The Mystery of Yawning in Physiology and Disease
Contents

VII  List of Contributors

IX  Preface
   Bogousslavsky, J. (Glion/Montreux)

X  Foreword
   Walusinski, O. (Brou)

1  Historical Perspectives
   Walusinski, O. (Brou)

22 Popular Knowledge and Beliefs
   Walusinski, O. (Brou)

26 Yawning throughout Life
   Giganti, F.; Salzarulo, P. (Florence)

32 Fetal Yawning
   Walusinski, O. (Brou)

42 Sleep, Sleepiness and Yawning
   Giganti, F.; Zilli, I.; Aboudan, S.; Salzarulo, P. (Florence)

47 Interplay between Yawning and Vigilance: A Review of the Experimental Evidence
   Guggisberg, A.G. (Geneva); Mathis, J.; Hess, C.W. (Bern)

55 The Hidden Sexuality of the Yawn and the Future of Chasmology
   Seuntjens, W. (Brussels)

63 Non-Human Primates: A Comparative Developmental Perspective on Yawning
   Anderson, J.R. (Stirling)

77 Punishment-Induced Fear Modifies the Daily Course of Yawning in Rats
   Moyaho, A.; Valencia, J. (Puebla)

84 A Thermoregulatory Behavior
   Gallup, A.C. (Binghamton, N.Y.)

90 Neuropharmacology of Yawning

107 Yawn, Yawn, Yawn, Yawn; Yawn, Yawn, Yawn! The Social, Evolutionary and Neuroscientific Facets of Contagious Yawning
   Platek, S.M. (Lawrenceville, Ga.)
113 Developmental and Comparative Perspectives of Contagious Yawning
    Senju, A. (London)
120 Methodological Problems in the Study of Contagious Yawning
    Campbell, M.W.; de Waal, F.B.M. (Atlanta, Ga.)
128 Exploring Yawning with Neuroimaging
    Nahab, F.B. (Miami, Fla.)
134 Associated Movements in Hemiplegic Limbs during Yawning
    Meenakshisundaram, R. (Chennai); Thirumalaikolundusubramanian, P. (Trichy);
    Walusinski, O. (Brou); Muthusundari, A. (Tirunelveli); Sweni, S. (Debrecen)
140 Associated Diseases
    Walusinski, O. (Brou)
156 Author Index
157 Subject Index
List of Contributors

S. Aboudan
Department of Psychology
University of Florence
Via di San Salvi 12
Complesso di San Salvi
Padiglione 26
50135 Florence (Italy)

James R. Anderson
Department of Psychology
University of Stirling
Stirling FK9 4LA (Scotland)

Julien Bogousslavsky
Center for Brain and Nervous Disorders
Genolier Swiss Medical Network
1272 Glion/Montreux (Switzerland)

Matthew W. Campbell
Living Links Center
Yerkes National Primate Research Center
Emory University
Atlanta, GA 30072 (USA)

Gregory T. Collins
Department of Pharmacology
University of Michigan
1301 MSRB III
1150 W. Medical Center Dr.
Ann Arbor, MI 48109 (USA)

Frans B.M. de Waal
Living Links Center
Yerkes National Primate Research Center
Emory University
954 Gatewood Dr.
Atlanta, GA 30322 (USA)

José Ramón Eguibar
Laboratorio de Neurofisiología de la
Conducta y Control Motor
Instituto de Fisiología
Benemérita Universidad Autónoma de
Puebla
Apartado Postal 406
Puebla, Pue. 72000 (México)

A.C. Gallup
Department of Biological Sciences
Binghamton University
Binghamton, NY 13902 (USA)

Fiorenza Giganti
Department of Psychology
University of Florence
Via di San Salvi 12
Complesso di San Salvi
Padiglione 26
50135 Florence (Italy)

Adrian G. Guggisberg
Department of Clinical Neurosciences
University of Geneva
Avenue de Beau-Séjour 26
1211 Geneva 14 (Switzerland)

