Yawning: Unsuspected avenue for a better understanding of arousal and interoception

Olivier Walusinski *

20 rue de Chartres, 28160 Brou, France

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Summary   Almost all the vertebrates yawn, testifying the phylogenetic old origins of this behavior. Correlatively speaking, yawning shows an ontogenical precociousness since it occurs as early as 12 weeks after conception and remains relatively unchanged throughout life. Thus, it is contended that these common characteristics and their diencephalic origin allow to model an approach from which emerges a pivotal link between yawning and REM sleep. Yawning and stretching reverse the muscular atonia of the REM-sleep and reopen the collapsed airways. Yawning appears as a powerful muscular stretch, recruiting specific control systems particularly the paraventricular nucleus of the hypothalamus, the locus coeruleus and the reticular activating system from which the vigor of this ancestral vestige, surviving throughout evolution with little variation, may increase arousal.

On the other hand, the James—Lange theory proposes that afferent feedback from muscles and viscera provides the brain with a feeling that characterizes the active motivational state and arousal. On this basis and using selected supporting findings from the literature and from data provided by daily life, it is contended that yawning takes part in interoceptiveness by its capacity to increase arousal and self-awareness. Adaptative behaviors depend on interactions among the nervous system and the body by a continuous feedback between them. The body's schema is a main component of the self, and interoceptive process is essential to awareness of the body and arousal. Yawning contributes to bodily consciousness as a behavior affiliating a sensory motor act and his perception from which pleasure is derived. Yawning can be seen as a proprioceptive performance awareness which inwardly provides a pre-reflective sense of one's body and a reappraisal of the body schema. The behavioral consequences of adopting specific regulatory strategies and the neural systems involved act upon attention and cognitive changes.Thus, it is proposed that yawning is a part of interoceptiveness by its capacity to increase arousal and self-awareness.
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I should like to work like the archeologist who pieces together the fragments of a lovely thing which are alone left to him. As he proceeds, fragment by fragment, he is guided by the conviction that these fragments are part of a larger whole which, however, he does not yet know.

<div align="right">Hans Spemann (1938).</div>

Introduction

Organisms exhibit cyclic variations in a variety of essential functions, including the sleep—wake

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* Tel.: +33 2 37 47 07 77; fax: +33 2 37 47 19 07.
  E-mail addresses: walusinski@yawning.info, walusinski@baillement.com.

cycle, feeding and reproduction, secondary, for example, to the daily alternation of darkness and light exerted by the rotation of the earth. Yawning, one of the most underappreciated of stereotyped behaviors, appears to be associated with each behavioral transition occurring at the beginning and the end of these functions. Our purpose is to give a new insight built on an evolutionary perspective of the wake/sleep system, and in particular, to argue that yawning shares links with REM sleep and arousal. The properties of yawning, thus revealed, help to give new explanations of its mysterious functions and of its survival without evolutionary variations postulating a particular importance in terms of needs. One might assume that yawning is a component of the interoceptive processes, essential to awareness and arousal. It is contended that yawning is a part of interoception by its capacity to increase arousal and self-awareness [2].

Yawning: its cycles, its life

Ethologists agree that most vertebrates yawn. Yawning is morphologically similar in reptiles, birds, mammals and fishs. There are three types of morphologically identical yawns occurring in three distinct situations: situations relative to circadian rest-activity rhythms, situations relative to feeding, situations relative to sexuality or social interactions [3].

Yawning is a stereotyped and often repetitive motor act characterized by gaping of the mouth accompanied by a long inspiration, a brief acme followed by a short expiration. In human, the expansion of the pharynx can quadruple its diameter at rest diameter, while the larynx opens up with maximal abduction of the vocal cords. These characteristics cannot be noticed in any other moment of life. Yawning is not just a matter of opening one's mouth, but a generalized stretching of muscles, those of the respiratory tract (diaphragm, intercostal), the face and the neck. It may be seen as a part of the generalized stretch, named pandiculation, with which it is generally associated [4]. It is necessary to notice that the function of stretching is actually not well understood. This association of complex and synergic movements occurs with an involuntary occurrence and shares no criteria of a classical reflex.

