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HYPOTHESIS

Pandiculation: Nature's way of maintaining the functional integrity of the myofascial system?

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Summary Pandiculation is the involuntary stretching of the soft tissues, which occurs in most animal species and is associated with transitions between cyclic biological behaviors, especially the sleep-wake rhythm (Walusinski, 2006). Yawning is considered a special case of pandiculation that affects the musculature of the mouth, respiratory system and upper spine (Baenninger, 1997). When, as often happens, yawning occurs simultaneously with pandiculation in other body regions (Bertolini and Gessa, 1981; Lehmann, 1979; Urba-Holmgren et al., 1977) the combined behavior is referred to as the *stretch-yawning syndrome* (SYS).

SYS has been associated with the arousal function, as it seems to reset the central nervous system to the waking state after a period of sleep and prepare the animal to respond to environmental stimuli (Walusinski, 2006).

This paper explores the hypothesis that the SYS might also have an auto-regulatory role regarding the locomotor system: to maintain the animal's ability to express coordinated and integrated movement by regularly restoring and resetting the structural and functional equilibrium of the myofascial system. It is now recognized that the myofascial system is integrative, linking body parts, as the force of a muscle is transmitted *via* the fascial structures well beyond the tendonous attachments of the muscle itself (Huijing and Jaspers, 2005). It is argued here that pandiculation might preserve the integrative role of the myofascial system by (a) developing and maintaining appropriate physiological fascial interconnections and (b) modulating the pre-stress state of the myofascial system by regularly activating the tonic musculature.

The ideas presented here initially arose from clinical observations during the practice of a manual therapy called Muscular Repositioning (MR) (Bertolucci, 2008; Bertolucci and Kozasa, 2010a; Bertolucci, 2010b). These observations were supplemented by a review of the literature on the subject.

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A possible link between MR and SYS is presented: The neural reflexes characteristically evoked through MR are reminiscent of SYS, which both suggests that MR might stimulate parts of the SYS reaction, and also points to one of MR's possible mechanisms of action.

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Note on terminology

Pandiculation (from the Latin: *pandicare* = stretching) is most often used to denote both the yawning and the involuntary stretching of somatic muscles, which together characterize the stretch-yawning syndrome (SYS). Though the yawn and the stretch are associated phenomena, each can occur independent of the other. Most studies about SYS focus on yawning, although the oft-accompanying stretch is occasionally described. It is less common for studies focus on the stretch component alone. In this text, SYS will be used to denote the combined behavior, while pandiculation will be used to denote the stretch behavior by itself.¹ Although such use is not the most common, the author rejected the term stretch to denote the involuntary stretching part of the SYS because it can be confused with voluntary muscle lengthening, which is part of a wide range of sports and bodywork activities, and is an entirely distinguishable phenomenon.

¹ Where other authors are quoted directly, the terminology is their own.

Pandiculation: determining and maintaining neural circuitry and peripheral motor effectors

Pandiculation is an old and almost ubiquitous behavior that occurs in similar form and circumstances across a wide spectrum of species (Baenninger, 1997). The regularity and vigor of pandiculatory movements suggest that they might be physiologically significant. Walusinski notes that according to Darwin's concepts, the cost of a behavior with high metabolic demand is likely to be outweighed by some adaptive benefit (Walusinski, 2006).

Indeed, the phylogeny and ontogeny of pandiculation reveal its likely role in the development and maintenance of motor function, in both its structural and neural aspects. Fraser (Fraser, 1989a), in connection with ultrasound fetal studies on sheep, refers to fetal pandiculation as a mechanism that influences functional determination of the moving parts of the musculoskeletal system and contributes to articular development and maintenance. He also identifies a bodily care and self-maintenance function of pandiculation, which restores muscle homeostasis in poultry, dogs, cats and horses, among other animals (Fraser, 1989a). In ostriches, a similar "maintenance" pandiculation has been described by Sauer and Sauer (Sauer and Sauer, 1967).

In man, pandiculation is also ontogenetically precocious, starting as early as 12 weeks of gestation (de Vries et al., 1982). It has been associated with the development of motor neural circuitry (Lagercrantz and Ringsted, 2001; Marder and Rehm, 2005; Briscoe and Wilkinson, 2004) and associated musculoskeletal effectors (de Vries et al., 1982; Walusinski et al., 2005). In fact, individual muscles are differentiated from primitive mesodermal condensations only after the establishment of their neural connections (Sadler, 1995), based on their specific motor actions, as discussed below:

Muscle development begins with primitive *myoblasts*, which aggregate and give rise to the *primary myotubes*. Around the 10th week of gestation, the primary myotubes

are invaded by spinal cord motor neurons, which give the primary myotubes contractile capacity. Within the primary myotubes, additional myoblasts aggregate, eventually giving rise to *secondary myotubes*, both sharing the same basement membrane at this stage. Later in fetal development, the secondary myotubes connect with tendon structures, at which time they develop their own basement membranes and become independent structures (Jones et al., 2004).

The differentiation of primary and secondary myotubes into discrete motor unit populations is implied by the differentiation of separate encasing fascial layers and gliding interfaces, which enclose and allow independent motion of their contents; *i.e.*, discrete fascial linings - and the areolar matrices between them, which allow them to glide against each other - are established upon functional grounds.