Christian W. Hess
Department of Neurology
Inselspital
University of Bern
3010 Bern (Switzerland)

Johannes Mathis
Department of Neurology
Inselspital
University of Bern
3010 Bern (Switzerland)
Ramachandran Meenakshisundaram  
Madras Medical College &  
Government General Hospital  
Park Town  
Chennai 600003 (India)

Alejandro Moyaho  
Laboratorio de Ecología de la Conducta  
Instituto de Fisiología  
Benemérita Universidad Autónoma de Puebla  
Apartado Postal 406  
Puebla, Pue. 72401 (México)

Arunachalam Muthusundari  
Tirunelveli Medical College & Hospital  
Tirunelveli 627011 (India)

Fatta B. Nahab  
University of Miami Miller  
School of Medicine  
1120 NW 14th Street, Suite 1347 (C215)  
Miami, FL 33136 (USA)

Steven M. Platek  
Georgia Gwinnett College  
Lawrenceville, GA 30043 (USA)

Piero Salzarulo  
Department of Psychology  
University of Florence  
Via di San Salvi 12  
Complesso di San Salvi  
Padiglione 26  
50135 Florence (Italy)

Atsushi Senju  
Centre for Brain and Cognitive Development  
Birkbeck University of London  
Malet Street  
London WC1E 7HX (UK)

Wolter Seuntjens  
J.-F. Leemanslaan 27  
1160 Oudergem Brussels (Belgium)

Shah Sweni  
University of Debrecen  
Medical & Health Science Center  
Nagyerdei krt. 98  
PO Box 48  
4032 Debrecen (Hungary)

Ponniah Thirumalaikolundusubramanian  
Chennai Medical College Hospital & Research Center  
Irungalur, Trichy 621105 (India)

Jaime Valencia  
Laboratorio de Ecología de la Conducta  
Instituto de Fisiología  
Benemérita Universidad Autónoma de Puebla  
Apartado Postal 406  
Puebla, Pue. 72401 (México)

Olivier Walusinski  
20 rue de Chartres  
28160 Brou (France)

I. Zilli  
Department of Psychology  
University of Florence  
Via di San Salvi 12  
Complesso di San Salvi  
Padiglione 26  
50135 Florence (Italy)
Along with laughing, crying, and even coughing, yawning is a mysterious and fascinating physiological phenomenon that has been poorly addressed. These phenomena share a complex paroxysmal motor-respiratory interaction that is strongly influenced by emotional factors. For instance, while the layman commonly associates yawning with boring situations, it also typically evokes a feeling of pleasure, especially during a full yawn with tonic extension of the limbs. However, many aspects of yawning remain unknown, and it will surely come as a surprise to many of us to read in the following pages that yawning may also be considered a strong sexual signal!

Dr. Olivier Walusinski is to be congratulated for putting together the fascinating chapters of this book, centered around a topic on which most neurologists would struggle to write more than a single sentence. The phylogenetic and ontogenetic (with fetal yawning) aspects highlight an interesting perspective on biological and human development, while the occurrence and features of yawning in neurological diseases also constitute an area that has only been explored by a few investigators. Dr. Walusinski is not merely one of these investigators, but an encyclopedic expert on yawning and its associated manifestations, as well as its neurobiological correlates. Moreover, it should be recognized that he has accumulated this large body of knowledge in parallel to his daily work as a general practitioner over the last 30 years! Acquiring scientific peer-recognition is not an easy task for an ‘outsider’, and we must say that the current result is beyond any of our initial expectations. Unlike most other books focusing on a specific neurological behavior or condition, the present work opens surprising windows into the history of neurology, human and animal behavior, and even philosophy; thus, making perfect ‘anti-yawn reading’!

Julien Bogousslavsky
Glion/Montreux
Foreword

It is an honor and a privilege for me to introduce the first textbook in English dedicated to *The Mystery of Yawning in Physiology and Disease*. It is interesting to note that 30 years ago, much of the information contained in this book did not exist. Since that time, there has been an increased awareness that yawning is indeed a very pertinent model for understanding a transitional behavior and its determinism in terms of neuroanatomy, neurophysiology, ontogenesis, phylogenesis and social cognition.