When animals change between behaviors, they are not merely responding in a passive way to conditions of the environment, like day—night succession, for example. Rather, they are following internally generated signals produced by homeostasis procedures originating from the hypothalamus (suprachiasmatic nucleus, SCN, and paraventricular nucleus, PVN, of the hypothalamus). This internal rhythm has the ability to anticipate the transitions and triggers behavioral and physiological changes in accordance with those transitions. This association has two advantages : predictability and the possibility to detect the unexpected. Yawning is a behavior which shares these characteristics and appears to be associated with transitions between periods of high and low activity or arousal. A circadian pattern has been found in spontaneous yawning. In normal, unstressed humans daily peaks of yawning are associated with transitions from sleeping to waking and from waking to sleeping [5,6].

Yawning: neurophysiology

Until now, no specific cerebral structure has been identified as a yawning center. A good number of clinical and pharmacological arguments indicate that yawning involves the hypothalamus (particularly the PVN), the bulbus and pontic regions, with frontal region connections in primates and to the cervical medulla. The PVN is an integration center between the central and peripheral autonomic nervous systems. It is involved in numerous functions ranging from feeding, metabolic balance, blood pressure and heart rate, to sexual behavior and yawning. In particular, a group of oxytocinergic neurons originating in this nucleus and projecting to extra-hypothalamic brain areas (e.g., hippocampus, medulla oblongata, and spinal cord) controls yawning and penile erection. Activation of these neurons by dopamine and its agonists, excitatory amino acids (N-methyl-D-aspartic acid) or oxytocin itself, or by electrical stimulation leads to yawning, while their inhibition by gamma-amino-butyric acid (GABA) and its agonists or by opioid peptides and opiate-like drugs inhibits yawning and sexual response. The activation of these neurons is secondary to the activation of nitric oxide synthase, which produces nitric oxide. Nitric oxide in turn causes, by a mechanism that is as yet unidentified, the release of oxytocin in extra-hypothalamic brain areas. Other compounds modulate yawning by activating central oxytocinergic neurons: sexual hormones, serotonin, hypocretine and endogenous peptides (adrenocorticotropin-melanocyte-stimulating hormone). Oxytocin activates cholinergic neurotransmission in the hippocampus and the reticular formation of the brainstem [7,8]. Acetylcholine induces yawning via the muscarinic receptors of effectors from which the respiratory neurons in the medulla, the motor nuclei of the

Vth, VIIth, IXth, Xth, and XIIth cranial nerves, the phrenic nerves (C1—C4) and the motor supply to the intercostal muscles.

Yawning: ontogenesis

The facial bone structure and the brain become distinct starting from a common embryonic structure, the ectoblast. The cephalic pole comprises an original embryological encephalo-facial and encephalo-cervical segmentation with a strict topographical correspondence: the naso-frontal and premaxillary structures are joined to the anterior brain; the maxillo-mandibular and anterior cervical structures are joined to the brainstem and its nerves. At the beginning of the third month, the embryo becomes a fetus with the occurrence of the first oral and pharyngal motor sequences under the control of the neurological development of the brainstem. The development of the suction-deglutition and yawning activity, sharing the same embryological origin, shows the importance of the brainstem in the neurophysiological development of the oropharyngeal activity coordinated with the respiratory, cardiac and digestive regulations which have the same neuroanatomical localization [9,10]. These circuits that generate organized and repetitive motor patterns, such as those underlying feeding, locomotion and respiration belong to the Central Pattern Generators in the medulla (CPG) which are genetically determined, subserving innate motor behaviors essential for survival [11]. Although in higher primates CPG are partially under neocortical control, reflexive control systems involving CPG contribute to swallowing, breathing and cough [12] which are all dependent on pharyngo-laryngeal muscles control [13]. Thus, it is argued that yawning takes part of this CPG for his motor aspect. Afferent somatosensory feedbacks, for both temporal coordination and intensity, provide simultaneous visceral sensation and autonomic response (PVN) by which yawning take part of the arousal homeostasis [14].

