Neurobiology

Current Comparative Approaches

Edited by
R. Gilles & J. Balthazart

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The Congress has been organized in relation with the 100th Anniversary of the School of Comparative Physiology and Biochemistry of the University of Liège.

The proceedings of the invited lectures to the different symposia of the congress have been gathered in five different volumes published by Springer-Verlag under the following titles:

Circulation, Respiration, and Metabolism
Current Comparative Approaches. Edited by R. Gilles

Transport Processes, Iono- and Osmoregulation
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Edited by R. Gilles and J. Balthazart

Respiratory Pigments in Animals: Relation Structure-Function
Edited by J. Lamy, J.P. Truchot and R. Gilles

High Pressure Effects on Selected Biological Systems
Edited by A. Pequeux and R. Gilles

Foreword

This volume is one of those published from the proceedings of the invited lectures to the First International Congress of Comparative Physiology and Biochemistry I organized at Liège (Belgium) in August 1984 under the auspices of the Section of Comparative Physiology and Biochemistry of the International Union of Biological Sciences. In a general foreword to these different volumes, it seems to me appropriate to consider briefly what may be the comparative approach.

Living organisms, beyond the diversity of their morphological forms, have evolved a widespread range of basic solutions to cope with the different problems, both organismal and environmental with which they are faced. Soon after the turn of the century, some biologists realized that these solutions can be best comprehended in the framework of a comparative approach integrating results of physiological and biochemical studies done at the organismic, cellular and molecular levels. The development of this approach amongst both physiologists and biochemists remained, however, extremely slow until recently. Physiology and biochemistry have indeed long been mainly devoted to the service of medicine, finding scope enough for their activities in the study of a few species, particularly mammals. This has tended to keep many physiologists and biochemists from the comparative approach, which demands either the widest possible survey of animals' forms or an integrated knowledge of the specific adaptive features of the species considered. These particular characteristics of the comparative approach have, on the other hand, been very attractive for biologists interested in the mechanisms of evolution and environmental adaptations. This diversity of requirements of the comparative approach, at the conceptual as well as at the technological level, can easily account for the fact that it emerged only slowly amongst the other new, more rapidly growing, disciplines of the biological sciences. Although a few pioneers have been working in the field since the beginning of the century, it only started effectively in the early 1960's. 1960 was the date of the organization of the periodical *Comparative Physiology and Biochemistry* by Kerkut and Scheer and of the publication of the first volumes of the comprehensive treatise *Comparative Biochemistry* edited by Florkin and Mason. These publications can be considered as milestones in the evolution of the comparative approach. They have been followed by many others which have greatly contributed to giving the field the international status it deserved. Since the 1960's, the comparative approach has been maturing and developing more and more rapidly into the independent discipline it now is, widely recognized by the international communities of physiologists, biochemists, and biologists. It is currently used as an effective tool of great help in the understanding of many research problems: biological as well as clinical, applied as well as fundamental.

The actual development of the field and the interest it arouses in a growing portion of the biological scientific community led some of us to consider the organization of an international structure, bringing together the major representative societies and groups around the world, which would aim at the general advancement and promotion of the comparative approach. This was done in 1979 with the incorporation, within the international Union of Biological Sciences, of a Section of Comparative Physiology and Biochemistry. The first International Congress of CPB I organized in Liège with the help of a few friends and colleagues, is the first activity of this newly founded Section. In 22 symposia it gathered some 146 invited lectures given by internationally renowned scientists on all major current topics and trends in the field. The proceedings of these lectures have been collected in 5 volumes produced by Springer-Verlag, a publisher long associated with the development of CPB. The organization of the CPB Section of IUBS, its first Congress and these proceedings volumes can well be considered as milestones reflecting the international status and the maturity that the comparative approach has gained, as a recognized independent discipline, in the beginning of the 1980's, some 20 years after it was effectively launched.

