the beak, against the cere or the forehead or close to the eye. This yielded definitely smaller-amplitude potentials than when the probe was placed against the auditory meati (Fig. 3). Completely covering the head and beak with a thick layer of a viscous paste, but taking care to leave free the auditory openings, did not affect at all the potentials evoked by acoustic clicks. However, blocking the meati with paste-soaked cotton-wool plugs considerably attenuated the amplitude of these responses. This attenuation remained the same irrespective of whether the remainder of the head was pasted or not. Subsequent removal of the ear plugs fully restored the amplitude of the potentials. Clicks delivered by earphone to the ipsilateral and contralateral ears yielded equivalent evoked potential amplitudes, the contralateral input being perhaps occasionally more effective (Fig. 3). This agrees with Iljitschew (20) who reported that, contrary to what is typical of medullary and mesencephalic auditory responses, the frontal telencephalic evoked potential amplitudes were unaffected by the direction of the sound source.

In the two birds with chronically implanted electrodes yielding auditory potentials, we attempted to bilaterally transect the three branches (ophtalmic, maxillary, and mandibular) of the trigeminal nerves as they course within the orbits using in part the approach described by Zeigler *et al.* (48). Under anesthesia an incision was made parallel to the posterior border of the bulbi and they were retracted frontally without removing them. An operating microscope and a small wire hook were used to search for the three trigeminal branches which were then cut with iris scissors or a small scalpel. After the birds recovered from this surgery, auditory potentials were again examined and found to be totally unaffected. Postmortem examinations 1 week later revealed, however, that in each subject one ophthalmic branch had not been severed. Therefore a third pigeon with implanted electrodes was bilaterally enucleated under anesthesia. After bleeding had been controlled, all the trigeminal branches were then cut under positive visual control as they emerge into the orbits. Again auditory evoked potentials recorded before and after such transectioning were virtually identical (Fig. 4). This bird was killed while still under anesthesia, and this time the postmortem showed that the trigeminal deafferentation had indeed been complete.

