THE ORIGIN AND EVOLUTION OF THE CALLS AND FACIAL EXPRESSIONS OF THE PRIMATES

by

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(With 35 Figures and 2 Plates)

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The study of the origin and evolution of displays began with the publication in 1872 of the 'Expression of the Emotions in Man and Animals'. The systematic study of primate displays not only began, but may be justly said to have ended with this book, despite the fact that human expressions and calls can be interpreted and understood only by comparison with those of other primates. The pages which follow represent a first attempt to resume this work, which is of great importance not only to the study of animal behaviour but to psychology and anthropology.

MATERIALS AND METHODS

The numbers of each species observed are given in the systematic account which follows. The literature on primate vocalisations and expressions has been reviewed up to the end of 1960.

Calls were recorded on an Ampex portable tape recorder and studied as sound spectrograms made with a Kay Sonagraph. This and much of the apparatus and materials used were bought with a National Science Foundation Grant (NSFG 12996). A sound spectrogram displays sounds visually; the vertical axis represents pitch, and the horizontal axis time from the beginning of the recording. A normal spectrogram would show sound over a period of a little over two seconds up to a pitch of about 7.5 Kc. By playing record-

1) Nearly all the Strepsirhines discussed were studied in the author's laboratory, thanks to the great generosity of Dr J. BUETTNER-JANUSCH. Cebus albifrons, Aotes trivirgatus and Lagothrix lagotricha have also been under prolonged study. The remaining primates were studied in the public collections at the Bronx Zoo; the author wishes to thank the authorities in charge of the Bronx Zoo for permission to make recordings there. His thanks are also due to Professor E. J. BOELL for the accommodation and facilities afforded by the Yale Zoology Department. He is extremely grateful to Dr T. TUGENDHAT and Dr O. ALDIS for comments on the paper in preliminary drafts. Finally, major support was afforded by US PHSG M 5127.

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ings at half or even quarter speed, spectrograms may be made reaching up to 15 Kc. or 30 Kc. and analysing sound over about one second or half a second. The recording system used responded to intense sounds at above 30 Kc., but its sensitivity began to fall above 15 Kc.

A typical mammalian sound results from the passive vibration of the partially closed and tensed glottis lips. (Active vibration due to very rapid rhythmic contractions of intrinsic laryngeal muscles is not involved, DUNKER and SCHLOSSHAUER, 1957.) Like any other vibrating system the glottis lips vibrate with a fundamental frequency, and also frequencies which are multiples of it (overtones). The greater the tension of the glottal lips, the higher is the fundamental. Often, the more vigorous the expiration the better the higher overtones are developed. Eventually they always become too faint to be represented on a spectogram. The sounds produced by the glottis are altered by passage through the nasopharynx or buccal cavity. Tones whose frequency approaches the natural frequency of vibration of one of these chambers will be emphasized; others will be reduced. The resulting emphasized bands on the spectogram have been termed 'resonant zones'. Their distribution is naturally altered by changes in shape or volume of the resonating chambers.

DEFINITION OF TERMS

The term 'sound' has been restricted in the present work to vocalisation with a tonal structure, whereas 'noise' is reserved for vocalisation which is continuously developed over wide ranges of pitch. Noise is best regarded as the result of sound generation by a number of sources, each with their own frequency. The glottis may produce noise when it is overblown as in a shriek, presumably because it ceases to vibrate as a unit. The vocalisations of each species have been divided into calls; that is, discrete patterns of sound and noise, which are sufficiently invariant to be recognisable as belonging to a particular type. Calls have been defined on form alone, with no consideration of causation. A variety of intermediates between calls always occur, so that any such classification is of necessity somewhat arbitrary.

Prosimians sometimes vocalise with the glottis lips fully closed. As a result air escapes in a series of little puffs, which produce clicks (narrow columns of sound or noise); these, when they follow each other rapidly, constitute 'vocal fry'. Such series of clicks may blur together, as the glottis lips become parted more completely, into a normal continuous vocalisation ('phonation'). A 'crackle' is the first result of blurring, in which undulations of the tones, (corresponding to fused clicks) result in their repeatedly meeting and parting, giving a very characteristic plaited appearance. 'Grunts'