Yawning and stretching have the original traits of related phylogenetic old origins and, as correlates, ontogenetic precociousness. Rhythmic motor patterns and movements are seen embryonically, before they are needed for behavior from which it is suggested that activity in immature networks is important for circuit formation and transmitter specification [11]. In the human embryo, yawning occurs as early as 12 weeks after conception and remains relatively unchanged throughout life. Its survival without evolutionary variations postulates a particular importance in terms of developmental

needs. The strong muscular contraction that signifies a yawn is metabolically expensive. If we accord with the terms of Darwin's evolutionary propositions, the costs of brain activity must be outweighed by the advantages gained in terms of developmental fitness. Thus, a structural hypothesis suggests activation in the synthesis of neurotrophins, which lead to a cascade of both new synapse formation or recruitment, and activation through the diencephalon, brainstem, and spinal cord. The phenomenon of activity-dependent development has been clearly shown to be one mechanism by which early sensory or motor experience can affect the course of neural development [15]. The ability to initiate motor behavior generated centrally and linked to arousal and respiratory function is a property of the brainstem reticular formation, which has been remarkably conserved during the phylogeny of vertebrates including agnathans, fishes, amphibians, reptiles, and birds [16,17]. Therefore, conservative developmental mechanisms orchestrating the organogenesis of the brainstem in all vertebrates are probably crucial for arousal and breathing.

As an example, it is possible to compare Ondine's syndrome, congenital or acquired (Chiari malformation) with the locked-in syndrome. It allows to distinguish brainstem from supramedullary regulatory mechanisms in humans. The former comprises loss of autonomic respiratory control, requires volitional breathing for survival, and points out the loss of any yawn. The latter entails loss of corticospinal or corticobulbar tracts required for volitional breathing, preserves autonomic respiratory control and characterizes automatic-voluntary dissociation with tenacious yawns [18]. Thus, yawning provides evidence for the emergences of stereotyped inborn fixed action patterns which may reappear as pathological states: epilepsy, stroke [19—21].

Sleep, arousal, and yawning

The phylogenetic appearance of sleep proposes that the nocturnal resting in poikilotherms most probably manifests in mammals as a form of rapid eye movement (REM) sleep or paradoxical sleep, which is characterized by peripheral muscular atonia originating in the dorsal part of the brainstem, rostral to the pons [22]. Based on numerous studies of fetuses and infants in a variety of mammalian species, it is widely believed that the earliest form of sleep is properly characterized as active sleep, that is an immature form of REM sleep and preponderant at birth. Accordingly, it is thought that

quiet sleep, an immature form of slow-wave sleep (SWS), emerges as REM sleep's predominance diminishes during ontogeny [23—25].

In the early intra-uterine life, a diffuse collection of phasic and cyclic motor events occur that gradually coalesce. For the fetus, sleep and wakefulness are reliably characterized, respectively, by periods of myoclonic twitching expressed against a background of muscle atonia and high-amplitude behaviors (e.g., locomotion or stretching—yawning) expressed against a background of high muscle tone. Movements of the limbs, such as stretching, yawning, and kicking, are typically considered to indicate periods of wakefulness [26]. Periods of twitching are almost always followed by the abrupt onset of high-amplitude awake behaviors, thus completing the cycle. Although myoclonic twitching during active sleep in infants is more prevalent and more intense than that seen during REM sleep in adults, its similarities to the adult behavior and its linkage to periods of atonia suggest developmental continuity between the infant and adult sleep states. The maturation of the central nervous system, based on myelinization, starts in the spinal cord and then proceeds to the brainstem and forebrain. Thus, paradoxical sleep mechanisms located in the brainstem are the first to mature and the only ones to function. Then, the slow-wave sleep and waking structures become mature [27—29]. Namely, the widespread control of neuronal activity exerted by specific REM sleep processes helps to direct brain maturation through activity-dependent developmental mechanisms. It may be inferred that REM sleep (and possibly yawning) directs the course of brain maturation in early life through the control of neural activity [11]. Behavioral pattern continuity from prenatal to postnatal life shows a strict parallelism between the ontogeny of REM sleep and yawning. Basically, REM sleep in the human declines from 50% of total sleep time (8 h) and a frequency of 30/50 yawns per day, in the newborn, to 15% of total sleep time (1 h) and less than 20 yawns per day, in the adult (see Fig. 1). This decrease takes place mainly between birth and the end of puberty. The emergence of distinct states is followed by dramatic changes in the amounts, duration, and cyclicity. An ultradian rhythm may be graded; in a period from 50 to 60 min appears an alternation of moment characterized by motor activity and by rest, as in newborns. Each period of rest switches over a period of activity by a yawn. Thus a periodicity of one or two yawns per hour can be noticed. Yawning appears 2 weeks before any discernible sleep—wake states, and its expression gradually becomes linked. No changes in the incidence of yawns between 20 and 36 weeks of gestational age have been observed by Roodenburg et al. [30] in the fetus. In preterm and full-term infants, yawns are frequently observed on the first days of life [31].

