

The Avian Brain

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Preface

The work of embryologists, histologists, pharmacologists, physiologists and zoologists has now provided a wealth of information about the avian brain. Such studies form an interesting and constructive comparison for workers in many aspects of brain studies and no single reference source, providing a summary, exists. It was therefore a pleasure to accept the suggestion of Academic Press and attempt to fill this gap. If the book is somewhat idiosyncratic then this reflects, at least in part, the rather diverse field. Should it assist biologists to see both bird brains and other structures in perspective I will feel that my objectives have been attained.

I would like to express my personal appreciation to a number of people. To Dr. E. A. Salzen, now of the Department of Psychology, University of Aberdeen, with whom I worked for all too short a time ; to Professor P. M. Sheppard, F.R.S., of the Department of Genetics, and Professor A. J. Cain, Dr. C. L. Smith and Dr. J. W. Jones of the Department of Zoology in this University, without whose encouragement this book would not have been written. Needless to say they are in no way responsible for any inadequacies which it may have.

Finally I would like to acknowledge a far older debt to Professor E. N. Willmer, F.R.S., who long ago convinced me that a study of structure must precede a study of function and I would also like to thank the Production Department of Academic Press for their very kind help.

University of Liverpool
January, 1972

RONALD PEARSON

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1 Introduction

I. GENERAL CONSIDERATIONS

In general terms both the gross and the detailed structure of the nervous system within a given taxon reflect the relative complexity of the morphological organization and behaviour. These are in themselves dependant upon the type of relationship which the animal has with its environment, and which its organ systems have with one another. The central nervous system of birds is no exception. Together with other amniotes, and more especially mammals, birds have a high degree of morphological differentiation. Furthermore, their behaviour patterns involve perceiving, and responding to, intricate visual, auditory and tactile cues. These facts pre-suppose the existence of a highly complex nervous system. The size of the brain itself exceeds that of reptiles, as can be seen from the often cited example of a lizard with a total body weight of 10 g. Such a specimen has a brain which weighs approximately 0.05 g. In contrast a small passerine bird of equivalent body weight has a central nervous system which weighs 0.5 g. Although this difference in size actually involves the entire brain it is particularly noticeable in terms of the cerebellum and forebrain hemispheres.

From a historical point of view it is interesting that the neuro-anatomical studies of these and other components of the avian brain, which were largely initiated during the closing decades of the last century, were somewhat interrupted in the latter part of the 1930s. This is of particular interest because it was at that very time that the complementary study of ethology was growing rapidly. Thirty or so years later the intellectual descendants of those early ethologists, and many behavioural psychologists, have now started to experiment widely upon avian brains. The particular interest of such workers lies in the possible neuronal pathways which may be implicated in the behaviour patterns that they observe. Although it would be ridiculous to suggest that there was not a continuing thread of neurological research on birds during the 1940s and 1950s, it is fair to say that at that time, when the work of ethologists was catching the imagination of both scientific and lay public alike, such research was spasmodic and largely confined to a limited number of isolated centres. During this period the information which did emerge was often an example of "spin-off", and was produced by interested individuals who considered that it would be informative to apply to the avian brain those

techniques which had been, or were currently being, developed by medically orientated research workers using mammalian material. It will be clear from subsequent chapters in this book that these techniques frequently fulfilled their user's expectations and produced fascinating results. If these results did not, perhaps, become as widely known as one might have expected, then this merely reflects the interests of the times—times during which such other subjects as molecular biology were beginning to compete successfully for the resources available to biologists.

It is also very instructive to notice how often the data which have emerged during the last twenty, and more especially the last ten years, corroborate at least some of the conclusions drawn by far older workers. These had painstakingly collated an immense number of anatomical results which are epitomized in the monumental works of Kappers (1921, 1947) and Kappers *et al.* (1936). The principal conclusions are represented in Fig. 140 of this book. Analogous compilations which represent a more physiological approach are those of Ten Cate (1936, 1965) and Buddenbrock (1953).

It is the intention of this present book to outline the extent of our knowledge on this whole subject, the anatomy, histology, physiology and overall integrative action of the avian brain. Naturally when doing so one necessarily indicates the extent to which its organization corresponds to that of vertebrate nervous systems in general. However, it is fair to say that, although a consideration of the brains of related species or classes frequently throws light upon the problems which particular research workers are encountering in the animals which interest them, this book is not written with the intention of providing an account of a type of brain which, although simpler, shares the characteristics of that found in mammals. It is clear that in the past a considerable proportion of the drive which produced descriptions of non-mammalian nervous material came from people whose primary interest lay in Man and mammals and who were seeking simpler, more easily investigated, but homologous, systems. Without any doubt at all this was both laudible and rewarding, but I would like to emphasize that in writing this book it has been my intention to consider the avian brain and sense organs *per se* and to emphasize that they are different from, but certainly not simpler than, mammalian brains. Where valid comparisons between avian and mammalian systems can be drawn, it is often beneficial to consider them. By doing so the answer to a particular problem may suggest itself. However, to go further than this and assume that just because a structure serves a particular function in one class it necessarily does so in another, is at best dangerous, and at worst ill-informed. Furthermore, to blithely assume that structures in different classes are homologous rather than analogous simply because they serve apparently related functions is also dangerous. In general, I have therefore limited this book to a consideration of the conditions which occur in birds.