Such mechanical-structural coupling is not confined to soft tissues; it can be extended to bone (Wolff, 1986), joint surface shapes (Kapandji, 1987) and virtually every tissue under mechanical stress (Moore, 2003; Silver et al., 2003). Besides shape, the *molecular compositions* of musculoskeletal structures are also functionally determined, involving the phenomenon of mechanotransduction (Ingber, 2006; Stevens-Tuttle et al., 2008; Banes et al., 1999), further discussed below.

In summary of the above, repetitive motion gradually determines shapes and compositions of moving structures, as well as their associated neural control pathways. The precociousness and stability of pandiculation suggest its contribution to such development.

Neuropharmacology and neurophysiology of SYS: an arousal function?

The SYS has been associated with the maintenance of arousal and attention; *i.e.*, it sets and maintains the central nervous and locomotor systems so that the animal is able to perceive environmental stimuli and respond to them with

appropriate motor actions (Baenninger, 1997; Walusinski, 2006; Askenasy, 1989).

Although no particular cerebral structure has been definitively associated with yawning (Argiolas and Melis, 1998), because yawning is seen in anencephalic newborns with only the medulla oblongata (Heusner, 1946), the brainstem appears to be involved. In addition, pharmacological and clinical evidence suggests the involvement of the hypothalamus, bulbous and pons. Since the 1960s, injection of various substances (e.g., adrenocorticotropin [ACTH], α -melanocyte stimulating hormone [α -MSH] and related peptides) into the CNS, has been shown to stimulate SYS activity in laboratory animals (Argiolas and Melis, 1998). More recently, it has been shown that rats' stereotypical yawning, including trunk stretching (SYS), can be triggered by stimulation of the paraventricular nucleus (PVN) of the hypothalamus *via* electrical or chemical (nitric oxide-releasing compounds) means (Sato-Suzuki et al., 1998).

Today, it is commonly believed that, once stimulated, PVN oxytocinergic neurons release oxytocin into extra-hypothalamic structures; and that these structures, in turn, mediate SYS and arousal responses (Walusinski, 2006). As SYS involves various behavioral and autonomic events, it is assumed that the PVN integrates the outputs of various origins and creates efferents on at least five different levels: respiratory, cardiovascular, facial motor, spinal motor and arousal systems (Sato-Suzuki et al., 1998), which are responsible, respectively, for the reactions of deep breath, drop in blood pressure, mouth opening, trunk stretching, and arousal response. Other neurotransmitters, including orexins, acetylcholine, dopamine, serotonin, and opioid peptides have also been shown to mediate the expression of SYS behavior (Argiolas and Melis, 1998; Sato-Suzuki et al., 2002).



Figure 2 Yawning is commonly accompanied by pandiculation of the upper extremities.

Sato-Suzuki's model on yawning/arousal responses in rats illustrates the main CNS pathways possibly involved in SYS (Sato-Suzuki et al., 2002) (Fig. 1).

Pandiculation can be considered a Modal Action Pattern (MAP) (Rosenbloom, 1994), an orderly sequence of reflexive behaviors, within which category evolutionarily important instinctual activities such as feeding, mating and other social behaviors important to survival are classified. As such, pandiculation seems to be elicited by complex array or sequence of stimuli, which might include both exteroceptive signals (e.g., light-darkness) and interoceptive ones (e.g., circadian endocrine cycles and somatic interoception) (Walusinski, 2006).

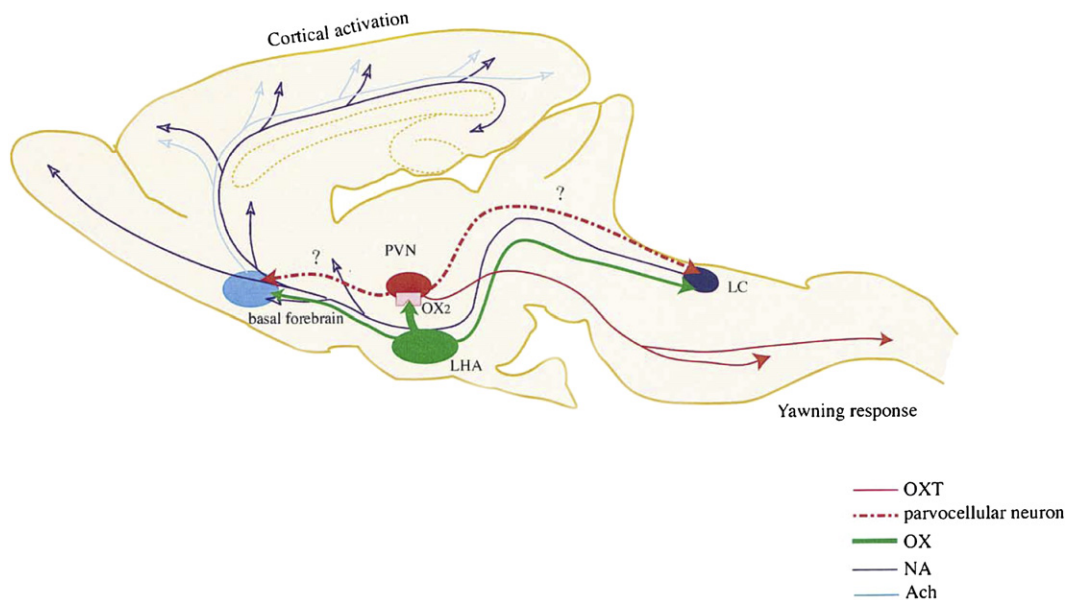


Figure 1 Schematic representation of Sato-Suzuki's model on yawning/arousal responses mediated through the PVN in rats. Orexin neurons from the lateral hypothalamic area (LHA) may directly activate neurons in the paraventricular nucleus (PVN), which in turn project to the locus coeruleus (LC) or the basal forebrain. Oxytocinergic neurons from the PVN project to the lower brainstem, including the facial nucleus and respiratory related neurons which are implicated in the yawning response. OXT, oxytocin; OX, orexin; NA, noradrenaline; Ach, acetylcholine. Reprinted with permission from: Ikuko Sato-Suzuki, Ichiro Kita, Yoshinari Seki, Mitsugu Oguri, Hideho Arita. Behavioural Brain Research 128 (2002) 169–177 Cortical arousal induced by microinjection of orexins into the paraventricular nucleus of the rat.

