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**Problems in the Behavioural Sciences**

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# Thirst

**Barbara J. Rolls and Edmund T. Rolls**

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## List of abbreviations

- ADH, antidiuretic hormone (vasopressin)  
AV3V, anteroventral region of the third ventricle  
CSF, cerebrospinal fluid  
ECF, extracellular fluid  
ICF, intracellular fluid  
OVLT, organum vasculosum of the lamina terminalis  
SFO, subfornical organ  
SIP, schedule-induced polydipsia

## Foreword

The space in which science lives and grows has some curious features. It is natural in some ways to imagine a tree diagram: a thick trunk (philosophy?) divides first into a few major branches (physico-chemical, biological, social sciences), then into somewhat thinner branches (physics, for example, now separating from chemistry), and so on repeatedly until the twigs that display the latest, developing buds ramify in all their recondite glory. The trouble with this image is that it leaves no room for the fusions between long-separate branches which make up one of the most powerful driving forces in contemporary science. If biology and chemistry once split off from each other as branches that aim at different places in the sun, how can we put them together again in our tree diagram to symbolize that modern prodigy, biochemistry?

Another image, avoiding this problem, is that of the bicycle wheel: a central hub (philosophy?) with spokes radiating in all directions, the distance between spokes being proportional to the distance between the sciences they stand for. Now, to celebrate the birth of biochemistry, we merely have to slot in another spoke, equidistant between the parent disciplines. And, to preserve the necessary metaphor of growth that is integral to the tree diagram, we can make our spokes expand proportionally to the maturity of the subjects they represent. But it is a consequence of this image that spokes get further and further from each other as they grow: the quickest route between two disciplines is always through the philosophical hub; and, as subjects mature, they become more isolated, more idiosyncratic. To be sure, this feature of 'bicycle wheel' space is, to some extent, veridical: Bear witness the latest journal devoted entirely (I invent, but barely) to the eating habits of the *ob/ob* mouse after lesions to the ventromedial nucleus of the hypothalamus. But, from another point of view, it is the growing points of science that are the closest together, the circumference of the wheel that is shorter than the hub. To take an example close to our interests, it is those workers who push the frontiers of brain science forward most vigorously whose research may be transformed overnight by developments in physics, chemistry or linguistics; the linguists, whose subject may be revolutionized by advances in brain science.



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The bicycle wheel is ill-designed for these paradoxes. Our series, *Problems in the Behavioural Sciences*, in contrast, is designed precisely to house them. Its intention is to provide a forum in which research workers on any frontier that relates to psychology *de facto*, even if not *de jure*, can communicate their discoveries, their questions and their problems to their peers in other disciplines, and to a new generation of students in their own. The central role played by psychology in this series guarantees that it will be multi-disciplinary; for psychology already draws on advances in fields as diverse as biophysics and biochemistry, logic and linguistics, social anthropology and sociology. Conversely, the increasing use of behavioural methods – often, alas, ill-understood and worse-applied – by scientists in other fields of biological or sociological enquiry means that they too need to keep a wary eye on how the battle rages at the frontiers of psychology. They will find in *Problems in the Behavioural Sciences* the latest war reports.

*Thirst* is by its very nature inter-disciplinary: indeed, it makes a mockery of the barriers erected between disciplines by history and accident. A correct fluid balance is vital for survival. Loss of water sets in train a whole host of physiological mechanisms that are intricately designed to preserve that balance. The study of these mechanisms is the domain of the physiologist, and especially the endocrinologist. But the only way in which, in the end, the animal deprived of water can put matters right is by behaving appropriately: it must find water – learn to find it, if necessary – and drink. That is the province of the psychologist. And the story does not stop there. A full understanding of the behaviour of the thirsty animal, and of the integration of that behaviour with the physiological response to water loss, requires an analysis of the brain mechanisms which control the behaviour that replenishes a water deficit. So now we are in the territory of the neuroscientist, that modern breed who, as often as not, is himself a hybrid between psychologist and physiologist.