Finally, I would like to consider that the selection of Liège for this first International Congress has not been simply coincidental. I thus feel that this brief foreword would not be complete without noting the privileged role Liège has played in some events associated with the development of the comparative approach. Liège had a pioneer in comparative physiology already at the end of the last century with Léon Fredericq. With Marcel Florkin, Liège had its first Professor of biochemistry and one of the founding fathers of comparative biochemistry. These two major figureheads of the comparative approach founded and developed what is actually called the Liège School of Comparative Physiology and Biochemistry, which was, at the time of the Congress, celebrating its 100th anniversary. This school provided early support to the European Society for Comparative Physiology and Biochemistry organized by Marcel Florkin and myself some years ago. The society, still headquartered in Liège, was, with the CPB division of the American Society of Zoologists, at the origin of the formation of the CPB Section of IUBS under the auspices of which this first International Congress, specifically devoted to the comparative approach has been organized. An essential particularly of the Liège school of CPB is that its two founding fathers, scientists interested in general, basic aspects of the organization of living organisms, were also professors at the faculty of medicine. This largely contributed in Liège to avoiding the undesirable structuration of a so-called "zoophysiology" or "zoobiochemistry" independent of the rest of the field. The conditions were thus realized very early in Liège for CPB to play its key role in canalizing the necessary interactions between the general, pre-clinical or clinical and the environmental, ecological or evolutionary tendences of physiology and biochemistry. The possibility of stimulating such interactions has served as a major guide line in the selection of the symposia and invited lectures from which these proceedings have issued.

Liège, Belgium, June 1985 R. GILLES

Preface

Comparative neurobiology is a rapidly growing field in the biological sciences. The discipline has taken advantage of major advances and refinements in a number of techniques including biochemistry, endocrinology, electrophysiology, neuroanatomy, and immunocytochemistry, and is now able to ask and answer questions which would have been considered science-fiction only a few years ago. This has certainly justified the inclusion of five symposia on comparative neurobiology within the first International Congress of Comparative Physiology and Biochemistry which was held in Liège in August 1984. This volume presents the proceedings of these symposia.

Five themes were developed, three of which are directly related to the control of behavior by the central nervous system and more specifically by steroid hormones. The first one presents recent views on the control of male and female sexual behaviour in mammals. This topic is considered at all levels of integration from population dynamics to interaction of steroids with their intracellular brain receptors.

Current trends in behavioural endocrinology of birds are presented in a second series of chapters. Birds have frequently been used as experimental tools in behavioural endocrinology and neurobiology in general, and have been instrumental in stimulating the emergence of new concepts and directions of research. Let us only mention in this context the fact that the first demonstration of the behavioural effects of testicular secretions was obtained in a bird, the domestic cock, by Berthold in 1849 about 50 years before this subject was studied in mammals. We can also quote the discovery by Nottebohm and collaborators of the neuronal multiplication in the brain of adult song birds in relationship with season and song control. This has undoubtedly renewed interest in studies on neuronal plasticity in adult vertebrates. Behavioral endocrinology of birds is still a very active field, and new trends such as the endocrine study of free-living animals in the field or the analysis of steroid metabolism in the brain and its behavioural implications are presented here.

The third "behavioural" section is devoted to the problem of sexual differentiation and its hormonal control. Important conceptual and technical advances have been made in this area during the last few years and they are presented here by renowned scientists from Europe and the United States.

The fourth section of the book presents current views on the aminergic neurons in the brain. Special efforts have been made here to present broad reviews of this complex and rapidly growing field and much emphasis is laid on the comparative aspects. Detailed information can be found on assay methods, distribution across the phylogenetic scale from protozoa to mammals, interaction with peptidergic systems and involvement in behaviour control.

The last series of chapters concerns photo-transduction in invertebrates. The visual system has always been a subject of intensive research and as a consequence it is now possible to analyze vision in refined electrophysiological and biochemical terms. These different approaches are exemplified here, together with genetical studies relating mutations affecting the visual system in *Drosophila* to specific biochemical alterations.

This book thus offers specific information, as well as broad reviews on selected topics of neurobiology. It will be of interest for all neurobiologists and neuroendocrinologists, as well as for biologists in general, by showing how modern techniques, in neurobiology can, turn the wildest dreams into reality.