SYS phenotype

The SYS has a similar and stereotyped phenotype along the evolutionary scale, having remained virtually unchanged. Yawning (Fig. 2) starts with a long and deep inhale, reaches a peak, and concludes with a short exhale. Respiratory, mouth, neck and upper spine muscles engage in co-contraction, simultaneously stiffening the joints and stretching the myofascial tissues (Walusinski, 2006).

The few references to pandiculation in the existing literature describe it as a series of coordinated actions that unfold sequentially, building up soft tissue contractile tension to a peak, at which point the joints of the limbs and trunk are maximally extended – or, alternatively, the trunk is arched in flexion (Fraser, 1989b). After the peak, the soft tissue tension level plummets, yielding a sense of pleasure and well-being (See section on Pleasure, below). The actions can be regional or involve the whole body, and are often bilaterally symmetrical (Fraser, 1989b).

SYS: compensatory response to temporary stiffness or immobility?

The patterns of full body pandiculation are, in general, similar to the ones used in striding and righting behaviors (Fraser, 1989b) - *i.e.*, they emulate ordinary functional movements - while pandiculation of limited bodily regions seem to be a corrective response to the stiffness induced by temporary positional stress or immobility.

During *turnover metabolism* extracellular matrix (ECM) components are continuously both reabsorbed and synthesized. Molecular interactions between glycosaminoglycans (GAGs), fibers and other components continuously change structural mechanical properties. The weaving of proto-collagen monomers into fibers is *spontaneous*, driven by hydrophilic interactions of hydrogen bonding between water and amino acid side chains. All that is necessary for this process are the physiologic conditions of temperature, pH, ionic strength and degree of hydration (Leikin et al., 1995; Giraud-Guille et al., 2003).

Mechanical stresses are the main determinants of form and relationship in this continuous and spontaneous re-weaving; *i.e.*, movement is crucial to the maintenance of the appropriate form and function of the ECM (Kjær et al., 2005, 2006, 2009; Tomiosso et al., 2005). For example, dense tissue is deposited in response to the mechanical need for tensional resistance, while areolar tissue is renewed where gliding is required. Without mechanical input, the ECM would be laid down amorphyously and its configuration would not meet physiological requirements.

For the configuration of the ECM to be physiologically appropriate, the mechanical input that stimulates it must first be appropriate. For example, a long striding movement will remain possible only to the extent it is *sufficiently* expressed, because only such expression will stimulate a supportive ECM configuration (Kjær, 2004; Kjær et al., 2009, Heinemeier et al., 2007).

But, most of the time, animals are *not* expressing their optimal qualities of movement, such as running at maximum speeds and attaining maximum range of movement (ROM) in the joints. What's more, sleep imposes a regular period of

immobilization, to which the patterns of collagen weaving and ECM relationships will accommodate. This suggests a continual tendency to "tie up" the animal's entire structure: cross-linking of collagen fibers directed by sub-optimal movements can limit function by diminishing (a) tissue length and strength and (b) the internal gliding capacity between parts necessary for attaining optimal motor potential. Unless it is counteracted, this process could lead to progressive loss of ROM in the joints and stiffening of tissues, both of which might compromise tissue health by restricting fluid distribution and distorting cell shape - and thus inhibiting appropriate gene expression. The mechanically driven modulation of genetic activity will be further discussed in the section on Mechanotransduction, below.

Pandiculation, with its specific and vigorous muscle activity, might be a means to compensate for the mechanical signals delivered by rest periods and sub-optimal movements. Fraser mentions, in connection with his studies of pandiculation among various species, that it might be considered a feedback from stiffness, and possibly be triggered by extended periods of immobility in asymmetrical positions. He concludes that if the body tends to stiffen, pandiculation "can serve to restore the limb (and related musculature) to an original (homeostatic) state (Fraser, 1989a, 1989b)". In fact, SYS has much in common with other homeostatic functions, as discussed immediately below.

Emotional motor systems and SYS

In humans, voluntary motricity involves the concerted activity of all constituents of the motor system. Movement planning is translated into actual motor responses through a chain of neural activity that starts at the prefrontal cortex, and then reaches the premotor area and the primary motor cortex sequentially (Kandel et al., 2000; Hallett, 2007). Neurons in the primary motor cortex project their axons directly to motor neurons *via* the *cortico-spinal tract*. As these axons descend, they form the *medullary pyramids*; thus, the entire projection is also called the *pyramidal tract*. The motor information the pyramidal tract carries is modulated not only by sensory information, but also by information from lower motor regions (basal ganglia, thalamus, midbrain, cerebellum, spinal cord), which information allows voluntary movements to be smooth, precise and well coordinated (Kandel et al., 2000). The modulation of information in the pyramidal tract is mainly unconscious and automatic; *i.e.*, the subcortical centers provide the unconscious, involuntary and patterned components essential to movement control (Jacobs and Horak, 2007; Guyton and Hall, 2006; Takakusaki et al., 2003), in contrast to the volitional components of motor action governed by the cortical centers.