Thus, the REM sleep and the yawning—stretch syndrome, are two opposite muscles tones, ontologically linked, and may be seen as ancestral vestiges surviving throughout evolution with little
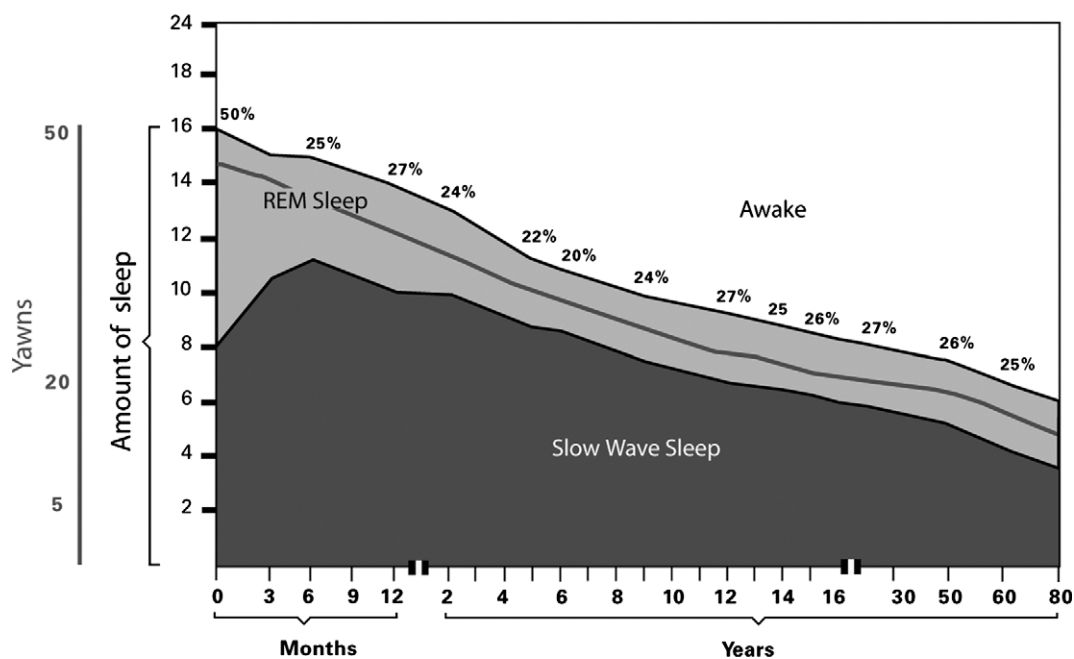

Figure 1 The similarity of the evolution of Yawn's frequency per day and the amount of REM sleep, throughout life.

variation. Decades ago, McLean postulated that these behavioral routines, similar across vertebrates, are evolutionarily conserved and mediated by the similarly conserved basal ganglia and related brain systems. Yawning is an example which validates McLean's postulates testifying that human behavioral medicine can profit from a broad comparative approach [32].

Yawning and awaking

Sleep is a reversible behavioral state of perceptual disengagement from and unresponsiveness to the environment but also the inner state. The sensory inputs and motor outputs are simultaneously blocked when the brain is activated during REM sleep, putting it off-line [33]. The preferred time to wake up from sleep is phase related to circadian rhythms. It is suggested that the homeostatic component of sleep regulation dominates in the first half of sleep, while the consistency in the second half of sleep mainly depends on circadian components. Awakenings show a characteristic distribution with a maximum immediately following REM sleep. This time preferentially coincided with the rising slope of the circadian rhythm of deep body temperature [34,35]. Campbell [36] found that sleep termination did not follow a completed REM sleep episode but rather interrupted REM sleep. He proposes ''REM sleep as a state with high neural activity which provides optimal physiological conditions for the transition from sleep to waking'' [36]. The transition from sleep to waking implies a physiological process which leads to a new behavioral state. Awakening essentially constitutes cortical arousal and is revealed by electroencephalographic desynchronization and a general increase of electrical excitability both in sensory and motor systems [37]. The activating system [38] is constituted by neurons located in midbrain reticular formation (the reticular activating system, RAS) projecting to the thalamus and to the cortex [39]. An intrinsic function of the RAS is its participation in responses such that alerting stimuli simultaneously activate thalamocortical systems, as well as postural and locomotor systems, in order to enable an appropriate response (fight versus flight). Neurons are, in the majority, noradrenergic and particularly concentrated in small nuclei like the locus coeruleus, having widespread projections to forebrain areas and to virtually all brain regions. Locus coeruleus activity varies first and foremost with the state of vigilance, as first reported in 1969 by Jouvet

[40] and has a role in regulating different types of cognitive abilities during alertness. Locus coeruleus neurons show low activity during low vigilance behavioral states such as grooming, but respond phasically to stimuli in all sensory modalities when they are novel and salient. The system contributes to the initiation and maintenance of behavioral activity necessary for the collection of sensory information and stays as a critical component of the central neural architecture supporting interaction with and navigation through the world [41].