Liège, Belgium, June 1985 J. BALTHAZART

List of Contributors

You will find the addresses of the beginning of the respective contribution

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Symposium I

Behavioural Endocrinology of Mammals

Organizer J. BALTHAZART

Neuroendocrine Control of Population Size in Rodents with Special Emphasis on the Mongolian Gerbil

H.H. SWANSON [1]

1 Introduction

Only rodents will be considered in this paper, although most premises will also apply to other mammals. In order for a species to survive, two major drives must exist in its members: (1) a drive for survival of the individual and (2) a drive for propagation of the species. Personal survival requires maintenance activities such as eating and drinking, as well as taking precautions against being destroyed by predators or unfavourable environmental conditions. At first glance these activities seem to operate within an individual which presumably takes appropriate action to alleviate unpleasant internal stimuli of hunger or thirst, or external stimuli such as heat or cold. Indeed most studies of the physiological mechanisms which regulate these homeostatic behaviours have concentrated on the stimulus-response sequence within an individual. On second thought it becomes obvious that social factors are also involved. Young animals must learn which foods are edible, where and how they can be obtained, and how predators may be recognized and avoided. As adults, individuals may cooperate in hunting, foraging, and warning of danger, or alternately, compete for food either directly or indirectly through competition for territory or a position in the social hierarchy.

Neuroendocrine interactions are involved in most of these processes. The interaction between the nervous and endocrine systems may be in either direction, i.e. neural stimuli may trigger hormone production or changes in hormone levels may affect neural input (such as changes in sensitivity to environmental cues) or output (behaviour). The action of hormones on behaviour is usually permissive. A particular endocrine state allows or facilitates the expression of certain behaviours if the conditions are appropriate. Hormones do not cause behaviour.

The second major drive, propagation of the species, requires the interaction of at least two individuals. Copulation, however, is only one link in the chain which begins at conception with sexual differentiation, progresses through maturation of the reproductive system, attraction of a mate, copulation, preparation of a nest, and culminates in birth and subsequent care of the young. At each stage neuroendocrine factors come into play.

The genetic sex of an individual is determined at conception, but the development of the reproductive tract and other sexually dimorphic structures is influenced by the

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presence or absence of androgens and other hormones secreted by the foetal testis. Structural and functional sex differences in the brain may also be programmed through androgen action during early development (De Vries et al. 1984; Swanson 1985). In the male, foetal testosterone is taken up by specific receptors in the brain, where it is aromatized to oestrogen and exerts permanent effects on the developing nervous system. Certain brain centres become "masculinized" whereas others become "feminized". The result is that the individual, when adult, will not only secrete gonadotrophins in the typical male acyclic manner, but will also make the appropriate behavioural responses to cues from receptive female (copulation) or male (perhaps territorial aggression) conspecifics.

The next important phase in reproductive development is sexual maturation. The mechanisms which trigger the sequence of events leading to first ovulation in females is still uncertain. One view is that an oestrogen-sensitive "negative feedback" system controlled by the hypothalamus becomes less sensitive to oestrogen as puberty progresses and ultimately, as oestrogen levels rise, a "positive feedback" threshold of oestrogen on luteinizing hormone (LH) is reached and phasic gonadotrophin release initiated (Ramirez and McCann 1963; Smith and Davidson 1968). An alternate suggestion is that the "positive feedback" threshold is reached well before sexual maturation, but that prior to this event LH release is inhibited by a "negative feedback" effect of prolactin or progesterone on the central nervous system (Wuttke et al. 1976; Döhler and Wuttke 1975). The rhythm of the oestrus cycle is regulated by neural stimuli produced daily at a precise time related to the onset of the light period.

Similar mechanisms may initiate sperm production and maturation of accessory sex organs in the male. It is clear, however, that in both sexes the timing of sexual maturity is influenced both by internal factors such as body size (Kennedy and Mitra 1963) and external seasonal factors such as light and temperature (reviewed by Sadleir 1969; Kappers and Pevet 1979). Social factors may also be involved. These have been extensively studied in the mouse, in which generally olfactory stimuli from females have been found to delay and those from males to accelerate the rate of sexual maturation in young females (Bronson 1971; Vandenbergh 1973; Drickamer 1977; Cowley 1978).