In general, the lower the structure, the simpler the motor information it conveys. For example, the spinal cord is at the lowest level; and the information it conveys serves to mediate simple reflexes related to rhythmic automatisms such as locomotion and scratching. Higher centers mediate more complex motor activity in a hierarchical organization of complexity (Kandel et al., 2000). For example, while lesions of the primary motor cortex can produce *contralateral*

hemiplegia in humans, some postural and stereotyped involuntary movements may be preserved (Kandel et al., 2000).

Similarly, components of certain instinctual behaviors can be executed without the intervention or modulation by the cortical centers. Instinctual behaviors evolved to guarantee the continuity of organisms' lineages, maintain internal homeostasis, and insure successful breeding (Dentona et al., 2009). They are mediated primarily by the limbic system and include those life-supporting activities (e.g., feeding, self-defense, sex) collectively named *emotional behaviors* (Guyton and Hall, 2006; Kandel et al., 2000).

In experimental animal models, stimulation of limbic structures, notably the hypothalamus and the amygdala, has elicited various emotional behaviors (Kandel et al., 2000; Guyton and Hall, 2006). - even in the absence of the cerebral cortex. For example, after decortication, an investigative procedure in which the connections between cortical and subcortical structures are severed, the latter continue to function without inhibitory influence of the former. Decorticated animals can feed themselves, express rage and fight, and have sexual intercourse (Magoun and Ranson, 1938; Smith, 1939; Guyton and Hall, 2006), which shows that the limbic system can produce such behaviors in the absence of cortical participation.

In fact, the limbic system sends diffuse and innumerable projections to the medulla. It is a system unto itself, able to produce motor activity independent of the voluntarily driven pyramidal system. Holtstege describes it as the *emotional motor system* because limbically regulated behaviors depend on the emotional state of the animal. The functions governed by the limbic system include different types of involuntary movements associated with olfaction and eating, such as licking, chewing, and swallowing; clonic and rhythmic movements (e.g., locomotion, shivering); sexual function; vocalization, laughing, and crying; and defense reflexes, among others (Guyton and Hall, 2006; Holstege, 1992). Indeed, in laboratory animals various stereotyped behaviors have been reproduced with electrical or chemical stimulation of mesencephalic nuclei, particularly the PVN (paraventricular nucleus) of the hypothalamus. Chewing, licking, lordosis in females, penile erection, and grooming have been observed (Argiolas et al., 2000; De Wied, 1999; Vergoni et al., 1998). The SYS is among these behaviors produced by the limbic system, and its phylogenetic longevity suggests an adaptive function.

One function of the PVN is to integrate the central and peripheral autonomic systems. The PVN projects onto *all* autonomic neurons in the brainstem and spinal cord, given that it is involved in various autonomic and endocrine functions relative to the maintenance of homeostasis (Kandel et al., 2000). These functions include: production of cortisol *via* secretion of corticotropin-releasing factor (CRF); production of oxytocin and vasopressin (hormones involved in milk production and water balance respectively); and regulation of factors such as food intake, heart rate, and blood pressure (Kandel et al., 2000; Holstege, 1992). That the SYS is mediated by the PVN suggests that the SYS might serve some general homeostatic function, which functions are carried out autonomously by the emotional motor system.

In man, the workings of the emotional motor system are illustrated by the involuntary movements of patients with

voluntary motor pathway lesions. For instance, when hemiplegic patients yawn, they have been observed to raise involuntarily an otherwise plegic arm (Graham, 1982; Töpper et al., 2003; Stewart, 1921), with the muscles of the paralyzed limb activated nearly as much as those of a normal limb would be in a voluntary movement (Omam et al., 1989). Also observed in hemiplegic patients are sinkinesias, in which voluntary movement of one part produces involuntary movement of another; e.g., thigh flexion and arm abduction during sneezing, or arm movements during micturition (Walshe, 1923). Similarly, patients with voluntary facial palsy show facial movements while laughing (Hopf et al., 1992; Töpper et al., 1995; Chernev et al., 2009), and patients incapable of voluntarily opening their mouths do indeed open them while yawning (Askenasy, 1989).

Taken together, the experimental and clinical observations summarized above illustrate that automatic (emotional) motor behaviors can express their patterns independent of the voluntary somato-motor system. Because in normal subjects the former is under the inhibitory influence of the latter (Marder and Rehm, 2005; Pincus and Tucker, 1974), involuntary limbic behaviors tend to appear when volitional motor circuits are damaged - naturally (as in hemiplegia) or artificially (as in decortication). The fact that normal human motor behavior includes the modulation of instinctual drives (Smith, 1992) might explain why SYS behavior tends to decrease as the person ages.

Pandiculation versus ordinary stretching: automatic versus volitional motor actions

If we attend to our interoceptive sensations, our experience tells us that pandiculation and SYS exhibit peculiar motor recruitment. If one "yawns" on purpose, one's internal sensations are quite different from those elicited by a spontaneous yawn. Similarly, the sensations produced by spontaneous pandiculation are different from those that accompany either "volitional pandiculation" or volitional soft tissue stretching.

The patterns of volitional stretching are cognitively established and the action purposely performed. They often involve relaxation of the muscles through a diminution of their actions: the subject muscle is elongated *passively*, as a result of either gravity or the activity of opposing muscles.

