

**Central Neural Mechanisms of Vocalizations
in Birds: J. D. Delius**

Because vocal learning is practically absent in mammals, that is, at least in those that lend themselves to laboratory investigation, birds may be the animals closest to man in which we can investigate physiologically this process fundamental for language acquisition. An indispensable basis for such investigation is knowledge about brain structures involved in controlling and generating vocal production. Available information on vocalization substrates in mammals is of little use because of the diverging structure of the avian brain. Electrical

brain stimulation, though suffering from serious inherent limitations, is a necessary method for this localization work.

Delius reported the main findings of two exploratory studies involving 250 stimulation sites in gulls and about 260 sites in pigeons (Delius, 1971b*). The subjects were largely unrestrained, and each site was stimulated by the electrode on at least 15 trials, usually on many more, over several sessions spread over a month or more. Information from similar studies by other workers has been taken into account to complete the picture (Brown, 1965a,b, 1969, 1971; Akerman, 1966; Putkonen, 1967; Maley, 1969; Allan, 1970; Potash, 1970,a,b; Newman, 1970,1972; Cannon and Salzen, 1971; Peek and Phillips, 1971; Andrew, 1973; see also Lanerolle, 1972). Little attention has been paid at this point to possible species differences, mainly because the information available on any one species is still too patchy to allow valid comparative conclusions. At some point in the future, however, this may well become an important issue; for example, when comparing stimulation results obtained in birds that have to learn and birds that do not learn their species-typical vocalizations.

Delius studied a brain area that all workers seem to find most consistent in eliciting vocalizations upon stimulation. First discovered by Popa and Popa in 1933, it is located in the midbrain and extends from the posterior commissure lateralwards, including the nucleus intercollicularis and the nucleus mesencephalicus lateralis. There is disagreement about whether the vocalization area comprises or merely surrounds the pars dorsalis of the nucleus lateralis, a structure that has been demonstrated to be the equivalent anatomically and electrophysiologically of the inferior colliculus of mammals, that is, a specific auditory relay nucleus (Biederman-Thorson, 1967; Boord, 1969). Delius's evidence, obtained by implanting concentric electrodes in which the core was a semi-microelectrode that could be used to locate the sound-sensitive neuronal pool and the outer ring was suitable for electrical stimulation, suggests, or at least does not exclude, the possibility that this area is directly concerned with mediating vocal-motor effects. Vocal responses can be elicited, when the stimulation electrode is located within the auditory neurons, with thresholds that are as low as the lowest found when eliciting vocalization from the areas surrounding the mesencephalicus lateralis dorsalis. Delius also noticed, as did Biederman-Thorson†, that the largest auditory evoked

*Also, J.D. Delius, unpublished work.

†M. Biederman-Thorson, personal communication.

potentials are not recorded from within that auditory neuron population but from the surrounding area. These results are contrary to Potash's (1970b) and Newman's (1970) results, which suggested that the areas from which unit potentials and evoked potentials are obtained coincide, and that stimulation only yields vocalizations when the electrode tip is outside the region that yields maximal response of either type. Rather, Delius's findings indicate that vocalizations can be obtained at comparable thresholds from the area yielding unit responses, from part of the areas yielding auditory evoked potentials, and from areas not yielding either type of response. However, the very small dimensions of the structures involved (the mesencephalicus lateralis dorsalis of a pigeon is a mere 1½ mm long and 1 mm in diameter) are close to the limits of what can be localized by brain stimulation. Further, while histological material stained to show cells and myelin might suggest a clean segregation between these structures, examination of silver-stained material corrects this view; the number of fibers that do not respect the nuclear boundaries is truly staggering. Furthermore, Golgi material from domestic chick indicates the presence of numerous interneurons that appear to specialize in interrelating the auditory colliculus with the surrounding structures.

Whatever its precise extent, several lines of evidence indicate that this mesencephalic vocalization area is, relatively speaking, on the efferent side of a system controlling vocalization: (1) As noticed by Andrew (1969), it is characterized by a comparatively short minimal latency, about 100 msec, whereas all other vocalization-eliciting structures considerably exceed this; their shortest minimal latency is never less than 500 msec. (2) Calling can be elicited under anesthesia, suggesting that few synapses can be involved in the pathway to the effector organs. (3) This area is characterized by high reliability; that is, if a given electrode elicits vocalization, it will do so on virtually every above-threshold trial, regardless of the surrounding conditions, unlike vocalization electrodes elsewhere. Similarly, it yields no detectable after-effects of any appreciable duration, a characteristic that distinguishes a high proportion of vocalization-eliciting electrodes elsewhere (see below). (4) The vocalizations induced are mostly, in Delius's experience, quite abnormal. They almost invariably consist of single syllables that are repeated with little variation for as long as the stimulation lasts and do not resemble any normal calls. They are not associated with postures normally associated with vocalizations. (5) Lesions in this area are reported to mute birds. Similar arguments led

Allan (1970) to postulate that this area is the location of neuronal oscillators responsible for the patterning of domestic chick calls and to formulate a theory of their mode of operation.

If the *intercollicularis mesencephalicus lateralis* area is a motor center of some sort, a pathway that descends from it to medulla levels must exist; one might expect that its stimulation would elicit vocalizations. Indeed, vocalization sites are found in portions of the lateral mesencephalon more ventral and more caudal than the above area, but their localization is remarkably scattered, suggesting that either the fibers making up the pathway descend in a broad front or that many different but discrete pathways are involved. Anatomical data indicate the presence of a descending pathway, but its termination in the medulla does not accord particularly well with a motor function (Karten, 1967; see also Murphy and Phillips, 1967). Clarification of this issue is one of the most important points for immediate research.

