Abstract: I discuss some concepts advanced for the understanding of the complex dynamics of brain functions, and relate them to approaches in affective, cognitive and action neurosciences. These functions involve neuro-glial interactions in a dynamic system that receives sensory signals from the outside of the central nervous system, processes information in frequency, amplitude and phase-modulated electrochemical waves, and control muscles and glands to generate behavioral patterns. The astrocyte network is in charge of controlling global electrochemical homeostasis, and Hodgkin–Huxley dynamics drive the bioelectric homeostasis of single neurons. In elastic processes, perturbations cause instability, but the system returns to the basal equilibrium. In allostatic processes, perturbations elicit a response from the system, reacting to the deviation and driving the system to stable states far from the homeostatic equilibrium. When the system does not return to a fixed point or region of the state space, the process is called homeorhetic, and may present two types of evolution: (a) In flexible processes, there are previously existing “attractor” stable states that may be achieved after the perturbation, depending on context; (b) In plastic processes, the homeostatic set point(s) is(are) changed; the system is in a process of adaptation, in which the allostatic forces do not drive it back to the previous set point, but project to the new one. In the temporal phase from the deviant state to the recovery of stability, the system generates sensations that indicate if the recovery is successful (pleasure-like sensations) or if there is a failure (pain-like sensations).

Keywords: homeostasis; homeorhesis; allostatic; elasticity; flexibility; plasticity; brain function; orienting response

1. Introduction

Investigation of the local and global temporal dynamics of neural tissue is necessary for scientific and technological approaches to brain function. Understanding the role of the central nervous system (CNS) in perception-action cycles, generating conscious sensations (named qualia in the psycho-physical and philosophical literature) is also necessary for the study of behavior, involving the whole living body in the interaction with the changing physical and social environment.

The current state of investigation of temporal brain dynamics benefits from the discovery of astrocytes as being responsible for the control of brain global homeostasis [1]. In the human brain, external signals captured by sensors are sent to neuronal sensory networks and processed feed-forward to other neuronal systems, reaching parietal, temporal, and frontal ‘associative areas’ and the motor system, which initiates voluntary actions. A large number of synapses are tripartite [2], including one astrocyte together with two communicating neurons. The transmitters released by the pre-synaptic neuron also reach the astrocyte, binding with metabotropic receptors, activating signaling pathways that induce the formation of calcium waves [3,4] by releasing the ions from the endoplasmic reticulum and propagation through gap junctions gated by connexins [5].

Besides this interaction with the environment, the SNC also interacts with the whole body in interoceptive cycles [6] mediated by neural and blood signaling, providing the SNC with ‘somatic markers’ [7]. The combination of perception-action with proprioceptive
cycles generates temporal processes with different phases, depending on the epigenetic history of the living individual, contextual initial and boundary conditions.

Homeostasis, in this context, refers to a basal “set point” or equilibrium class of states of the CNS that compose, in elastic systems, the initial and putative target of the temporal process. Within the process, there are other phases to be considered; the phase corresponding to the deviation from equilibrium, and the phase of return to equilibrium, when an “orienting” response [8] is generated by the system, corresponding to a sensation [9] that helps to guide the process of homeostasis recovery.

There are conceptual and semantic issues in the neurosciences regarding the understanding of the “quality” of the orienting response. This response is a subjective experience of the system that is not accessible to the external, scientific observer. Besides many philosophical attempts to understand qualia, here, I put the emphasis on the efforts of neuroscientists such as Walter Freeman [10], Jaak Panksepp [11] and Antonio Damásio [12] to approach this issue, by means of concepts such as “meaning”, “affect” and “feeling”, respectively. In this paper, instead of a speculative view, I relate this type of subjective experience with a phase in the temporal dynamics of the CNS.