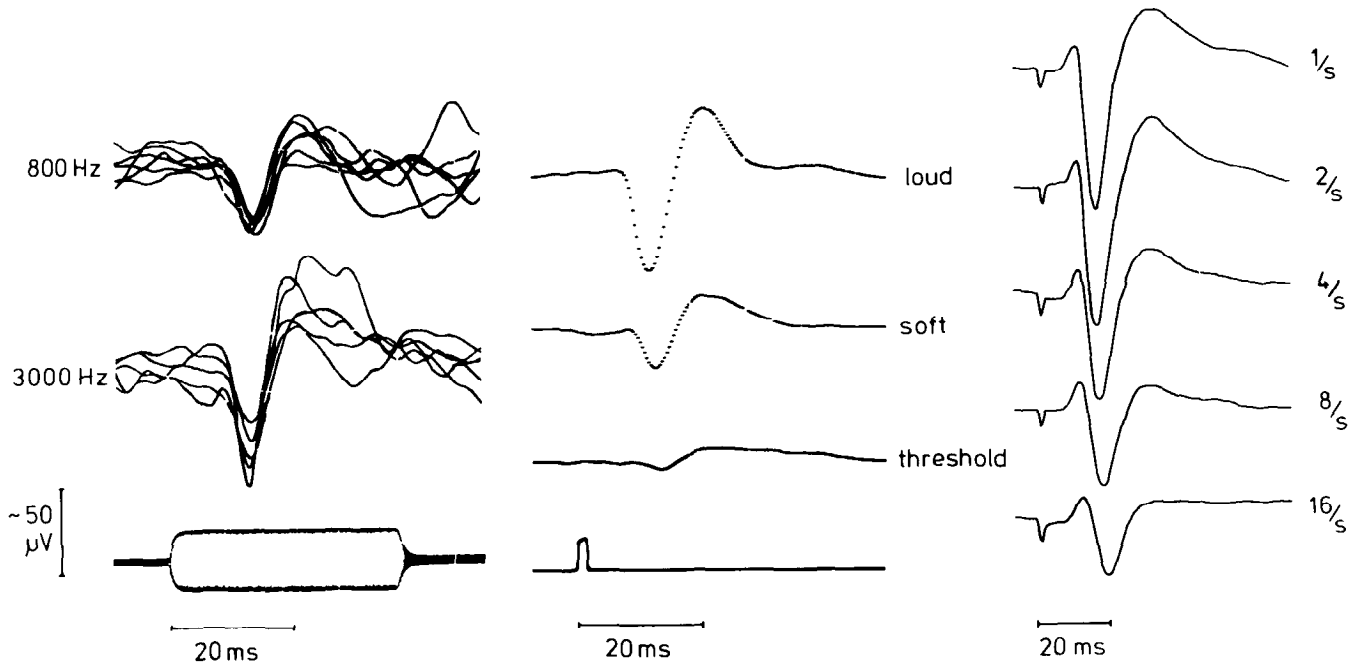

FIG. 2. Auditory evoked potentials from the frontolateral forebrain of the pigeon. Left—superimposed single potentials evoked by sine-wave tone bursts of two different frequencies. Middle—average potentials evoked by clicks at human loudness threshold and above. Right—effect of increasing click repetition rates on averaged potentials.

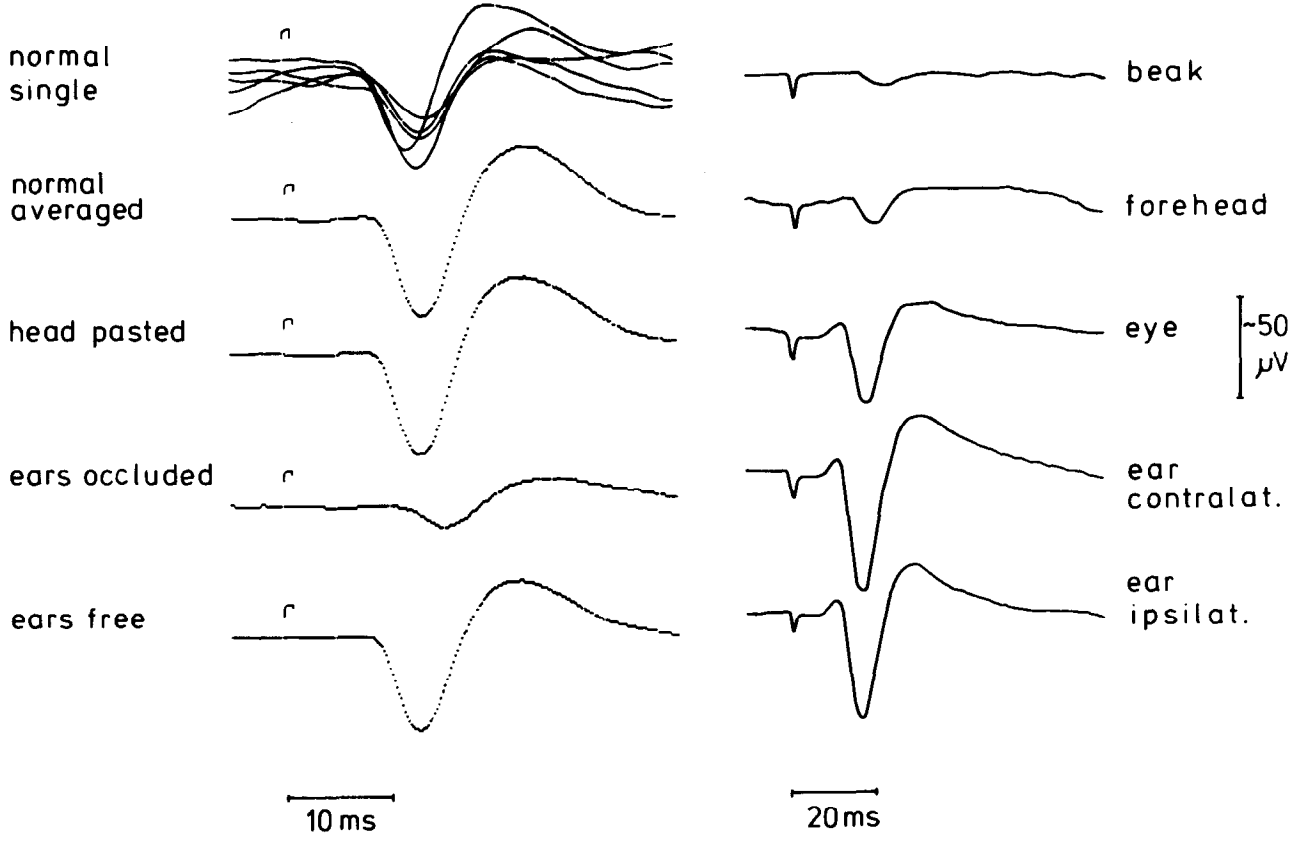

FIG. 3. Auditory evoked potentials from the frontolateral forebrain of the pigeon. Right—potentials evoked by clicks applied to various parts of the head. Left—potentials evoked before and after thickly covering the head and beak with a paste and plugging the auditory canals with paste-soaked cotton-wool.

