# THIRST

*Proceedings of the First International Symposium*

*On Thirst in the Regulation of Body Water*

*Held at the Florida State University*

*in Tallahassee, May 1963*

Edited by

MATTHEW J. WAYNER

*Syracuse University*

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# THIRST

E. F. ADOLPH

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# WELCOMING ADDRESS

JOHN W. CHAMPION
Florida State University

FROM both a physiological and psychological point of view the role of water in the life of virtually all living matter is clearly basic to an understanding of both behavior and survival. Most every high school graduate is familiar with some of the basic facts of water content in living organisms, the balance of body fluids and the fundamental role of water in both phylogenetic and ontogenetic development. Only a group of scientists such as the distinguished participants of this conference are familiar with the molecular phenomena underlying these basic facts, or with the detailed interactions between body fluids and the resulting behavior of intact organisms.

To a layman such as myself thirst connotes a dryness of the throat and a heightened effort to obtain fluids. To many people these are all the facts they need to know and constitute a naïve tautological explanation, i.e. "I'm thirsty because my throat is dry and my throat is dry because I'm thirsty". It is quite clear that this is a totally inadequate account of a basic part of our life cycle. Together with air and food the role of body fluids demands explanation with respect to every possible part of our physiological and psychological make-up: research at the molecular level; at the cellular level; at the level of different body systems; digestive, circulatory, and nervous, and finally at the level of the intact behaving organism.

An examination of the program reveals that this conference will involve each of these levels and that current research problems and findings will play a prominent part in the presentations and discussions of the next several days.

Although there have been many national and international scientific conferences, symposia, and meetings, and there will be many more in the future, it is my understanding that this is the first conference on the problem of thirst in the regulation of body water.

We are extremely pleased to have this conference at the Florida State University. I am sure that much that will be discussed during this conference will have a tremendous effect on the future planning and thinking of all who are participating in this conference.

On behalf of the Florida State University I am pleased to welcome you here officially and personally. We are glad that you are here and we are confident that this will prove to be a most successful conference.

# INTRODUCTORY REMARKS AND ACKNOWLEDGEMENTS

MATTHEW J. WAYNER
Conference Chairman

IT is indeed a pleasure to welcome you to the Florida State University and the first international conference on thirst in the regulation of body water. We are particularly fortunate to have Professor Adolph, whose long and distinguished career in the field of physiological regulations has been a continuous source of stimulation and enlightenment to all of us, here as a participant. We hope that our foreign visitors will enjoy Tallahassee. Unfortunately C. P. Richter, K. Schmidt-Nielsen, and A. V. Wolf, whose wealth of knowledge we will miss, were unable to attend.

I would like to acknowledge the financial support of the Life Sciences Division of the U.S. Army Research Office, the State of Florida, and the Florida State University. As we plan to publish these proceedings, I believe they will complement very well the proceedings of the UNESCO conference in Lucknow, India, on Environmental Physiology and Psychology in Arid Conditions; the formal and informal discussions on the regulation of caloric intake during the International Physiological Congress in Leiden; the symposium on Olfaction and Taste in Stockholm; and other symposia, for example, the one on the Development of Homeostasis held in Liblice near Prague.

Many people have helped to make this conference possible: Dr. Eugene Sporn of the Life Sciences Division of the U.S. Army Research Office, Dr. E. L. Chalmers, Assistant Dean of the Faculties, and Mrs. Virginia Hopkins, Administrative Assistant. Mr. Wade Hitzing who operated and maintained the recording equipment during the conference. Miss Diane De Armon who organized the graduate students of the Psychology Department who operated the slide projectors. Mrs. Eunice Vittoria, our secretary, to whom we are all indebted for her help not only during the conference but for transcribing the discussion and editing the manuscripts. Dr. Henry S. Odbert, Program Director, Psychobiology, NSF, whose help early in the planning stages and Dr. Gordon Blackwell, President of the Florida State University, whose help in the end proved to be invaluable. I am also indebted to my wife, Therese, whose help was always available when we required it.

We are grateful to the publishers of the following books and journals who have cooperated by permitting us to reproduce figures and other material: The Aerospace Medical Association, *Aerospace Medicine;* Academic Press, *International Review of Neurobiology;* Academy van Wetenschappen Amsterdam, Afdeling Natuurkunde, *Verhandling;* American Academy of Neurology, *Neurology;* American Association for the Advancement of Science, *Science;* American Medical Association, *Archives of Neurology;* American Physiological Society, *American Journal of Physiology* and *Journal of Applied Physiology;* American Psychological Association, *Journal of Comparative and Physiological Psychology;* American Society for Artificial Internal Organs, *Transactions;* Brookhaven National Laboratories, *Brookhaven Symposia in Biology;* Budapesti Orvostudomanyi Egyetem Ánatomiai Intezet, *Sonderdruck aus, Zeitschrift fur mikroskopischanatomische forschung;* Department of Pharmacology, Emory University, *Journal of Pharmacology and Experimental Therapeutics;* Karolinska Institutet, *Acta Physiologica Scandinavica;* J. B. Lippincott and The Endocrine Society, *Endocrinology;* Macmillan, *Nature;* Pergamon Press, *Olfaction and Taste;* Rockefeller Institute Press, *Journal of General Physiology;* Ronald Press Company, *Physiological Regulations,* by Edward F. Adolph; Southern Universities Press, *Psychological Reports;* U.S. Naval Institute, *U.S. Naval Institute Proceedings;* University of Montreal, *Revue Canadienne de Biologie;* and the Wistar Institute of Anatomy and Biology, *Anatomical Record.*