By contrast, the patterns of pandiculation are automatic. Through intense and involuntary deep muscle co-contractions, the soft tissues *actively* elongate themselves against the bony structures as the joints are stiffened. Each movement within the pattern emerges in sequence, apparently from the recruitment of a mosaic of reflexes, the sequence of which can neither be anticipated nor purposely performed. Just as a spontaneous yawn feels quite different from a deliberate imitation of one, spontaneous pandiculation feels quite different from a voluntary pandiculation-like stretch. Because the voluntary and emotional motor systems have discrete neural pathways, pandiculation's distinctive internal sensations might be attributable to the motor unit recruitment sequences dedicated to automatic movement patterns. Indeed, the

contrast between interoceptive experiences during automatic versus volitional motor actions has been documented (Hommel, 2009). What's more, operation of the hierarchically higher volitional system can inhibit that of the lower automatic system; this inhibition can disrupt the characteristic spontaneity of the SYS in favor of a cognitively directed stretch.

Automatic arm abduction during yawning in hemiplegia shows the non-volitional nature of SYS: the patients did not show any arm movement when they *imitated* a yawn (Töpper et al., 2003). In other words, voluntarily imitation of the automatic motor pattern (*via* the cortico-spinal system) will not reproduce immediately the instinctive patterns originated in the limbic system (*via* the emotional motor system). Moreover, if the motor patterns are discrete, their physiological effects should be discrete, as well.

The importance of stretching to the maintenance of musculoskeletal health is well-known. In humans, each of the myriad of physical fitness regimens that include stretching has its own rationale; and although all muscle groups should be stretched, different regimens address particular problems and are intended to compensate for various patterns of muscle shortness or consequent joint mobility restriction. But how do animals in the wild maintain musculoskeletal health? They perform no voluntary stretching and still maintain their motor capabilities. Might SYS be responsible?

If so, and if it were possible to stimulate SYS, might SYS be employed to achieve therapeutic goals? Various somatic practices encourage the SYS because of its apparent homeostatic effects, e.g., Hanna Somatics, Joyflexing, Eutonia (Hanna, 2004; Johnson, 2002; Vishnivetz, 1995). In Eutonia, the SYS is observed to be evoked by certain attentional states and forms of mechanical stimulation. Similarly, the specific mechanical stimulation of Muscle Repositioning might also stimulate the SYS. (see section on responses induced by MR, below).

Pleasure and health

Ancient biological behaviors associated with the maintenance of homeostasis are directed through interoception - the sensory experience reflective of the physiological condition (Craig, 2003). Sensory experiences of displeasure and pleasure define the *affective* qualities of stimuli, which influence an animal's behavior (Guyton and Hall, 2006; Bozarth, 1994). The *positive affects* of pleasurable experiences support many life-supporting behaviors: satisfaction of hunger and thirst, sexual intercourse, and vesicle and bowel evacuation are examples of instinctive behaviors that, once accomplished, reward the animal with an experience of pleasure, which biologically reinforces their expression. Preservation of health (salutogenesis) is intimately linked to the perception of positive affects (Esch and Stefano, 2004). Such *positive affect* states are closely related to ancient sub-neocortical limbic brain regions common among humans and other mammals, in which various neuropeptides appear to mediate homeostatic satisfactions (Burgdorf and Panksepp, 2006; Vincent, 1994; Cabanac, 1992).

The instinctive behaviors, contributing as they do to the maintenance of the internal milieu, can be considered

homeostatic drives (Sherwood, 2010), a category within which pandiculation may also be included. Not only has pandiculation been associated with pleasure and well-being (Fraser, 1989a; Sauer and Sauer, 1967; Russel and Fernandez-Doz, 1997; Walusinski, 2006; Steward, 1921), but it also shares with the other homeostatic drives involvement of the PVN nucleus of the hypothalamus. Homeostasis is maintained chiefly by the parasympathetic division of the autonomic nervous system (Recordati and Bellini, 2004), and increased parasympathetic activity has been detected during SYS (Askenasy and Askenasy, 1996).

What's more, the frequency of SYS is correlated with degrees of health or convalescence: Fraser (Fraser, 1989b) notes that pandiculation is absent in animals with some systemic illnesses, but returns as the animal recovers. Similarly, in recovering hemiplegic patients, SYS and synkinesias characteristically re-emerge (Töpper et al., 2003; Hwang et al., 2005) in advance of voluntary limb movements. Notably, patterns of involuntary synkinesias have been proposed as a parameter for assessment of post-stroke hemiparesis recovery, as the timing of how the patterns emerge seems to be related to the patient's functional outcomes (Hwang et al., 2005). During coma, yawning foretells the approach of wakefulness (Braunwald et al., 1987). Therapeutic application of transcranial electromagnetic fields in the treatment of Parkinson's disease and multiple sclerosis has elicited SYS. In a multiple sclerosis investigation, SYS reappeared in those patients whose disease had gone into remission in response to treatment (Sandyk 1999, Sandyk, 1998).

However, excessive pandiculation is associated with certain diseases and the use of certain drugs (Askenasy, 1989). This suggests a possible distinction between a complete (and successful) and an incomplete (and unsuccessful) pandiculation. Perhaps the former, having fulfilled its purpose, physiologically recurs; while the latter, seeking completion, pathologically repeats. Consider, for example, the palpable frustration that accompanies the interruption of a yawn or sneeze!