Barbara and Edmund Rolls chart these complex waters with the ease and skill that can come only to those who are expert in all these various fields. Psychologists will find in the story they tell an easily accessible account of a topic that is central to the field of motivation – and this is itself central to the whole of psychology. Roughly speaking, motivational systems can be divided into those which obey principles of homeostasis (i.e., whose object is to maintain the equilibrium of the *milieu intérieur*) and those which do not conform in any obvious way to these principles. The emotion of fear is probably the best understood example of a motivational system belonging to the second of these

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*Foreword*

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categories; and fear will form the subject of a later monograph in our series. Thirst, in contrast, is the very type of a homeostatic motivational system. It has so far figured less prominently in the textbooks of physiological psychology than its more complex relative, hunger; but, as this book shows, it has yielded sufficiently far to physiological, behavioural and neural analysis as now to serve as an excellent general model for the way in which homeostatic motivational systems work. Thus a reader keen to know what is generally afoot in the field of motivation, no less than one with a more specific interest in the subject of thirst, will find here plenty of nourishment.

## Preface

Drinking is essential for most terrestrial species and requires integrated behavioural responses to physiological stimuli and environmental demands. Because the stimuli which produce drinking can often be identified, drinking provides an opportunity to analyse behaviour in terms of its physiological and neurophysiological bases as well as at the psychological and ethological levels. We have written this book on thirst to bring together these different approaches. It is particularly important to have a clear and integrated understanding of thirst because disturbances in the balance of body water and electrolytes can occur in many clinical conditions.

This book has several aims. One is to provide a text useful to students of psychology, physiology, medicine, biology and zoology. Another aim is to consider not only the analysis of mechanisms that can produce drinking, but also the extent to which the different mechanisms underlie normal drinking, whether it occurs for example following water deprivation or spontaneously. For example, not only is drinking which can be produced by activation of the renin-angiotensin system analysed, but the role of activation of this system in normal drinking is also considered. A third aim is to make the discussion of thirst as relevant as possible to man, and therefore studies in non-human primates and man are included. A fourth aim is to introduce the investigation of subjective aspects of thirst, and studies in which these aspects have been investigated quantitatively are described. A fifth aim is to discuss clinical disorders of fluid intake in relation to our understanding of thirst mechanisms. With these aims, it is hoped that this book will be of interest not only to students, but to all those interested in the scientific study of thirst, and in the physiological and neural bases of behaviour. At this point historically in the study of thirst, we have tried to give a generally useful account of thirst and also, in the ways described above, to introduce themes which we believe will be important in the future development of the subject.

Thirst is defined and introduced in Chapter 1, and in Chapter 2 useful background information on fundamental aspects of the body fluids and their measurement is presented for those readers who have not previously covered this topic. After a historical review of the investigation of thirst in Chapter 3, Chapters 4, 5 and 6 describe the

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initiation, maintenance and termination of drinking. The neural and pharmacological controls of thirst are described in Chapters 7 and 8. We have included a separate chapter (Chapter 9) on clinical problems of thirst. Particular attention is paid in Chapter 10 to the factors that control spontaneous drinking. To encourage our readers to think about this subject further, we have pointed in Chapter 11 to some areas in which fruitful developments can be made.

To assist the reader, summaries of important points appear at the ends of most sections of this book.

We would like to thank all of our colleagues, including A. N. Epstein, J. T. Fitzsimons, J. G. Gibbs, J. G. G. Ledingham, H. Lind, R. W. Lind, D. J. McFarland, S. Maddison, G. J. Mogenson, D. J. Ramsay, and R. J. Wood, who have collaborated in many of the experiments described. Our research was supported by The Medical Research Council of Great Britain. D. J. Ramsay, R. J. Wood, and P. A. Phillips made many useful suggestions for improvement of the manuscript, and we thank them.

*Oxford*

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