Yawning has fascinated and mystified humankind for ages. The bizarre and evanescent qualities of yawning have invited boundless speculation about its origin, meaning and purpose. The neurobiological underpinnings of yawning have become increasingly well understood and it is now possible to describe the brain mechanisms responsible for the expression of this behavior in detail. Modern neuroscience is still looking for a complete explanation of its intimate purpose. We propose a broad-based cultural, ethological, neurophysiological, neuroimaging and medical overview of the related concepts.

Yawning is a stereotyped and often repetitive motor act characterized by gaping of the mouth accompanied by a long inspiration, followed by a brief acme and a short expiration. It is not merely a simple opening of the mouth, but a complex coordinated movement bringing together a flexion followed by an extension of the neck, a wide dilatation of the laryngopharynx with strong stretching of the diaphragm and anti-gravity muscles. Highly stereotypical because no environmental input changes the sequence of movements, it is observed in cold-blooded and warm-blooded vertebrates – from reptiles with rudimentary ‘archaic’ brains to human primates – in water, air and land environments. The ethology, neurophysiology and neuropsychology literature associates yawning with wake/sleep rhythm fluctuations, eating and sexuality, where it externalizes a group of possible vigilance-stimulating mechanisms and attests to the central role of the hypothalamus in homeostasis.

The chapters in this book represent the best thinking on the role and function of yawning, and they address what has become central to most contemporary accounts – the link between arousal, sleep, vigilance, satiety, sexuality and social communication linked to emotion.

As Winston Churchill said: ‘The farther back you can look, the farther forward you are likely to see.’ In this way, the first chapter tells the story of the prolonged effort in
Western thought to define yawning and to interpret it scientifically. Interest in yawning has existed since the dawn of history. Some of the world’s greatest thinkers and physicians, such as Hippocrates, Descartes, Diderot, Boissier de Sauvages, Haller and others, have attempted to explain the physiological and psychological bases of yawning. What is emphasized here for the benefit of the scientist or the practitioner is the evolution of the key concepts that define discoveries and developments in the field. For example, in his 1755 book *De perspiratione insensibili*, Johan de Gorter was the first to describe yawning as a mechanism to accelerate blood flow, supposedly to improve oxygenation of the brain, in response to cerebral anemia. Well into the 20th century, there were regular references to this notion, even though it had never been demonstrated. The inaccuracy of this hypothesis was formally shown by Provine, Tate and Geldmacher in 1987. In the chapter that follows, we shall continue to investigate popular thinking on yawning. We offer a broad-based cultural overview of the related conceptions and myths by comparing popular views in Arabic, Western and Indian cultures.

All the movements that a newborn is able to produce originate during fetal life and are performed throughout the life span. F. Giganti and P. Salzarulo explain that yawning is a behavior beginning in the first epochs of life. Their chapter examines frequency and time course changes of spontaneous yawning across the life span, taking into account hypotheses about its function and role. In recent years, there have been dramatic technical advances in diagnostic sonography. This procedure has become essential to the modern management of pregnancy. Fetal motility is considered to reflect the developing nervous system, but also involves functional and maturational properties of fetal hemodynamics and the fetal muscular system. Yawning is recognizable in ultrasound images from the 14th week of pregnancy, and like the appearance of oromandibular movements and swallowing, it signals functional maturation of the brainstem and basal ganglia. We hope to underscore the importance of fetal yawning with this chapter and depict how disturbances over time can lead to an earlier diagnosis of disharmonious brainstem maturation.