If REM sleep may facilitate for the brain a smooth transition to wakefulness, it must be noticed that REM sleep is characterized by a peripheral muscular hypotonia (potent tonic suppression) which may immediately switch to a reversible state of basal muscle tone. It is suggested that the trigemino-cervical-spinal projections on the locus coeruleus, which convey afferent stimulations, resulting from the yawning—stretch syndrome, would favor behavioral adjustment, through an enhancement of 'bottom-up' information processing. This signal would have a general reset function. His activation is tightly related to stimulus and induces cognitive shifts by promoting reset of functional networks [42]. Each motor pattern is controlled by a specific functional network, defined as a dynamic assembly of neurons establishing specific spatiotemporal interactions. The powerful muscular contraction involved in the yawning—stretch syndrome triggers an abrupt dissolution of the preexisting functional network controlling the REM sleep motor pattern and facilitates the emergence of a functional network controlling the awaking motor pattern. Reconfiguration of networks is thus snappily achieved and their reorganization promotes rapid behavioral adaptation [43].

To recapitulate, at becoming awake, yawning and stretching reverse the muscular atonia which characterize REM sleep. The wide inspiration triggered by the yawn, which can be seen as a form of sigh, improves lung compliance by ensuring re-inflation of collapsed airways and alveoli.

Drowsiness and fatigue may be linked to the disruption of neural networks involved in tonic attention, such as the reticular activating system and related structures involved in the subcortical attentional network. In the course of the day, muscle tone tends to diminish as drowsiness approaches and the upper airway would tend to be drawn inwards. The stretching of skeletal muscles would tend, on one hand, to overcome the reduction of muscle tone in the ''antigravity'' muscles and, on the other hand, to restore normal airway resistance [44].

How yawning is triggered?

Awareness and more precisely arousal, are essential components of total consciousness. They require the ability to integrate sensory informations from external environment, from internal bodily states and modulation by emotions and memory.

The trigeminal nerve, the facial nerve, the glossopharyngeal nerve, the vagus nerve and the C1—C4 spinal nerves provide sensory information and terminate topographically in the nucleus of the solitary tract (NTS). NTS is involved in central integration for the regulation of arousal, sexuality and feeding. The major outputs from the NTS is the parabrachial nucleus which in turn provides extensive projections to a wide range of sites in the brainstem, hypothalamus, basal forebrain, and thalamus. The NTS and the parabrachial nucleus project to the cerebral cortex, especially the insular visceral sensory field, the amygdala, the sensory and laterofrontal cortex. A part of the NTS's neurons projects directly to the locus coeruleus, the hypothalamus, mideline thalamic nuclei, each of which has direct and diffuse cortical projections. Sensory afferents from the musculoskeletal joints converge via the spinothalamic and the spinoreticular tracts which passes through the brainstem and have two divisions. The medial pathway, coming from diaphragm, projects to the thalamic formation and caudal raphe nuclei and then towards cortical sensory regions. Many afferents end in the parabrachial subnucleus, which provides a diffuse input to the intralaminar thalamic nuclei and thus is involved in arousal response to musculoskeletal and visceral stimuli. A key feature of this ascending pathway is that it provides collaterals that converge with the cranial nerve sensory pathways at virtually every level. Some of the afferents may be responsible for autonomic reflex responses to visceral stimuli, and it is argued to yawning. To keep in account, the thalamic nucleus and the PVN belong to a neural loop circuitry sending and receiving histaminergic projections from the tuberomammillary nucleus, and noradrenergic projections from the locus coeruleus. The basal ganglia, as a rule, are highly interconnected with the peduculonpontine tegmental nucleus (PPN). PPN shows motor function by controlling postural muscle tone and plays a role for the regulation of the sleep—wake cycle and is a limbic—motor interface for reward predictions [45,46].