Mechanotransduction, tensegrity and health

Arguably, a cell's function is fundamentally dependent on its shape. No longer considered mere gelatinous cytoplasm enveloped by a flexible membrane, the cell is now believed to be structured by an internal cytoskeleton consisting of a complex array of microtubules and microfilaments (Ingber, 2008a). Mechanical stimuli govern the synthesis of the cytoskeleton, which determines the cell's form (Patwari and Lee, 2008; Bischofs et al., 2008). What's more, mechanical links between the cytoskeleton, on the one hand, and cellular components such as protein synthesis machinery (e.g., ribosomes and mRNA) and membrane receptors, on the other hand, mechanically modulate the components' functions by a mechanism known as *mechanotransduction* (Ingber, 2008b; Bischofs et al., 2008; Chiquet et al., 2009). Through mechanotransduction, mechanical stimuli are transduced into chemical responses (Humphrey and Delange, 2004), such as protein synthesis. By modulating gene expression, the activity of membrane surface receptors and ion channels, and related cellular

functions, mechanical forces govern the cell's development, maintenance, functions and fate (e.g., Dahl et al., 2010; Chiquet et al., 2009; Patwari and Lee, 2008; Haudenschild et al., 2009).

A cell's shape, molecular constitution and functions reflect the mechanical stresses put upon it. For example, in response to particular dynamic mechanical load patterns, human mesenchymal stem cells enable distinctive gene expression patterns, which in turn produce changes in cell shape and volume (Haudenschild et al., 2009). It appears that each tissue is developed and maintained to bear the stresses to which it is exposed; e.g., tension stimulates both fibroblastic and osteogenic genes, while compression stimulates genes associated with chondrogenesis (Haudenschild et al., 2009). Evidence suggests that mechanical stimuli alone can even help a genomic-defective cell to attain a normal phenotype (Gieni et Hendzel, 2008).

But because cells are not isolated, cell shape is also influenced by the cell's relationship to the extracellular matrix (ECM) surrounding it. Through interactions at adhesive sites on the cell membrane, components of the ECM affect the net mechanical outcome of the externally acting forces (Streuli, 2009; Bischofs et al., 2008). For example, fibroblasts and other adherent cells sense the physical parameters (e.g., rigidity) of the ECM and modify their protein expression accordingly, and thus alter their own morphology (Döbereiner et al., 2005; Chiquet et al., 2009).

In connection with the influence of the ECM, note that it seems to behave as a liquid crystal (Giraud-Guille et al., 2003; Giraud-Guille, 1992; Bouligand, 1972; Kreis and Boesch, 1994). Therefore, the growth, shape and function of living tissue - not unlike those of macromolecular crystals produced in reactors - also seem to be governed by mechanical stimuli independent of biological activity (Lappa, 2003). Thus, mechanical stresses seem to direct the ECM's composition and form (and therefore the organism's shape and patterns of mobility) both biologically (*via* mechanotransduction) and non-biologically (*via* its liquid-crystalline properties).

Macroscopically, the ECM can be conceptualized as a fibrous skeleton (Bienfait, 1987) linked to the bony skeleton. These two skeletons are believed to constitute a *tensegrity* structure (Ingber, 2008a, 1998): the bones, which resist compression, maintain the distance between joints and counteract the basal tension (pre-stress) imposed by the soft tissues. The soft tissues are the tensional elements, which maintain the relative positions of the bones. *Tensegrity* exists on smaller scales, as well; *i.e.*, structural hierarchies link the macroscopic assemblage of bones and soft tissue to the mechanosensitive cytoskeleton, which is linked to the cellular components governing gene expression (Ingber, 2006). Movement and posture - acting simultaneously in macroscale and microscale - mechanoregulate cell function and ECM form and relations (Kjær, 2004; Kjær et al., 2009; Heinemeier et al., 2007).

The variety of locomotion on display in any crowded street illustrates how individual human movement is. Within the wide variety of motor patterns, one observes *qualities* of movement: coordinated, fluid, and aligned movement, on the one hand - and encumbered, abrupt and

misaligned movement, on the other hand. Not all qualities of movement present equally beneficial stimuli for cell shape and function, and positive and negative stresses might play their parts in health and disease.

Perhaps optimal movement is that which properly distributes mechanical stress through the various tissues and cells, stimulating them according to their needs. Each cell requires particular mechanical stimuli to its normal function (Ingber, 2006), and the structural and mechanical characteristics of the ECM are the ever-changing products of the various mechanical stresses imposed upon it.

In short, the mechanical balance between hard and soft tissues dictates stress distribution, which plays a key role in cell shape and metabolism. In pandiculation, the intense mechanical stimuli produced by forceful co-contraction of antagonist muscle groups might serve as appropriate organizing signals to the cells and tissues by re-optimizing the mechanical conditions of their environment.

Optimal mechanical stimuli might maintain potential for optimal motor function

The vigorous mechanical stimulus of SYS produces maximum soft tissue span and joint extension, which, in turn, maximize body *dimensions*; e.g., yawning enhances pharyngeal diameter fourfold and separates vocal cords to a degree that "cannot be noticed in any other moment of life (Walusinski, 2006)". SYS might be a biological compensation for periods of immobility and/or vicious body positions, restoring the animal's mobility by breaking up abnormal ECM cross-links formed by inactivity or sub-optimal activity.

Abnormal ECM cross-links might shorten soft tissues and reduce internal lubrication, leading to motor rigidity. SYS might restore soft tissue length and normal internal gliding movements, at the same time as mechanotransduction maintains tissue composition by matching ECM constituents to the mechanical demands of the cells, thus protecting the cells from mechanical damage (Banes et al., 1999; Ingber, 2006).