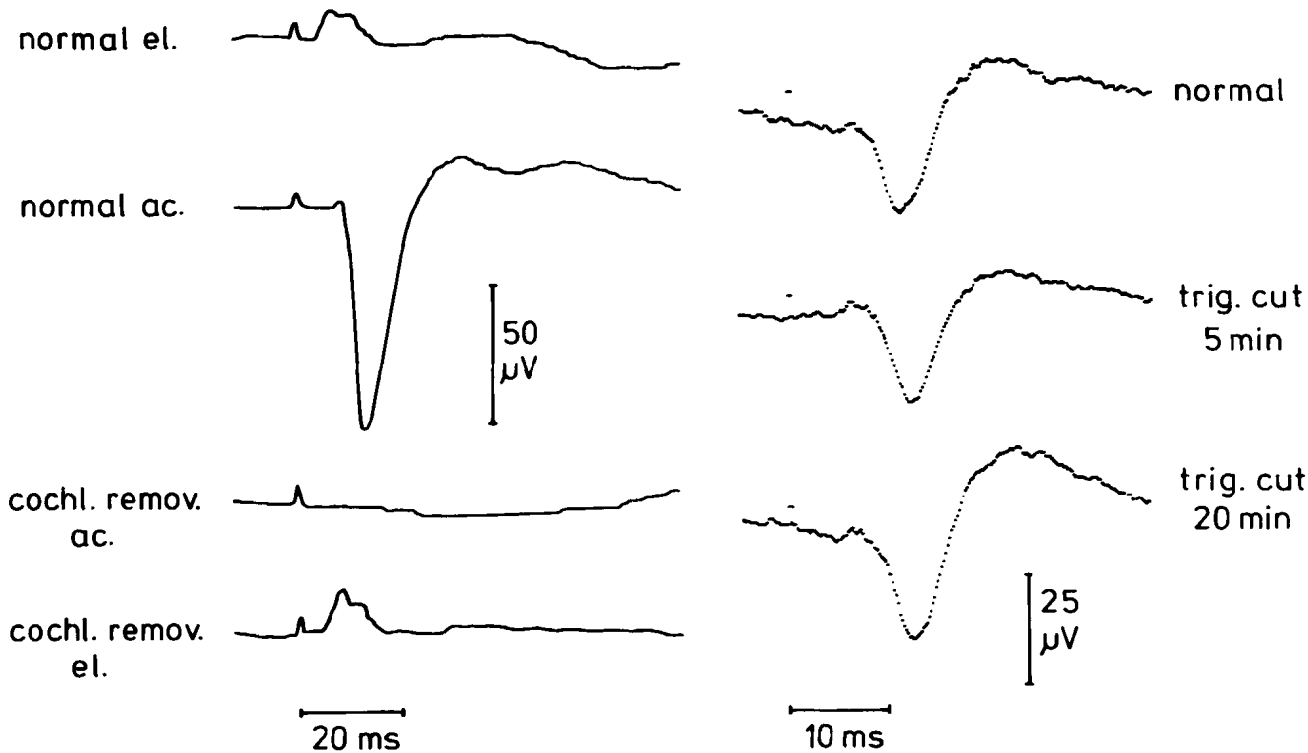

FIG. 4. Evoked potentials from the frontolateral forebrain of the pigeon. Left—averaged potentials evoked by electrical pulses (el.) delivered to the beak and clicks (ac.) before and after bilateral removal of the cochlea. Right—averaged evoked potentials elicited by clicks before and after bilateral transection of all branches of the nervi trigemini. The amplitude increase seen 20 min after the transection could be due to a lightening of anesthesia.