Another area that authors agree yields vocalizations upon stimulation is the medial, paraventricular hypothalamus. In Delius's experience, vocalizations elicited from this region are usually associated with posturing. This posturing and the calls themselves are generally indistinguishable from those given by normal, unstimulated birds. A high degree of unreliability is characteristic for loci in this area compared with the mesencephalic sites. The results of a particular stimulation trial are markedly dependent on present and recent stimulus contexts. Furthermore, a substantial proportion of the sites show lasting after-effects following stimulation, which can be best described as changes of mood (see also Delius, 1973). These can sometimes be measured in terms of changes of threshold, changes in probability of the same or other behavior being shown, changes in the completeness of behavior evoked, etc. The postures and vocalizations elicited are fairly constant for a given site, but over several sites a large portion of the normal repertoire of a species can be elicited. Probably there is a degree of discrete localization for the various types of calls and associated postures among the medial hypothalamic nuclei, but this is still uncertain. The minimal latencies for eliciting vocalizations for this area, typically several seconds, are longer than those characteristic for the mesencephalic area. A few vocalization-eliciting sites are found in the immediate neighborhood of the nucleus ovoidalis, the avian equivalent of the mammalian medial geniculate (Boord, 1969; Biederman-Thorson, 1970). It is thus possible that, as in the case of the mesencephalic nucleus, the thalamic auditory nucleus is enveloped, or

even overlapped, by a vocal motor area. Delius hypothesized that sensory neural filters functioning in the recognition of vocalizations are partially enmeshed with motor neural oscillators responsible for the production of vocalizations. He discussed this notion in the context of Nottebohm's electrophysiological investigations, currently in progress, and Brown's (1971) work on the red-winged blackbird. Delius felt that discrepancies between the findings of various workers in this field might be due to species differences. In any event he thought that evidence is mounting for the close proximity of the vocalization motor area to auditory projection, the area L, an avian equivalent of the auditory cortex (Boord, 1969; Biederman-Thorson, 1970). Incidentally, in all stimulation data no evidence is mentioned for any lateralization; this could be due to the fact that researchers have not looked for it.

Some other telencephalic structures have been fairly consistently found to elicit vocalization. These are the archistriatum, the occipito-mesencephalic tract, and some septal nuclei. These structures are, in part, homologous with the amygdala, the stria terminalis, and the bed nuclei of the latter in mammals (Zeier and Karten, 1971) and are well known to be involved in the control of emotional behavior, including vocalization. It seems likely that they link up with the medial hypothalamic vocalization area mentioned earlier.

Delius indicated that the picture of the neural substrates of avian vocalizations described above is misleading without some additional, restricting comments. The concordance among the results of various authors is less than perfect. Part of this may be due to species differences, to differences in stimulation techniques, to differences in environmental conditions under which tests were conducted. One variable that undoubtedly is important is the hormonal state of the subjects. Indirect evidence for this comes from comparing the proportion of vocalization-eliciting sites found in juvenile, sexually immature gulls (8 out of 250) and in adult, sexually active pigeons (48 out of 260), and more direct evidence from the demonstrated vocalization-(with displays)-facilitating effect that hormones implanted in the archistriatum, occipito-mesencephalic and medial hypothalamus have (Barfield, 1969; Hutchison, 1970). In Delius's data there were several instances of anatomically identical electrode placements that in one individual yielded vocalizations and in another did not. This is difficult to explain. Interspersed among clusters of positive sites in any of the areas mentioned earlier, there were invariably electrode loci that did not result in vocalizations, and similarly, in the midst of hosts of

negative sites, it was not rare to find the odd positive locus that could not be easily dismissed because it did consistently and persistently elicit calling. The rather frequent occurrence of sites that, after having produced no vocalizations for hundreds of trials, suddenly begin to do so and persist in doing so is also disturbing.

Other discordances are similarly puzzling. For example, by selecting "spontaneous vocalizer" and "spontaneous nonvocalizer" pigeons, Delius* finds that the "vocalizers" yield a considerably larger proportion of vocalization sites when electrodes are implanted in likely areas. Castration, though partially abolishing the "spontaneous" vocalization differences, does not seem to affect the number of sites evoking calling.

Delius believes that vocalizations in birds are not controlled by anything like a tidy hierarchical neural system of the type that ethologists might fancy. The control is, rather, achieved by a highly meshed network, partially overlapping with sensory systems engaged in the recognition of vocalization, widely distributed among neural structures. Components may at times, by virtue of variable programming, be vicariously incorporated in systems controlling functions other than vocalization. Electrical stimulation, due to its inherent coarseness, permits us only the most imperfect insights into such complex systems. The approximately 10^8 neurons with some 10^{11} synapses in the average bird brain unfortunately allow some room for sophistication!

**The Development of Auditory Sensitivity in Relation
to Mother-Young Vocal Communication in Birds:
M. Konishi**

Interspecific differences in the rate of prenatal and postnatal development of hearing are an important factor in the comparison of the ontogeny of vocal behavior among different species. In some mammals, such as the rat, normal adult hearing does not develop until 10 days after birth (Crowley and Hepp-Reymond, 1966; Gottlieb, 1971b). Precocial birds, such as chicks, start walking and feeding for themselves shortly after hatching. Among these birds a considerable amount of vocal-auditory interaction between parents and chicks in eggs takes place before hatching. In guillemots (*Uria aalge*), chicks in eggs can learn to recognize individual characteristics of the calls of their

*J.D. Delius, unpublished, preliminary experiments.