The attainment of sexual maturity is usually synchronized with the seasons, so that young will be born at the most advantageous time of year (Hutchinson 1978). Indeed, the gonads of many rodents living in the lower latitudes regress during the winter and undergo changes similar to puberty every spring. The endocrine changes may produce alterations in character usually manifested in the male by increased aggressiveness towards other males. Success in defeating rivals will allow an individual to either gain access to a desirable territory or to attain a sufficiently high place in the social hierarchy to allow him to participate in breeding. The same hormones then cause him to become receptive to stimuli from females and to seek a mate. At the same time females will show proceptive (soliciting) and receptive behaviour towards the advances of a male. Most female rodents are only sexually motivated during the oestrous phase of their cycle, which coincides with ovulation and thereby maximizes the chance that fertilization will follow mating.

If the female becomes pregnant, she will engage in maternal activities, which include building a nest and feeding and caring for the young after birth (Gubernick and Klopfer 1981; Elwood 1983a). Maternal behaviour seems to be initiated and maintained by a combination of the appropriate endocrine balance and stimulation by pups (Rosenblatt 1967). Depending on the species, the father may or may not engage in parental care (Kleinman and Malcolm 1981; Elwood 1983b). Stimuli from the pups are able to induce parental care in males or virgin females if exposure is prolonged over several days (Rosenblatt 1967). In parturient females, hormones serve to increase sensitivity to pup stimulation, thus reducing the latency to a few minutes after birth (Pedersen and Prange 1979; Bolwerk and Swanson 1984). Weaning of the young completes the reproductive process, which may of course be reinitiated at an appropriate interval.

Most studies on the neuroendocrine control of reproduction have focussed on a specific phase, i.e. sexual differentiation, puberty, the oestrous cycle, intermale aggression, sexual, or maternal behaviour, rather than examining how the system is integrated as a whole to ensure that the species will survive in a particular ecological niche.

2 Studies on the Mongolian Gerbil

In the present paper I will try to present a picture of how neural and endocrine factors interact in regulating population size in one particular species, the Mongolian gerbil *(Meriones unguiculatus)*. This work was done over several years in the Department of Anatomy at the University of Birmingham and formed the basis of a Ph.D. thesis by B. Payman (1980). Although the studies were carried out in the artificial conditions of laboratory enclosures, what is known about the ecology of the gerbil suggests that the mechanisms observed may also operate under natural conditions. Field observations indicate that in this rodent, which inhabits desert and semi-desert regions of Mongolia and northern China, young of the season spend the winter in a burrow with their parents, but do not hibernate (Bannikov 1954). Hence, exposure of young to their parents beyond weaning is a situation which could be encountered in the wild.

Rodents and other small mammals with a high reproductive capacity use various strategies to limit population size so as not overexploit their habitat (Wynne-Edwards 1962; Ebling and Stoddart 1978; Lidicker 1975, 1978; Swanson 1983). In most mammals the family is the basic social unit. The size, complexity, and cohesion of the family group is characteristic of the species. One or more families form a social group or colony within which stable relationships between individuals become established (Lidicker 1965). In the case of the gerbil, each colony occupies a complex burrow system which is defended against intruders. The spacing between colonies depends on the local availability of food and shelter.

In the present study family groups of gerbils were established in enclosures in which all extrinsic factors for population control were absent (climate, predators, food shortage). As there was no opportunity for emigration or immigration, stabilization of such a freely breeding population must be accomplished by social controls. Behavioural interactions between individuals were systematically observed and related to their position in the social hierarchy and their breeding performance. Each family group showed a distinct pattern. This variability suggests that rodents show individual differences which are worthy of study in their own right. This is an alternative to the usual approach of observing the behaviour of a sufficient number of animals so that individual differ-