SYS and arousal: restoration of postural tonus and tensegrity

Yawning is reportedly more common in carnivores, which exhibit pronounced cycles of rest and activity, than in herbivores, the behavior of which exhibits less frequent cycles of arousal (Baenninger, 1997). This is further evidence of the arousal function of SYS. Upon awakening, the reticular formation relays activating stimuli not only to the thalamo-cortical systems, but also to the postural and locomotor systems. This activation makes the fight-flight response readily available (Walusinski, 2006).

The fact that animals most often awaken immediately following REM sleep (which is characterized by muscle atonia), led Walusinsky (Walusinski, 2006) to postulate an opposing relationship between REM sleep and SYS, during which strong muscular contractions elicit an immediate shift of the previous neural patterns controlling the REM sleep, facilitating the appearance of a functional network appropriate for the control of the wakeful motor pattern.

Apparently, SYS restores to the myofascial system the elevated level of tonus required for activity in gravity: because in sleep the myofascia is slack and relaxed, the body segments must be *reassembled* upon awakening before the organism can move properly in the field of gravity.

In a tensegrity structure, the orderly distribution of pre-stress permits rapid mechanical communication throughout the entire body. Whatever the entry point and direction of an external mechanical stimulus, the reciprocal tensions within the body allow the stimulus to reach and affect mechanoreceptors throughout the entire system. A tensegrity structure thus exhibits much greater mechanosensitivity than a slack system, in which the influence of external stimuli remains local. The absence of slack in a well-balanced tensegrity structure also means that mechanical communication is virtually instantaneous. This facilitates fast and accurate motor responses (Ingber, 2006, Ingber, 2008b; Chen and Ingber, 1999), the adaptive value of which is evident. Such structural coupling among elements in a tensegrity structure, named “morphological communication”, has already been proposed even to assist in controlling movement, alongside the nervous system (Rieffel et al., 2010).

For the basal tension of a tensegrity structure to be efficiently distributed, the links among the tension elements must be precisely located. In addition, the compression elements must approximate *precisely* relative to each other, which requires both free articular ROM and free *gliding* among associated – and precisely located – myofascial structures. A functional combination of *linking* among *tensional* elements with *gliding* among *compressional* elements is essential to the “assembly” of bony and fibrous skeletons that exhibit full tensegrity properties. Each body form (particular arrangement of intersegmental relative positions) implies a certain combination of precisely located structural linking and gliding configurations to distribute pre-stress evenly. The immense variety of body forms that movement implies, each one affected by gravity, allows us to imagine how innumerable are the linking-gliding configurations.



Figure 3 Dogs often paniculate in this pattern of extension of the forelimbs and trunk; yawning is also frequently simultaneously present. Paniculation involves progressive co-contraction and stretching of soft tissues, which may extend to virtually every muscle in the body.



Figure 4 The downward dog yoga asana is reminiscent of a panting dog.

Perhaps the vigorous co-contractions of paniculation systematically reshape the structural linkage among segments and simultaneously signal the cells (*via* mechanotransduction) to synthesize the ECM components required to maintain the appropriate environment (Fig. 3). If so, paniculation might help restore optimal musculoskeletal arrangements, and thus optimize motor capabilities.

The paniculation connection: yoga and martial arts

The *downward dog* position (Fig. 4), like many yoga *asanas*, is reminiscent of an animal paniculation position (Iyengar, 1979). In fact, some say yoga is derived from *automatic* and *spontaneous* actions of sages deep in meditation, and that yoga should be practiced spontaneously (Muni, 1994). Eastern martial arts might also have a connection with paniculation. Qi Gong, for instance, requires the body to be fortified with automatic (involuntary) tonus in the deep postural muscles at the same time the superficial muscles associated with voluntary activity are relaxed (Fig. 5).



Figure 5 Qi Gong posture. The stretching of the whole myofascial system is reminiscent of paniculation.

Under these conditions, the body is integrated as a whole and all its parts relate with one another in movement (see http://www.caiwenyu.com.br/09_Fotos_p_ing.htm). These conditions cannot be produced by voluntary motor action, but emerge spontaneously with appropriate states of attention in which mechanosensing is enhanced. A person in such state could take advantage of elastic potential energy stored in the body when performing a blow. This characteristic of Qi Gong suggests a tensegrity-based mode of action with a high pre-stress level. In fact, potentiation of performance has already been shown in prestretched muscles, due to their ability to store potential elastic energy (Bosco et al., 2008; Ettema et al., 1990; Ishikawa et al., 2006).

Elements of martial arts training forms are often described in terms suggestive of animal pandiculatory patterns (Johnson, 2002). This invites reflection upon the fact that decorticated cats and dogs do exhibit instinctual behaviors, such as eating, copulating and fighting (Argyle, 1988); *i.e.*, that basic life-supporting behaviors can happen without cortical participation. In fact, fighting appears to be a largely reflexive behavior, the expression of which is associated with subcortical structures such as the hypothalamus and midbrain periaqueductal gray (PAG) (Ulrich and Azrin, 1962; Shaikh and Siegel, 1994).

Responses induced by MR might be similar to those of pandiculation

Like pandiculation, MR's manual local loading of the myofascial system integrates body parts, apparently by inducing co-contraction of opposing muscle groups (Bertolucci, 2008; Bertolucci and Kozasa 2010a, Bertolucci, 2010b), at the same time as it evokes a measurable rise in tonic muscle activity indicative of an overall increase in load. The client's subjective experience is similar to that evoked by pandiculation, which suggests a common element among pandiculation, yoga and martial arts and MR.