Where, as in the chapter on brain biochemistry, the available data suggest that the situation is comparable with that in other vertebrates, I have indicated that this is the case, referred to general reviews, and restricted the text to the actual information which is available about avian material.

Wide ranging summaries of nervous systems and their function in numerous animals and experimental situations are provided by many works (see, for example, Bourne, 1968). Previous synoptic reviews of avian material include, besides those of Kappers *et al.* (1936) and Kappers (1947), those of Papez (1929), Portmann and Stingelin (1961) and Stingelin (1962). In recent decades the development of the Nauta-Gygax histological process (Nauta and Gygax, 1951, 1954) together with the stereotaxic atlases of both Tienhoven and Juhasz (1962) and Karten and Hodos (1967) promise great rewards in the future. Where no recent information on anatomical structures is available I have drawn on my own studies of avian material which are derived from specimens kindly provided by the Director of Chester Zoo and other local sources.

It is worth mentioning at this point the very interesting review of electrical stimulation studies on the brain of birds which was provided by von Holst and Saint Paul (1963). This has received a considerable amount of attention from ethologists and was discussed in detail by Hinde (1966). Sceptical of the existence of discrete and localized centres within the central nervous system of the hen, they concluded that:

1. A stimulation field may appear silent or active at different times;
2. Changing behaviour patterns may be evoked over a period of hours as the result of activating a particular stimulation field;
3. The same pattern or action can often be released by stimulating different fields.

Central to their interpretation is the concept of "mood shifts". They suggest that in life it is to be expected that stimulus fields remain silent in the presence of a dominant behaviour pattern such as fleeing or postural freezing which suppresses other activity. They conclude that, under these conditions, to say that the stimulus field is silent is incorrect. The activity which would normally result from such focal stimulation does not occur because it is being blockaded elsewhere. To explain the changing reactions which can be evoked at different times from one and the same field they invoke both the obvious and widely noted variations in the distance from the site of stimulation to which excitation may be propagated, and also the huge differences in individual behaviour thresholds which result from mood shifts and adaptation. Making the assumption that there are structures related to a number of neuromotor systems within the stimulus field and that all these are therefore excited, they concluded that the resultant behaviour is determined by the total dynamic situation which is currently prevailing, rather than by specific

anatomical projections of the stimulus field. The fact that identical reactions can result from stimulating widely separated fields reflects, in turn, the fact that many movements are common to a variety of behaviour patterns. Locomotor unrest which may in one case be directed at an enemy may, in another, reflect thirst etc. Although to completely deny the existence within the avian brain of foci which are predominantly associated with at least certain sensory modalities and motor output would be to fly in the face of much of the evidence which is reviewed in the later chapters of this book, this highly critical assessment of many basic assumptions is a valuable background to any such considerations.

II. AVIAN TAXONOMY

As birds constitute the most homogeneous class of the vertebrates it is not surprising that their systematic relationships are not easily stated with precision. It is certainly true that no single classificatory scheme is universally acceptable to ornithologists and zoologists. The particular difficulties relate to a limited number of orders and genera, are somewhat idiosyncratic, and reflect the preconceptions or predisposition of the relevant writer. Universally recognized as originating from the diapsid reptiles, from which they can be theoretically derived by relatively slight modifications of basic anatomy, there are some 25,000 known species or sub-species of living birds. Besides the exact interrelationships of these forms their degree of affiliation to fossil forms, such as the Jurassic sub-class Archaeornithes and the Cretaceous *Hesperornis*, are also difficult to establish with any great degree of confidence. A summary of these problems is provided in such works as Romer's "Vertebrate Paleontology", and Young's "Life of the Vertebrates". It is for this reason that the classificatory schemes which have appeared since the days of Linnaeus vary, as does their credibility. This variation not only reflects the items of knowledge which were either new, or considered to be critical, at the time they were produced, but also as was noted above the personal idiosyncracies of the particular workers. It is certainly clear that, as a result, the schemes which are considered acceptable today are markedly different from those which were put forward by for example Linnaeus himself, Buffon and Cuvier.