Taking together, these characteristics suggest that the visceral and musculoskeletal sensory pathways are connected to the same subcortical structures that provide arousal and attention mechanisms [47]. Under this perspective, yawning triggers the stimulation of the locus coeruleus beyond musculoskeletal and visceral sensory inputs.

For example, the control of muscle tone of the neck (trapezius) and of the masseters is one of the elements contributing to the triggering of our awakening [48]. The modification of this tone would be one of the triggering events of yawning. During the powerful contraction caused by yawning, the spindles of the masticatory muscles (masseters, temporal, pterygoids), which have receptors that respond to stretching, send stimuli via afferent nerve of the Ia category, which are located in the mesencephalic root of the trigeminal nerve (ascending visceral parasympathic pathway). With the motor neurons of the same muscles these nerves form a monosynaptic link. This is the basis of the masseteric reflex. These nerves have projections on the RAS and the locus coeruleus which are anatomically close to the nucleus of the trigeminal nerve. Through the massive contraction of the masseteric muscles, yawning stimulates those structures responsible for cortical activation. The fact that the amplitude of the masseteric reflex varies in parallel with the level of vigilance constitutes another argument [49].

What is interoception?

School children are still routinely taught that there are five senses (sight, hearing, touch, smell, taste, a classification first devised by Aristotle). But it may be argued that there are at least six different senses in humans. The five senses belong to what is called exteroception, the perception of stimuli which come from an external source. Nociception, the perception of pain, is a distinct phenomenon that intertwined with all other senses, including touch. In addition, some animals have senses that humans do not, including the following: electroreception, magnetoreception, and echolocation.

By contrast, the sixth sense is the interoception, the sensory perceptual process for events occurring inside the body. It is the perception of body awareness and frequently not aware. The term ''interoception'' was introduced in 1905 by Sherrington [50]. It includes proprioceptive sensations and labyrinthine functions but refers also much more broadly to all bodily sensations, most frequently at the border of consciousness [51].

Yawning: the inside story

There are reciprocal connections between insula and thalamus, hypothalamus, RAS, the locus coeruleus. Yawning engages any of these structures related to the representation and/or regulation of organism state, for example, the brainstem, the hypothalamus and the insula. These regions share a major feature in that they are all direct and indirect recipients of signals from the internal milieu, visceral, and musculoskeletal frame. In addition, some brainstem nuclei, the hypothalamus, and subsectors of the insula and cingulate, also generate regulatory signals necessary to maintain homeostasis. The results underscore the close anatomical and physiological connection between yawning and homeostasis, and between yawning and mapping of the ongoing state of the organism. The neural patterns depicted in all of these structures constitute multidimensional maps of the organism's internal state and they form the basis for an aspect of the feeling state. Some of these maps, such as those in brainstem and hypothalamus, are coarse. The maps in insula and cingulate regions that receive regulatory signals from brainstem and hypothalamus in addition to direct sensory signals from the organism, are more refined, and their information is accessible to consciousness, thus providing integrated perceptual maps of the organism state [52].

After a yawn, humans experience an unfolding feeling of well-being. Physical movement (somatic motor system) and respiratory activity are coordinated by interactions involving brainstem mechanisms and structures such as the NTS, the PVN, and the RAS. Visceral-somatic sensations are functionnally and anatomically linked. Subjectively experienced feelings as well as emotions might be bases on higher-order re-representations of homeostatic afferent sensory activity in human forebrain. Direct ascending projections from these sites activate insular cortex by way of the basal (parasympathetic) and posterior (sympathetic) parts of the ventromedial nucleus of the thalamus. These modality-specific, topographically organized projection pathways are phylogenetically distinct to primates and are well-developed only in humans. These pathways progressively activate higher-order homeostatic afferent re-representations in more anterior portions of the insula. The anterior insula (particularly right, nondominant) is activated predominantly by homeostatic afferents. Indeed, the insular cortex is involved in higher somatic integration, in relation to both somatic, autonomic and limbic systems [53]. The ventral anterior insula is most important for core affect, a term that describes broadly-tuned motivational states with associated subjective feelings [54].

