Neural Substrates of Vocalizations in Gulls and Pigeons

JUAN D. DELIUS

Department of Neurosciences, UCSD, La Jolla (U.S.A.)
and Department of Psychology, Durham (England)

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Summary. Vocalizations were obtained by electrically stimulating the inferior colliculus, the auditory thalamic nucleus and a medial hypothalamic nucleus of awake, unrestrained herring gulls, lesser black-backed gulls and pigeons. The significance of the involvement of auditory centres in the motor control of avian calling is discussed. The wide gammut of calls and accompanying behaviour that was elicited is described and related to the normal behaviour, typical of the species concerned. A difference between immature gulls and adult pigeons regarding this relationship is attributed to their differing hormonal states. Attention is drawn to the heterogeneity of temporal characteristics associated with the stimulus induced responses even when elicited from virtually the same site. Incorporating earlier work on the central mechanism of avian vocalizations and based on anatomical, physiological and behavioural considerations it is tentatively concluded that the neural structures involved are linearly organized into a telencephalofugal, efferent system. It is suggested that the inferior colliculus incorporates the origin of a final common pathway to medular motor centres for all vocalization generating structures.

Key Words: Electrical brain stimulation — Evoked vocalization — Birds

Introduction

Vocalizations play an important communicatory role within the social behaviour of birds. It is not surprising therefore, that they have been the subject of intensive research (Thorpe, 1958; Hinde, 1969). But only few of the studies, well summarized by J. Brown (1969) have been concerned with the neural mechanisms of avian sound production. These could, however, be of interest from various points of view.

Many bird calls are stereotyped but complexly patterned sounds; the neural substrate producing them might be suitable for studying the neurogenic generation of non-periodic patterns (Murphey and Phillips, 1967). The songs of some species are learned; the structures underlying them may be promising material for studying the neuronal changes that accompany learning (Konishi and Nottebohm, 1969). Some vocalizations are uttered only during certain hormonal states; hormones must be impinging on the vocalization mechanisms and hence these could
be good sites for studying humoro-neural interactions (Hutchison, 1967). Bird individuals that could be induced with electrical stimulation to utter particular calls at specified times would be invaluable for the analysis of the communicatory function of vocalizations (John Smith, 1969). The fact that the avian syrinx differs fundamentally from the mammalian larynx (Greenwalt, 1969), in conjunction with the divergent brain organisation of the two vertebrate classes (Kappers, Huber and Crosby, 1965), provides an interesting background for a comparative study of the functional neurology of vocalizations.

Before such studies are possible it is necessary to identify and delineate with some precision the central nervous structures involved in controlling and pattern ing avian vocalization. This paper presents results relevant to this problem arising from a systematic exploration of the brain of herring and lesser black-backed gulls with electrical stimulation (Delius, 1967, in prep.) and some results of a more specific study on pigeons using the same technique, which expand the information obtained by earlier workers.

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Methods

The herring and lesser black-backed gulls (Larus argentatus and L. fuscus) were hand-reared from eggs, keeping them in semi-isolation for 5 weeks; this made them reasonably tame. Then they lived in large aviaries in groups of 6—8, feeding on fish, meat and dog biscuits. Water was available in small ponds. When at least 8 months old, but always before they reached sexual maturity at the age of 3 years, they were implanted under pentobarbital anaesthesia (Delius, 1966a) with up to 8 stainless steel electrodes of 0.1 mm diameter and with 0.25 mm² uninsulated tips. A subcutaneous bare wire served as the indifferent electrode (Delius, 1966b). After a week's recovery they were tested for 10—20 sessions spread over 2—3 months in a 4 m³ cage. During each session each electrode was stimulated several times with 50 cycles sine wave current up to 200 μA. The brains were then conventionally processed and the electrode tips localized on sections stained for fibres and cells.

The domestic pigeons (Columba livia) of the white carneau variety were adults from the Palmetto Pigeon Plant, North Carolina. Under Equithesin anaesthesia (Karten and Hodos, 1967) they were stereotactically implanted with staggered, multiple electrodes made of 0.2 mm diameter stainless steel wire with 0.5 mm² uninsulated tips. A subcutaneous length of bare, stainless steel wire was used as indifferent electrode. Beginning some 5 days after the operation they were tested for 5—10 two hour sessions in their homecage, each electrode being repeatedly stimulated with 60 biphasic pulses per sec of 1 ms duration, and of up to 5 volts in strength. While usually the stimulation current was passed between the electrode tips and the indifferent (monopolar stimulation) in some cases the current was passed between two closely neighbouring electrode tips (bipolar stimulation). Electrode tips were located in conventionally prepared histological sections.

In both the gull and pigeon experiments it was made certain that the behavioural responses obtained were not incidental, but due to the stimulation itself, by randomly interposing control periods in which all the routine procedures of a stimulation trial were followed except that the bird was disconnected from the stimulator. Also in at least two trials for each electrode another bird was present in the testing cage to check for a possible communicatory role of the vocalizations elicited.