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# OPENING ADDRESS

# REGULATION OF BODY WATER CONTENT THROUGH WATER INGESTION

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WATER intake, considered as a part of the body's water economy, usually compensates for water deficit. All the processes and behaviors concerned in intake may be activated by this deficit. Deficit is a sort of stimulus that arouses regulatory responses; therefore, also, it is a motivation. Since these responses tend to remove the stimulus, they evidently figure as part of a feed-back loop. As in any study of physiological regulations, the relations of stimulus (deficit) to response (drinking) are quantitative ones. A great advantage is gained by experimentation with water intake rather than with "thirst". Intake represents an operant response and an operational measurement; it employs no uncertain terminology.

## HISTORY

Historically, water intake was regarded as an occult phenomenon because no sense organs to arouse it were recognizable. Progress actually came through realization that intake responses could be measured without knowledge of specific organs of sense.

Abnormalities of intake in man (*diabetes insipidus*) were known to Galen[1] in A.D. 180. That water drinking served the bodily economy was apparent to Descartes[2] who wrote:

> When we stand in need of drink, there arises from this want a certain parchedness in the throat that moves its nerves, and by means of them the internal parts of the brain; and this movement affects the mind with the sensation of thirst, because there is nothing on that occasion which is more useful for us than to be made aware that we have need of drink for the preservation of our health.

This statement introduced the concept that water drinking compensated for specific water need or deficit.

Later, an experimental approach to the study of water ingestion resulted from an accident described by Gairdner[3]. A would-be suicide succeeded in

cutting his esophagus and trachea but not his arteries or veins. In a couple of days he developed an intense desire for water, but as fast as he drank it by mouth, all the fluid ran out of his esophagus. The physician then placed water in the lower half of the esophagus and the urge to drink was soon assuaged. Years later, physiologists beginning with Bernard[4] produced esophageal and gastric fistulas in dog and in horse. By their means it was found that water passing through the mouth only temporarily suppressed the urge to drink.

Meanwhile, Dupuytren[5] devised another experiment. Water deficit was produced when a dog ran in warm sunshine. At the end of exposure to water loss, water was injected into a vein, and after that the dog refused to drink. Therefore, water, when distributed throughout the body, need not enter through the alimentary tract in order to satisfy the demand for water.

From these two experiments have arisen today's techniques for the study of water drinking. We can classify procedures into those that modify the anatomical conformation of the animal (alimentary, nervous, endocrine lesions) and those that modify the physiochemical state (osmotic pressure, solute, taste, timing, location, heterologous stimuli). These altogether are the resources of the experimenter.

In all experiments one must look for two kinds of response: onset of drinking, and cessation of drinking. Water intake is obviously accomplished by such a discontinuous or on–off response. At once we recognize this familiar type of regulation, of the kind typified by a house thermostat which periodically turns on a supply of heat to the house. The same supply also warms up or satiates the sensitive device inside the house.

## WATER BALANCE

My initial interest in water drinking consisted in a study of the quantitative relation between water deficit (a stimulus) and water drinking (a response). Was the amount of water drunk proportional to the amount of water deficit, and perhaps, equal to it? Water deficits of varying amounts resulted when dogs were force-fed diets deficient in water content for diverse periods of time.[6] At the end of each deficit period, the dog drank to satiation in a few minutes. On the average the amounts drunk were proportional to deficits, and about equal to the deficits (Fig. 1).

It seemed evident therefore that the act of drinking was a response to the amount of water deficit. In the dog the drinking ended long before the water reached any tissue where the water was to be deposited. The alimentary intake was accomplished by specific muscular activities, and almost certainly the nervous system managed those activities and received signals indicating how much water had been ingested.