Broadly speaking, one can differentiate amongst living forms between the Ratites, Impennae and Carinates. The first group includes the Struthioniformes, or Ostriches; the Rheiformes, or rheas; the Casuariiformes, including the cassowary and emus; and the Apterygiformes or Kiwi. The second group comprises the penguins, and the third all other living birds.

By using zone electrophoresis Gysels (1970) showed that *Rhea*, *Casuarius* and the tinamiform genus *Crypturus* are clearly different from each other

although showing similarities which suggest a closer relationship than with other birds. This would agree with the conclusions of Parkes and Clarke (1966). It is also interesting that, of the other avian orders, it is the Galliformes which have the closest similarities, in terms of lens protein reactions, with the ratites and tinamous. This corroborates the suggestions that tinamous are more closely associated with the ratite birds than with other carinates, and that the Galliformes are closer to the ancestral stock than are other carinates. On the other hand Sibley (1960) found that the tinamou pattern resembled neither the rheiform nor the galliform one. Stresemann (1927-34, 1959) favoured polyphyletic evolution.

TABLE 1

Systematic list of the orders of living birds based on Wetmore's classification (1934). The approximate numbers of species in certain orders after Mayr and Amadon.

Struthioniformes	Ostrich (1)
Rheiformes	Rheas (2)
Casuariiformes	Cassowaries, emus (5)
Apterygiformes	Kiwis (3)
Sphenisciformes	Penguins (16)
Tinamiformes	Tinamous (33)
Gaviiformes	Divers or loons (4)
Colymbiformes	Grebes (20)
Procellariiformes	Albatrosses, petrels, etc. (90)
Pelecaniformes	Cormorants, gannets, pelicans, etc. (54)
Ciconiiformes	Hérons, storks, etc. (105)
Phoenicopteriformes	Flamingoes (6)
Anseriformes	Geese, Ducks, Screamers (148)
Falconiformes	Diurnal birds of prey (271)
Galliformes	Game-birds, etc. (241)
Gruiformes	Cranes, rails, cariamias, etc. (199)
Charadriiformes	Waders, gulls, auks, etc. (308)
Columbiformes	Sand-grouse, pigeons (308)
Psittaciformes	Parrots (316)
Cuculiformes	Turacos, cuckoo (147)
Strigiformes	Owls (134)
Caprimulgiformes	Nightjars, etc. (97)
Micropodiformes	Swifts, Humming-birds
Coliiformes	Mouse-birds (6)
Trogoniformes	Trogons (35)
Coraciiformes	Rollers, kingfishers, bee-eaters, hoopoes, hornbills, etc. (194)
Piciformes	Puffbirds, barbets, woodpeckers, toucans, etc. (381)
Passeriformes	Perching and singing birds (5072)

Apart from the conjectural relationships of the orders grouped together under the heading of Ratites, and the degree of independence between the three groupings themselves, the inter-relationships of the neognathous orders produce a number of difficulties. Wetmore's classification is generally used and this is summarized in Table 1 but it has some inadequacies, and I have, for personal preference, followed the somewhat more anarchic system which is particularly favoured by some French speaking authors. In particular this affects the auks, gulls, waders and humming birds and throughout this book they are ascribed to the independent orders Alciformes, Lariformes, Charadriiformes *sensu stricto* and Trochiliformes. It is also worth emphasizing that some inconvenience awaits the unwary in the differing usage which occurs on the two side of the Atlantic for the ordinal names of the divers, grebes, herons, storks and rails. A comparison of these terms is provided by Table 2. Furthermore the status of the flamingoes also varies. They are usually relegated to a separate order by British, if not all European ornithologists, although Wetmore included them as a sub-order of his Ciconiiformes.

TABLE 2

A comparison of the principal differences in nomenclature on each side of the Atlantic.

Wetmore's nomenclature	British nomenclature	Common names
Gaviiformes	Colymbiformes	Divers or loons
Colymbiformes	Podicipidiformes	Grebes
Ciconiiformes	Ardeiformes	Hérons and storks
Gruiformes	Ralliformes	Cranes, rails, cariamas, etc.

Note: Wetmore's order Ciconiiformes differs from the Ardeiformes as it includes the Phoenicopteriformes or Flamingoes.

III. DISSECTION OF THE BRAIN TO SHOW ITS GENERAL CHARACTERISTICS

Detailed guides for the dissection of the avian brain occur in most textbooks of practical vertebrate zoology but for completeness one can briefly outline the principal considerations at this point. They serve as an introduction to the overall anatomy and enable one to highlight the particular

characteristics which are peculiar to birds. Prior to attempting any such gross dissections the brain should have been hardened in alcohol. It is situated very close to the roof of the skull and it is therefore necessary to remove the bone very carefully. When this has been done and the dorsal surface of the brain is exposed it can be viewed *in situ*. The olfactory bulbs are of variable size but often very small, and lie at the extreme anterior end. The forebrain has a pair of large hemispheres which have a relatively smooth surface in the chick, but which bear various surface structures in other birds. These grooves and prominences, together with their position, reflect the relative degree of development of the internal components such as the neostriatum, and the ventral, dorsal and accessory hyperstriatum which are discussed in detail in Chapter 13.