The auditory canal occlusion experiments mentioned above suggest that the sensitive area is associated with the meati. The trigeminal transections just described could have spared smaller nerve branches innervating this area. To check for this possibility we locally anesthetized the relevant areas in an awake chronically implanted subject. The lining of both auditory canals, including the tympanic membranes and the surrounding skin, was treated with xylocaine spray and novacaine instillations. Needle pricks then no longer elicited withdrawal reflexes from the relevant areas. Nonetheless the potentials evoked by clicks were still indistinguishable in every respect from those obtained from the same animal before the treatment. Sound applied to the ear openings continued to be the most effective stimulation.

From two additional pigeons with implanted electrodes which yielded reliable auditory evoked responses, the cochleae were removed bilaterally. Following the surgical procedure described by Schwartzkopff (36) and under anesthesia, the middle ear cavity was opened from the rear. With the aid of an operating microscope and a small wire hook, the membranous cochlea and lagena were removed through a perforation which gave access to the inner ear. The effectiveness of the resection of the cochleae was later checked in postmortem dissections. After recovery from this operation the frontal forebrain evoked responses to acoustic stimuli had disappeared entirely: Even the loudest clicks that could be generated failed to yield any observable response. This lack of auditory response persisted as long as 2 weeks after the operation, when the last tests before despatching the birds were made. In one of these birds a short-latency potential was evoked by electrical stimulation of the beak. The response was unaffected by cochlear extirpation. Thus surgery had not inadvertently affected fifth nerve afferent fibers (Fig. 4). Incidentally, the fact that the electrically evoked potential had an inverse polarity suggests that the tissue generating it was situated differently from that producing the auditory response.

In four additional pigeons, lesions were placed at the tips of the electrodes which had yielded good auditory responses, by passing a radio-frequency coagulation current between the electrode tips and a brass olive placed in the subject's cloaca. After decapitation, the head of each subject was perfused through a cannulated carotid artery with saline and formalin and further fixed 10 days in formalin. After removal from the skull the frontal forebrain was cut transversally on a freezing microtome at 40 μm and stained with cresyl violet. The brain sections were examined, and the electrode tip loci were transferred onto drawings based on the Karten and Hodos (24) pigeon brain atlas. Figure 1 summarizes these findings. It is apparent that the lesions span portions of the neostriatum frontale closely surrounding the nucleus basalis.

Preliminary unit recordings were carried out with eight additional birds. They were anesthetized with either Equithesin (as before) or urethane (intraperitoneally, 200 mg/100 g body weight). After intubation of the trachea and puncture of the sacral bone air sac diverticula they were ventilated by a through-flowing air stream. For stability the bird's skull was cemented with dental acrylic to a crossbar. Both tungsten electrodes, with platinum-blacked tips and impedances of about 10 MΩ at 1 kHz, and 3 M NaCl-filled glass capillaries with a resistance of 15 to 20 MΩ were used. Acoustic stimuli were generated by feeding either 0.3- to 3- ms pulses or 50- to 200- ms sine-wave bursts with a fusiform envelope into an earphone. The latter was connected to the hollow contralateral earbar via a 10-cm length of polythene tubing.

It proved difficult to locate auditory units, suggesting again that the responsive region is of a quite restricted extent, but the stereotaxic locations of successfully isolated units coincided with the immediate neighborhood of the nucleus basalis. A total of 22 auditory units were recorded. Twelve units responded phasically to the stimuli but adapted quickly, and a response could be maintained only by altering stimulus parameters (click duration, tonal frequency) for every few repetitions. In these cases, after a suitable stimulus had been found, it elicited one to three spikes for three to five stimulus repetitions. The 10 remaining units yielded small-amplitude spikes. Most of these units gave a phasic–tonic response to maintained tones, followed sometimes by an inhibitory poststimulus pause. There was a clear optimal-response frequency, and best frequencies ranged between 0.8 and 3 kHz with a clustering at around 2 kHz. Five of the auditory units were thoroughly tested with tactile stimuli applied to the head and beak, but they could not be driven by them. Sound delivered to the ear openings was clearly superior to the same stimulus delivered elsewhere on the head and beak (Fig. 5).

DISCUSSION

To the extent that we replicated some of Iljitschew's experiments we can confirm his findings. There can be little doubt that there is a frontolateral forebrain region in the neighborhood of the nucleus basalis telencephali that reliably yields evoked potentials to acoustic stimuli and with a relatively short latency. It is believed that there is now sufficient evidence to permit the definite rejection of the hypothesis that the evoked responses in question are due to an inadvertent stimulation of peripheral trigeminal receptors being relayed to the nucleus basalis by way of the tractus quintofrontalis (23, 44).