From the neurochemical point of view, serotonin is known to modulate the regulation of the sleep/wake cycle. Serotonergic (5HT) neurons are found in the hypothalamus and the raphe nuclei. These neurons innervate many different regions of the brain and spinal cord, and play also, important modulatory roles in regulating locomotor coordination, neuro-endocrine systems, motivation and reward, emotional balance, mood, attention, and social behavior [55]. It is argued that this serotonergic system is involved in the well being induced by yawning-reward. Thus, psychotropic drugs, such the selective serotonin reuptake inhibitors, has given a rich iatrogenic pathology, triggering yawns salvos.

Based on these numerous lines of evidence, it is proposed that yawning associated with arousal indirectly activates insula, anterior cingulate cortex and somato-sensory cortex. Subjective ratings of feeling from yawning are correlated with homeostatic afferent activity, including pleasant feeling. The capacity of extract informations from this well-being, stays as a substrate for subjective awareness of being aware, consistent with the James-Lange theory of emotion [56,57] and Damasio's somatic marker hypothesis of consciousness [58,59]. Yawning appears ''one body perspective experiment'' and gives the opportunity to enhance responses of the bodily frame to higher cognitive level (brain's representation of the body). Yawning plays a multi-level role in that it not only stimulates arousal but also regulates the level of alertness and the ability to perform adaptively during the waking state by resetting the representation of body configuration [60].

Tentative conclusions

The development of adaptive behavior includes not just an interaction between the brain and the environment external to the organism, but also the ongoing involvement of the body in this process in both motor and sensory aspects. Damasio postulates that consciousness arose as a consequence of sensory processes and argues that visceral sensations contribute to the development of consciousness. He attributes importance to interoceptive processes as a general factor in ongoing organismic functioning. Bodily input provides stability, contributing to the sense of the self as consistent and persistent over time. The body's schema is a

main component of the self and interoceptive processes that is essential to awareness of the body. Total muscle relaxation appears to lead to loss of conscious imagery and phantom limb phenomenon depends on the persistence of sensory feedback produced by residual muscular activity. Thus, it may be argued that the sensory and motor systems are one system and cognitive functions apparently are related to motor processes. A sensory experience would imply a motor response to issue the consciousness of the self. Yawning contributes to bodily consciousness as a behavior affiliating a sensory motor act and his perception from which pleasure is derived. Yawning can be seen as a proprioceptive performance awareness which inwardly provides a pre-reflective sense of one's body and a reappraisal of the body schema. It displays three levels: embodiment (constrained and enabled by motoric possibilities), communication (making public an arousal state), cognition (feeling well and rewarding) and remaps the link unifying body and mind. Yawning connects consciousness as well as unconscious (or subconscious) interoception to higher mental functions [61—63].

Acknowledgment

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Echokinetic yawning, theory of mind, and empathy

Humans are social beings. One of the primordial functions of the brain is to enable optimal interaction with others. The success of social interaction resides in the capacity to understand others in terms of motor actions (intentionality), emotional perception, and a mnemic and comparative cognitive integration which separates the self from others (empathy, altruism). In psychology, all these capacities are referred to collectively as Theory of Mind (TOM). It has long been known that yawning is "contagious"; ethologists speak of behavioural imitation and neurologists refer to echokinesis, a term coined by JM. Charcot. How does such echokinesis turn yawning into a form of nonverbal social communication related to TOM and empathy?

The discovery of mirror neurons by Rizzolatti and Gallese (1) offers a neurophysiological explanation for TOM. In most vertebrates, developing the capacity to explore the environment, making decisions (especially in a life-or-death response to a predator) and general preparation for action involve the activation of these mirror neurons, along with motor neurons, in cortical motor areas. Mirror neurons are activated when the movements and actions of conspecifics are perceived, indicating that intentional action and the corresponding mental imagery share the same neuronal structures. Hence, when a single pigeon senses the approach of a pedestrian, the entire flock automatically flies away, even though most of the birds did not actually perceive the danger. This cooperative motor automatism is a result of adaptive responses selected by evolution. It serves the group by providing protection from predators. Echokinesis-induced yawning does not correspond to this mechanism, as indicated by its latent appearance and its inconsistency. In fact, echokinesis only occurs in situations of minimal mental stimulation (public transport); during prolonged intellectual effort, people are not susceptible to this phenomenon. Using functional MRI (fMRI), Schürmann et al. (2) confirmed that during echokinetic yawning, there is no activation of mirror neurons in motor areas of the human brain (left posterior inferior frontal cortex), whereas these neurons are activated during observation of other types of facial gestures (decoding of intentionality). These ethological and neurophysiological elements demonstrate that, strictly speaking, echokinetic yawning is not motor imitation.