Esophageal fistulas were produced in dogs by Bellows[7]. When fistulous

dogs were subjected to water deficits, their drinking,[6] like that of intact dogs, was proportional to the deficits. But the water passed only through the mouth and pharynx; the dogs drank twice as much to reach a temporary satiation. Since they too stopped after a specific amount of drinking

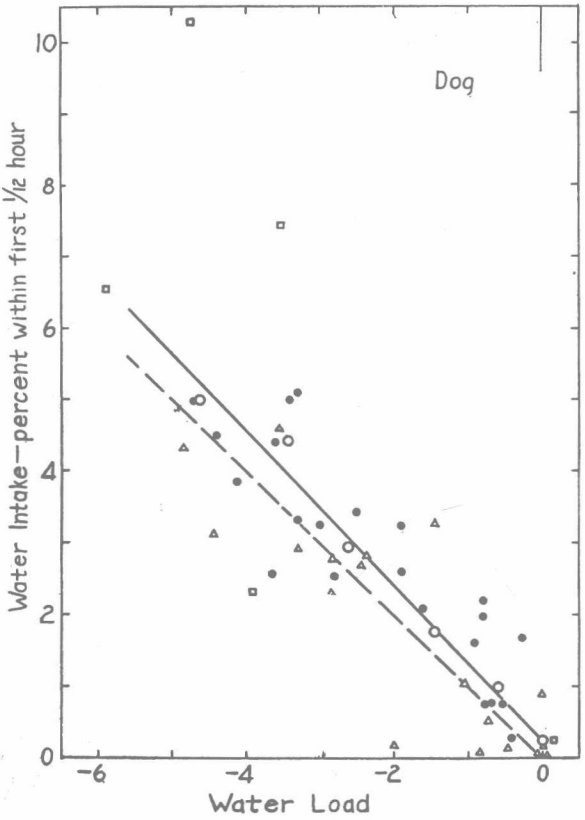


FIG. 1. Water intakes of dogs offered water at the end of dehydration periods of various extents. Large circles mark the mean for each per cent of water deficit. (From Adolph, 1943.)

activity, they evidently metered the intake. Thus, part of the neuromuscular activity (initiated through the central nervous system) aroused sensory components (in the acts of lapping and swallowing) which in turn led to a sort of satiation.

But the satiation became permanent when an amount of water equal to the deficit was allowed to reach the stomach and to be absorbed from the gut. Towbin[8] demonstrated that the distention of the stomach itself helped to supply sensory information that led to an early part of this satia-

tion, for the dogs drank appreciably less than their deficits, according to the amount of distention imposed by a gastric balloon. The effect of distention was abolished by disconnection of the vagi nerves from the stomach;

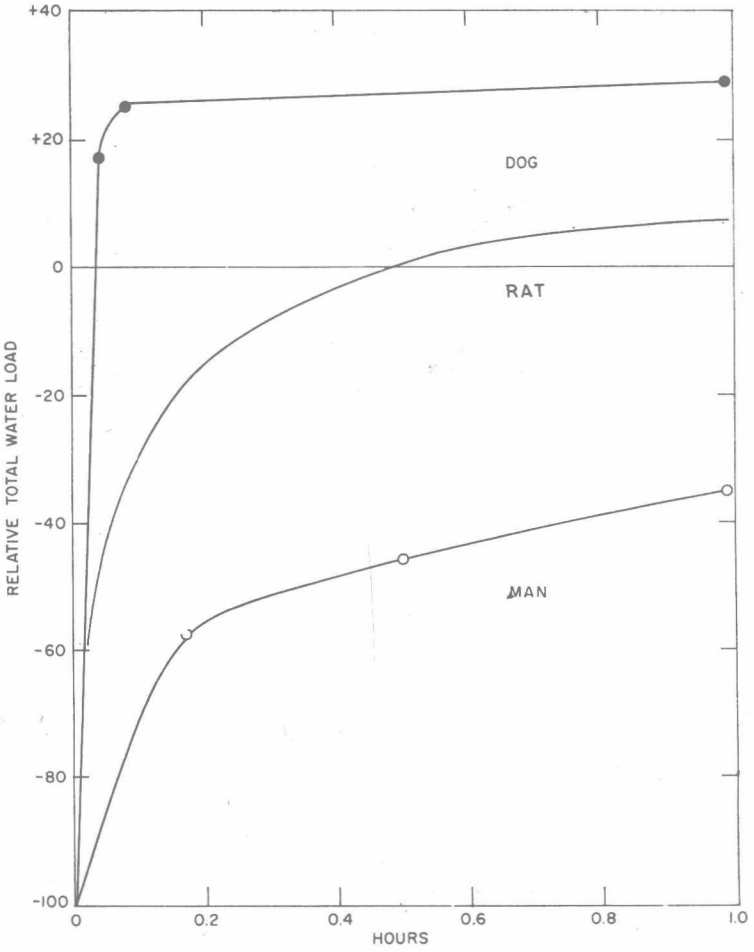


FIG. 2. Water intakes during the first hour of drinking in three species. (From Adolph, 1943.)

therefore an effective sensory pathway accompanied those nerve trunks. Possibly the sensory nerves concerned were the ones (contained in the vagi) that have been shown by Paintal[9] to carry afferent impulses when the stomach is distended.

At this point it should be noted that other species, including man, drank water much more slowly than did dogs (Fig. 2). Man did not drink an