Delivery of a sound stimulus to the auditory meati was more effective than the application of the same stimulus to any other locus of the head or

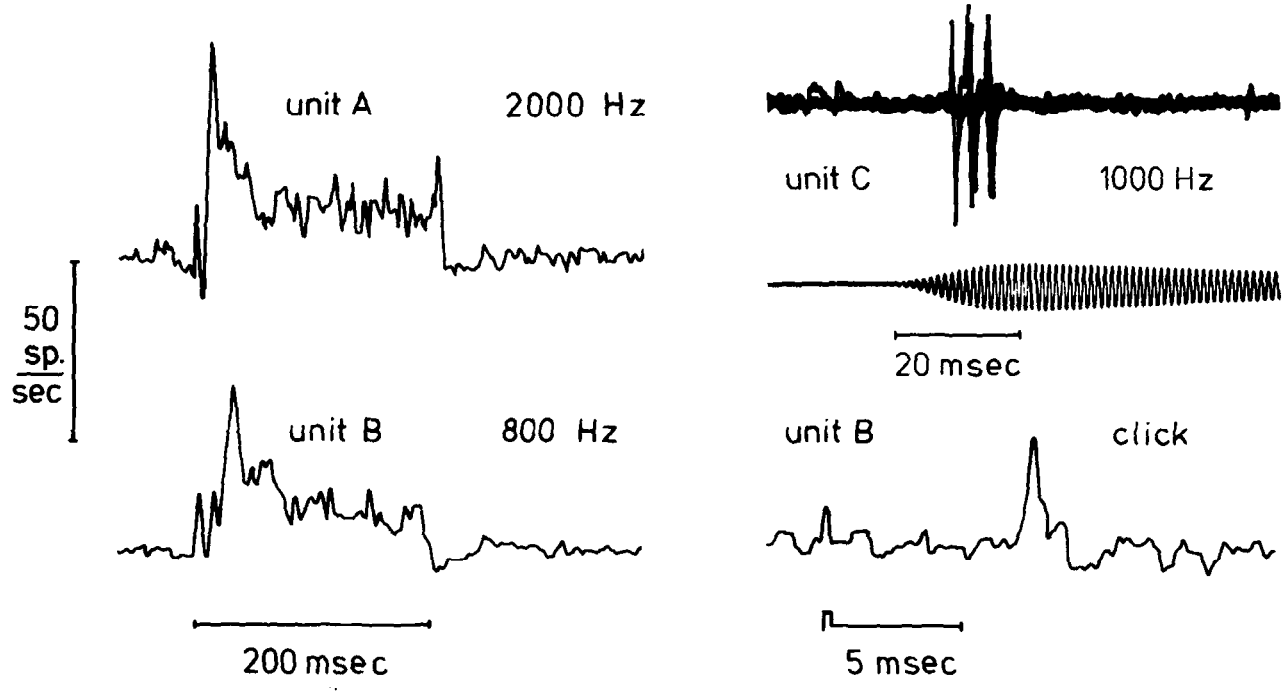

FIG. 5. Auditory evoked unit activity from the frontolateral forebrain of the pigeon. Left—poststimulus histograms of units responding to 200-ms tone bursts. Lower right—poststimulus histogram of unit responding to click stimuli. Upper right—spike responses of a unit to a 1000-Hz tone burst (three traces superimposed, spikes retouched).