The relationship between spontaneous yawning and sleepiness is obvious. Sleepiness is a basic physiological need state linked to hunger or thirst, which are physiological need states essential to the survival of the individual. This implies a common functional basis, both physiological and biochemical, between sleep, arousal and yawning. Which structures and substances are implicated in the transition between waking and sleep and, at the same time, involved in yawning production? F. Giganti and P. Salzarulo review the relationship between yawning and sleep and highlight the contrast between morning and evening yawning. What can explain the fact that yawning, an expression of sleep pressure, can occur in its arousal time course (i.e. directly after sleep)? Further experimental studies can be considered after reading their chapter.

A. Guggisberg, J. Mathis and C. Hess also address this question in their chapter in which they review behavioral studies and electroencephalographic recordings of brain activity before and after yawning. The authors assess consistent evidence indicating that yawning occurs during states of low vigilance. For the authors, this substantiates
the notion that yawning is provoked by sleepiness. However, studies analyzing autonomic nervous activity and EEG-based indices of vigilance in yawning subjects have not found specific autonomic activations or increased arousal levels after yawning. During sustained periods of taxing cognitive work, humans typically display time-on-task effects, in which performance gets steadily worse over the period of task engagement. Persistent effects of cognitive fatigue in the frontoparietal region after a period of heavy mental work indicate the critical role of this attentional network in mediating task effects. Can yawning be a marker of the level of fatigue in the neural attentional system by which a reverse attentional stimulation occurs, but not an arousal enhancement? Perhaps yawning is more a sign of some impending change of state rather than a statement of tiredness itself.

After completing his psychology studies, W. Seuntjens reviewed the scientific literature on yawning and found there was no simple and straightforward explanation of this phenomenon. He undertook his own research and wrote a thesis in 2004: ‘On yawning or the hidden sexuality of the human yawn’. Here, he presents a summary of the data collected. Amassing circumstantial evidence, he substantiates the discovery of a hidden sexuality of the human yawn. Seuntjens uses the word ‘chasmology’, derived from the Greek, to describe the new field of research on yawning and foresees a bright future for it. Perhaps more philosophical than scientific, his chapter certainly appears to be the most original in this book.

Non-human primate yawns are usually categorized according to context (e.g. as a threat, anxious, rest or emotivity yawn), but there has been little consideration about whether these yawns are best regarded as a unitary behavior that only differs with respect to the context in which it is observed. James A. Anderson discusses the current view of yawning as non-verbal communication, whether champanzees can trigger voluntary yawns and how yawning by non human primates can be an opening into empathy. Reflecting the growing wave of research investigating these abilities, this chapter reviews the comparative literature and offers some thoughts relevant to the intriguing question: why does contagious yawning exist?

On the one hand, research on human stress has traditionally relied mostly on physiological and psychological measures with a relatively minor emphasis on the behavioral aspects of the phenomenon. A promising approach to the study of the behavioral correlates of stress is to analyze those behavior patterns that ethologists have named displacement activities. On the other hand, anxiety-related disorders are among the most common behavioral problems in humans and animals. On these occasions, animals frequently present lip licking, yawning or scratching, for example. In humans, yawning may even be a general preparation for some new mental experience. Certainly, people expecting something novel to happen indulge in yawning quite frequently; for example, parachutists about to jump tend to do so. Thus, yawning and stretching, like all forms of behavior, occur within definable contexts. Displacement activities are behavior patterns characterized by their apparent irrelevance to the situation in which they appear. Scratching, autogrooming and yawning are among the
most commonly reported displacement activities in non-human primates, rodents, dogs and cats. Displacement behavior appears in situations characterized by social tension and is likely to reflect increased autonomic arousal. In such contexts, yawning gives more veridical information about the subject's emotional state than verbal or vocalized statements and facial expressions. We are proud to present new research, conducted by A. Moyaho and J. Valencia, in this promising field. Their work suggests that yawning is a delayed response to fear produced by response-dependent punishment in rats. The precise mechanisms whereby rats respond by yawning to emotional conditions remain to be elucidated, again suggesting a new field of investigations.