Lying between the anterior hemispheres at their posterior end is the small pineal body. The front part of the cerebellum is immediately adjacent to the hemispheres in this region; consequently, the optic lobes are not visible at this point although they can be seen to the side of it. Posteriorly the cerebellum projects backwards as far as the hind end of the roof of the fourth ventricle and covers the front part of the medulla oblongata. The medulla itself is wide and merges with the spinal cord. In such a dissection as this it becomes clear that the avian brain, as represented by, say, the pigeon, is bent and the axis of the brain is not merely a forward projection of the main axis of the spinal cord. The principal point of flexure is in the region of the mid-brain or mesencephalon, but although the results of this flexure can be seen in dorsal view its actual location, in terms of the brain areas, necessitates at least a gross section.

After exposing the anterior part of the spinal cord the brain can be removed by transecting the cord near to the medulla, raising the brain and severing the various nerve roots as they are exposed. On the ventral surface (see Fig. 1) the olfactory lobes can be seen anteriorly, and either behind or above them, depending on the species of bird, lies the ventral surface of the hemispheres. The optic chiasma is a well-defined and large structure which is situated in the mid-line. The optic tracts can be seen leaving it and passing outwards to run dorsally and reach the optic lobes. Behind the chiasma the infundibulum projects into a small depression but unless considerable care is exercised the hypophysis is usually detached from the tuber cinereum when the brain is removed from the cranial cavity. In this case it will be found still remaining in the sella turcica which is a pit in the floor of the cavity. Behind the infundibulum is the large medulla which has a broad band of pontine fibres in its anterior region. With two exceptions the cranial nerves originate from regions which are comparable to those of other vertebrates.

If one makes a parasagittal section through the brain at a transverse level close to the mid-line of one forebrain hemisphere a number of further

characteristics emerge. The hind part of the forebrain hemispheres overlaps the optic lobes dorsally and the ventricle of the forebrain is a very narrow cavity. This is predominantly restricted to the dorsal region and has a relatively thin roof. A detailed discussion of the components which surround it is

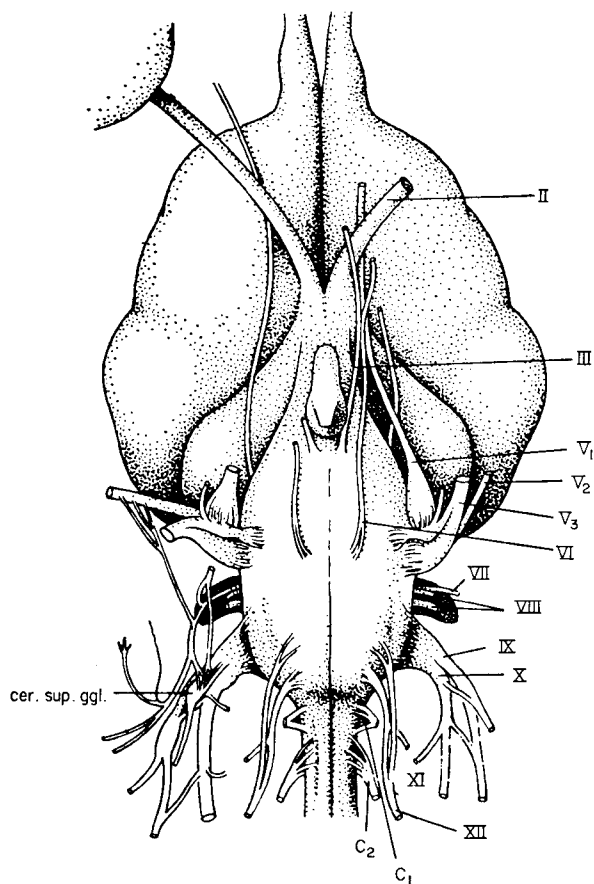


FIG. 1. A ventral view of the brain of the goose showing the cranial nerves (Portmann and Stingelin, 1961). $V_{1,2,3}$, branches of the trigeminus; $C_{1,2}$, cervical nerves; cer. sup. ggl., superior cervical ganglion.

again contained in Chapter 13, but it can be seen that there is an extensive development of telencephalic nuclear material. A vertical sagittal section which passes along the line separating the hemispheres shows that their posterior regions completely cover the mid-brain. Indeed it is as a result of the development of the forebrain on the one hand, and the cerebellum on the