beak surface. Damping of the head and beak surface with a paste layer did not affect the auditory potentials in any way. Obstruction of the auditory canals with plugs drastically reduced the responses. Trigeminal denervation or blocking was ineffective in modifying the evoked auditory responses but removal of both cochleae totally suppressed them. Incidentally Karten's (23) statement that Naumov and Iljitschew (30) had found the potentials to be unaffected by destructive lesions of the auditory canal is somewhat misleading. The lesions in question involved only the shaving of the periauricular feathers. This indeed did not appreciably modify the responses. The evoked potential's sensitivity to the intensity of airborne acoustic stimuli is equivalent to that shown by the established neostriatum caudale (field L) responses. Certainly the sensitivity to specific frequencies clearly agrees more favorably with the notion that the potentials are auditory rather than somesthetic in nature. The most effective frequency for eliciting auditory responses was 3 kHz according to Iljitschew (17) and is certainly above 2 kHz according to our data. This agrees reasonably with the best hearing frequency of pigeons, as determined by various physiological or behavioral measures (15, 16, 34, 39), but does not correspond very well with the best frequency for the vibration sensitivity of birds, as established by behavioral and physiological methods [bullfinch, *Pyrrhula pyrrhula* (36); duck (8, 9, 12, 26)] which generally lies below 1 kHz. The fact that Witkovsky *et al.* (44) found that the acoustically responsive units surrounding the nucleus basalis also reacted to tactile stimulation of the head and beak does not, by itself, conclusively show that their acoustic responsiveness is not a true auditory one as these units may have been polysensory. According to Gogan (11), such polysensory units predominate throughout the pigeon telencephalon. The few auditory units that were tested in this study, however, could not be activated by tactile stimuli.

If the lateral neostriatum frontale is a real auditory projection and receives information derived from the output of the cochlea, then the question may be asked as to what anatomic pathway does carry the information? Obviously it is no longer possible to refer to the somesthetic pathway to the nucleus basalis (41, 44) or to the nearby hyperstriatal somesthetic projection (6) in order to account for the auditory responses. In the latter case long latencies are involved (14 to 16 ms), which are incompatible with the shorter latencies characteristic of the auditory potentials (5 to 8 ms) described in this study. Based on this relatively short latency, Harman and Phillips (14) speculated that the pathway might originate from the auditory mesencephalon and bypass the thalamus altogether. Karten (23) specifically reported not finding such a pathway and argues against the possibility that medullary auditory centers might be projecting directly to the peribasalis region. He also quotes Boord (personal communication) as

specifically failing to find any such tract [see also Boord (4)]. However, there are reasons to believe that the anatomy of the auditory pathways in the pigeon is, as yet, incomplete. Johnston (21), for example, found evoked auditory responses in the nucleus ruber. Whitlock (43) and Gross (13) reported finding auditory evoked potentials and unit responses in certain parts of the cerebellar cortex. The afferent pathways responsible even for these projections remain essentially unidentified. Thus it is a reasonable assumption that an oligosynaptic pathway to the frontolateral forebrain from medullary or mesencephalic auditory centers may have been, as yet, overlooked by anatomists. It is quite remarkable in this context that Iljitschew (19) reported that transection of the ipsilateral forebrain peduncles reduced the amplitude of the auditory evoked potentials in the frontal forebrain by only 30% whereas transection of the anterior commissure attenuated them by about 90%! We note that Zeier and Karten (46) in fact found that the anterior commissure contains fibers ending in the nucleus basalis neighborhood but the origin of this particular commissural component is uncertain. Retrograde axonal tracing techniques, such as that using horseradish peroxidase, seem the most promising approach to resolve this question.

It remains to speculate on the functional role that the frontal auditory projection may have. One possibility is that it may provide short-latency feedback to the nearby vocalization-controlling motor area X paraolfactorii which has been identified in the canary, *Serinus canarius* (31). However, it is uncertain whether the pigeon, which differs from the canary in having "innate" vocalizations, possesses an equivalent nucleus as it cannot be identified cytoarchitectonically. Another possibility is that it may play a role in feeding. The nucleus basalis is undoubtedly involved in the control of food uptake by birds as lesion studies showed (47). The results of electrical brain stimulation in herring gulls, *Larus argentatus*, (5) suggested that the nearby neostriatum frontale might be involved in the elaboration of complex food searching patterns [see also Salzen and Parker (35)]. Auditory afferents to such a region might be important for bird species that hunt at least partially by acoustic cues. The pigeon, as a granivorous species, is admittedly an unlikely candidate for auditory foraging [for indirect evidence on this see Delius and Emmerton (7)], but it may nevertheless exploit auditory (bone-mediated?), in addition to tactile, feedback to decide whether it is hitting grains or grit when pecking more or less blindly in the dirt as it often does in nature. Indeed there is recent evidence that pigeons will orient their food-related pecking by acoustic cues (38). It seems possible that the frontolateral telencephalic auditory projection, discovered by Iljitschew and confirmed by this study, is specialized in processing peck-generated noises in the service of food uptake behavior.

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