The past 30 years of research have led to a much greater understanding of the neuropharmacological regulation of yawning. While many of the early studies concluded that yawning was primarily driven by changes in cholinergic neurotransmission, Gregory T. Collins and Jose R. Eguibar expertly discuss the state of knowledge for each of the major neurotransmitters and neurohormones (dopamine, glutamate, serotonin, oxytocin, GABA and others) involved in the regulation of yawning, their interactions with one another, and their place in the hierarchical organization of yawning. This chapter is the most complete text ever published on the topic, and we predict it will be the most cited in the future.

A. Gallup has emerged as a leader in new perspectives on the function of yawning. His research provides support for the view that yawning is a behavioral response to transient hyperthermia, acting to counter intermittent increases in brain temperature and promote thermal homeostasis. Brain activity never stops. The brain is one of the most metabolically active tissues, generating large amounts of heat. Dissipating this heat as well as heat absorbed from the environment has been a major evolutionary hurdle necessary for continued brain development. It seems that the evolution of emissary veins (i.e. ritia mirabilia; the vascular network in the scalp and face removing heat from the brain) solved this problem. Brain cooling mechanisms have been described during fever to protect brain tissues and activities. There is no work (to my knowledge) indicating that cerebral activity modifies the internal temperature of the brain in a variable way according to the level of attention. Except during fever, the brain temperature remains constant; thus, how could yawning be necessary for brain cooling? This is the challenge that A. Gallup faces.

It has long been known that yawning is ‘contagious’; ethologists speak of behavioral replication and neurologists refer to ‘echokinesis’, a term coined by J.-M. Charcot. The neural mechanisms responsible for spontaneous yawning as well as contagious yawning have been incompletely characterized. Fatta B. Nahab details how neuroimaging can be an essential tool for helping to identify the seminal neural structures and their inter-related functions to carry out this complex stereotyped motor program. Matthew W. Campbell and Frans B. M. de Waal point out that the various contagious yawning studies are confusing because researchers analyze their results differently. The authors go on to make recommendations for more rigorous, thorough and informative analyses. Their goal in raising awareness of these issues is to encourage
new experiments and improve discussion of existing research. In particular, they propose more standardized studies of contagious yawning to test its hypothesized link to empathy.

Steven Platek summarizes the suggestion that contagious yawning is a primitive expression of social cognition, in particular empathy. Susceptibility to contagious yawning is correlated with speed in recognizing one’s own face, theory of mind processing and is also associated with activation in regions of the brain that have been associated with social cognitive processes. This suggests that contagious yawning may be an evolutionarily old process that begat a higher level of social cognition in certain species. Atsushi Senju reviews the current evidence from developmental studies with typically and atypically developing populations and comparative studies in non-human animals. Developmental studies have revealed that contagious yawning is disturbed in individuals with autism spectrum disorders and schizophrenia, suggesting that contagious yawning may share a developmental basis with the capacity for theory of mind. He also presents comparative studies suggesting that contagious yawning can be observed in non-primate species and, perhaps, domestic dogs. His results seem consistent with the claim and previous statement that the mechanism underlying contagious yawning relates to the capacity for empathy.

As with all physiological behaviors, deregulated yawning reveals disorders. However, a property unique to yawning, which is nevertheless physiological, is its ability to trigger certain disorders and, conversely, to cure others! We successively cover all forms of yawning disorder – i.e. anhedonia, disappearance of yawning, excessive yawning – in a wide-ranging chapter.

The central nervous system in vertebrates follows a common organizational pattern and shows gradually increasing complexity with higher and higher levels of independence and functionality. A promising new field of research describes the pattern of associated movements observed in hemiplegic limbs during yawning. Thus, Ramachandran Meenakshisundaram and colleagues from India have collected 75 clinical cases of stroke. They indicate how, in certain stroke localizations, functional levels become disconnected; thus, functions may reappear that are normally inhibited by a phylogenetically more recent and functionally more sophisticated structure.

I would especially like to thank all my coauthors for their valuable work, which is essential to the success of this book. I would also like to extend a special thanks to Tanja Sebuk and Peter Roth at Karger for their active support and professionalism.

Dr. Olivier Walusinski, Brou