In pandiculation, muscle activation begins locally and spreads to neighboring areas until it reaches a peak of distribution and intensity; *i.e.*, joints progressively stiffen through a chain of reflexes, in which neighboring segments are sequentially engaged to form an ever-larger block that eventually encompasses the entire body. Following the peak, the tissues release.

MR induces a similar progressive engagement of body segments. The inclusion of each segment increases the overall tension within the block until, following the peak, the practitioner feels an abrupt soft tissue release. The progressive segmental engagement is paralleled by an increasing involuntary tonic muscle activity observable both by palpation and by electromyography (Bertolucci, 2008; Bertolucci and Kozasa, 2010a; Bertolucci, 2010b).

Let us imagine how it might be that MR and pandiculation would evoke similar muscle activity. The author hypothesizes that the manual forces applied during MR maneuvers mimic internal forces, and therefore induce mechanoreceptor afferents, similar to those characteristic of pandiculation.

In the clinical setting, recipients of MR treatments have exhibited spontaneous pandiculation-like movements (see

videos at <http://musclerepositioning.blogspot.com/>), and have described their subjective experiences during MR as similar to their experiences during pandiculation. Some clients also report having resumed the habit of pandiculating in the morning, to which they attribute a greater sense of bodily well-being along with relief from musculoskeletal symptoms. These observations support the hypothesis of a similarity between MR and pandiculation.

Perhaps MR is a blend of myofascial release and "assisted pandiculation", with the soft tissue release evoked by a combination of the practitioner's manual input and the internally generated forces of tonic pandiculation-like reactions. This combination of forces might produce a greater effect in the soft tissues than either manual input or pandiculation alone.

Is SYS culturally inhibited?

SYS recruits the medullar, genetically determined Central Pattern Generators which, in higher primates, are under neocortical control (Marder and Rehm, 2005). Humans, unlike other primates, have been observed to yawn less frequently as they age (Walusinski et al., 2005); however, in various old world monkeys (*Cercocebus albigena*, *Macaca fuscata* and *Macaca fascicularis*) yawning has been shown to become more frequent as plasma androgen levels increase (Deputte, 1994; Troisi et al., 1990).

As yawning has negative social connotations in most cultures and religious traditions (Walusinski et al., 2010), perhaps cultural conditioning inhibits the SYS in humans. Given the likely homeostatic function of SYS, any such inhibition might contribute to the high incidence of human musculoskeletal disorders.

Biological clocks and health

Maintenance of homeostasis is closely related to biological rhythms, which are controlled by both environmental and endogenous stimuli (Aréchiga, 2003). Biological rhythms are generated by intracellular mechanisms called *circadian clocks*, which are present in both specific CNS centers and most peripheral tissues (Duguay and Cermakian, 2009; Aréchiga, 2003). In particular, they are present in fibroblasts, the cells responsible for the synthesis of ECM constituents. The intrinsic biological rhythms of fibroblasts have been shown to be involved in various metabolic functions (*e.g.*, cytoskeleton protein synthesis, cell cycle control and enzyme synthesis, among others) (Bursian, 2009). While the fibroblast's metabolic machinery has a rhythm of its own, it is at the same time influenced by mechanical stimuli – including, presumably, those generated through other biological rhythms. This raises the question of whether various biological rhythms mutually influence each other.

It is already known that various biological rhythms are related: *e.g.*, heart rate, respiration, and periodic somatomotor excitation have been shown to interact (De Haro and Panda, 2006 Niizeki et al., 1993). The existence of such complex relationships among biological rhythms led to the concept of *multi-oscillatory systems*, as well as the hypothesis that synchronization among various co-existing

rhythms is a determinant of gene expression and biological activity in both plants and animals (Lloyd, 2009; Bell-Pedersen et al., 2005). Quite possibly, the circadian clocks intrinsic to the fibroblasts might correlate regularly with other bio-cyclical phenomena such as the sleep-wake transition associated with SYS.

Sleep-wake and other biological rhythms have already been shown to be related to the immune response (Shepard and Shek, 1997), which indicates their importance to general health and inspires further study as to the possible role of rhythmic activities (such as SYS) in the maintenance of homeostasis in both particular tissues and in the organism as a whole. Tissue microdialysis, serum metabolic-tracers, neuroimaging, EEG and EMG are all possible resources for further investigation of the physiological role of SYS.

Conclusion

The concept of myofascial force transmission (Huijting and Jaspers, 2005) assumes the presence of ECM links among musculoskeletal components, which links unite those components into an integrated system; *i.e.*, the fascia itself is assumed to play an integrative role. Integrated movement *both requires and stimulates* appropriate matrix connections. However, animals engage in a great deal of non-optimal movement, of which immobilization (*e.g.*, during sleep), trauma and bad postural habits are among the causes.

Should normal activities generate both “good” and “bad” mechanical signals to the ECM, the bad signals would need to be countermanded by good ones for the animal to maintain full movement capabilities throughout life. Pandiculation might provide one source of good signals by (i) breaking bad connections while stimulating better ones, and (ii) resetting postural muscle tonus to produce integrated movement, which movement is a further source of good mechanical signals. In short, pandiculation might be a form of neuro-myofascial hygiene.

If this be true, might we encourage pandiculation to enhance general health? This would require a reassessment of the cultural stigma against yawning and pandiculation, as well as further investigation of therapeutic approaches, such as Muscle Repositioning, that seem to stimulate it.

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