Visual recognition of one's environment involves various neuronal circuits which distinguish inanimate objects from living creatures (3). Recognition of human faces involves specific dedicated neurons in the temporal area. The inferior temporal region (IT) allows immediate overall recognition of faces, both their identity and their expression, apparently through its own autonomous, non-hippocampal memory (4). As for the superior temporal sulcus (STS), it is specifically activated during perception of eye and mouth movements, which suggests its implication in the visual perception of emotions, once again by the activation of mirror neurons. These neurons mime the expression perceived, helping the observer to understand it. Schürmann et al. (2) demonstrated that the STS is activated during echokinetic yawning. This activation, automatic and involuntarily, is transmitted to the left amygdala, the posterior cingulate cortex and the precuneus. These structures are thought to play a role in differentiating emotions expressed by the human face and, especially, in evaluating the sincerity of the sentiment expressed.

Using fMRI, Platek et al. (5) found a correlation between personality traits and the activation of neuronal circuits beyond the STS. « In contrast to those that were unaffected by seeing someone yawn, people who showed contagions yawing identified their own faces faster, did better at making inferences about memal states, and exhibited fewer schizotypal personality characteristics. These results suggest that contagious yawning might be related to selfawareness and empathic processing »(6). Subjects considered empathetic, who were very susceptible to echokinetic yawning, activated the amygdala and the cingulate cortex, whereas schizotypal subjects, who were not susceptible to this type of yawning, did not activate these structures. Neurophysiological studies of empathy (7) show similar zones of activation (STS, insula, amygdala, cingulate cortex). These data imply that contagious yawning may reside in brain substrates which have been implicated in self-recognition and mental state attribulion, namely the right prefrontal cortex.

During echokinetic yawning, frontal lobes show no inhibitor activity. Therefore, it appears that while the understanding of intentionality (motor mirror neurons) and the sharing of the emotions (mirror neurons in the insula, amygdala and right parietal cortex) require a common action-perception neuronal activation and, simultaneously, frontal inhibition (orbitofrontal activation) to prevent motor exteriorisation, echokinetic yawning cannot be inhibited involuntarily due to the potentially absence of frontal inhibiting relays. In contrast, the right temporoparietal activation makes it possible to differentiate between the self and others, and thus identify on a conscious level that another person's yawn has acted as a trigger (8). Yawning could thus illustrate the simulation theory of mind.

Whereas yawning is universal amongst vertebrates, it appears that only primates are capable of echokinetic yawning. Anderson (9) reported that chimpanzees yawn while watching a video of their conspecifics yawning, but not while watching other facial expressions. Chimpanzees thus appear to be susceptible to echokinetic yawning in the same way humans are. Although the existence of a TOM in chimpanzees remains controversial (10), the observation of echokinetic yawning in this species argues in favour of different levels of TOM, which are perhaps secondary to the different evolutionary paths of cognitive development in hominids. Human psychiatric pathology also dissects TOM in a similar way (11).

Senju et al. showed video clips of people either yawning or simply opening and closing their mouths to 49 children who were 7 years or older, half of whom were autistic. The yawning faces triggered more than twice as many yawns in non-autistic children than in their autistic counterparts. This study suggest that contagious yawning is impaired in autism spectrum disorders, which may relate to their impairment in empathy (14).

Anderson (12) showed that children were only susceptible to echokinesis-induced yawning during their sixth year, i.e. after acquiring the ability to reflect on what others are thinking and attribute mental states accordingly. In other words, one must possess a state of cognitive maturity on a functional level to be susceptible to echokinetic yawning. Consequently, there is a phenomenological link between the capacity to attribute mental states to others (TOM), which is the basis for empathy, and what is commonly referred to as contagious yawning. In addition to the neuroanatomical hierarchy separating TOM into sensorimotor, emotional and cognitive levels, echokinetic yawning makes it possible to disassociate TOM, via its ontogenesis and its phylogenesis, into various developmental levels, an approach which is reinforced by the differential activation of specific neuronal circuits (13). This type of yawning may have conferred a selective advantage by synchronising the level of vigilance between the members of a social group. It may also take part in a form of involuntary instinctive empathy, which could be qualified as rudimentary and probably appeared late in the course of hominid evolution (in the neomammalian brain proposed by P. McLean).

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