The astrocyte network controls global brain electrochemical homeostasis [1], while the Hodgkin–Huxley dynamics of depolarization and repolarization drives the bioelectric homeostasis of single neurons generating action potentials at the axon hillock. In complex systems as the brain, there may exist several stable regions of the state space (‘attractors’), in which the system may rest far from the homeostatic equilibrium region. In this type of situation, we refer to a flexible system, instead of the elastic one. Furthermore, the system shaped by a series of changes affecting the molecular structure and functions and instantiating new stable regions is a plastic one. During development, there are changes in the state space of the system [13], implying changes in the distribution of set points; these changes are often labeled as “neural plasticity” [14]. In terms of dynamical systems theory, there is a change in the class of ‘attractor regions’ [15] of the state space, forcing the system to become adapted to new patterns of stability.

The theoretical framework I propose here is that the physiological dynamics of neural systems can basically be homeostatic (attached to an equilibrium point or region), or homeorhetic [16], when the dynamics drive the system away from the equilibrium point or region. Allostasis, in this context, refers to types of processes when homeorhesis leads to a new stable region of the system’s state space. The temporal dynamics of the CNS after a perturbation may be elastic, when the process is strictly homeostatic; or flexible and/or plastic, when the process is allostatic. In the cases of flexible systems, the new stable region that is reached is a previously existing one that was kept “recessive”. In the case of plastic systems, a new stable region is built by the process of interaction of the system with the whole body and environment.

2. Signals, Homeostasis and Sensations: Orienting Reflex and Projective Models

Signal processes in the CNS may be generated internally or externally of neural tissues. Each signal elicits a response from the tissue, which can be bioelectrical (ionic waves, spikes), chemical (release to transmitters, hormones) or molecular (activation of signal-transduction pathways by means of electrostatic protein conformation changes). The incoming signal perturbs the previous basal homeostatic state, causing a response that tends to drive the system back to homeostasis. This response and the resulting process back to stability are based on signaling processes and physiological responses.

In this temporal process, “differences make differences”. The first differences are differences within the signals (non-redundancy), and the second difference is the deviation from homeostasis caused by the signal. The sentient [9] capacity of neural systems depends on the process during which sensations emerge, corresponding to a phase in the process of allostasis. A perturbation (difference in stimulation) causes a deviation from homeostasis (difference in physiological activity), to which the system reacts by returning to the homeostatic basal state. At this moment, sensations are experienced together with the effort
to return to homeostasis. If the system is successful (e.g., drinking water to satiety), then sensations are “positive” (pleasure-like); but if the system fails (e.g., continued lesion of tissue) then sensations are “negative” (pain-like).

A crucial step in understanding the dynamics of allostasis and generation of sensations was initially given by Sokolov’s observation that the presentation of a habitual stimulus does not elicit a recognition process, but the withdrawal of such a stimulus does. As Martindale describes, “According to Sokolov, the cortex compares all incoming stimuli with models or expectations. If the incoming stimulus matches a pre-existing cortical model, the cortex blocks the reticular system and ... no attention is paid to the stimulus. On the other hand, if the stimulus is novel—that is, if it does not exactly match any cortical model—then the cortex does not block the reticular system” [17].

The withdrawal of a previously habitual stimulus constitutes in itself a new stimulus, to which attention is directed. The whole dynamics of recognition processes can be summarized in Sokolov’s match-mismatch rule: “If a percept exactly matches a set of cognitive units, nothing happens other than passive perception. If a percept matches the best-fitting set of cognitive units, then the arousal system activates the cortex. This arousal response is accompanied by an orienting reflex, attention, and the construction of a new cortical model” [17].

E. Sokolov and O. Vinogradova [8] related the orienting reflex with the functions carried by the limbic system. In this expression, the word “reflex” does not mean a response elicited by an external conditioning; on the contrary, it refers to a constructive response (based on unconditioned affective dispositions) that guides behavior, in the following kinds of situations:

(a) When a stereotyped pattern is initiated, without being triggered by a specific stimulus, e.g., a chicken searching for food, in the absence of any specific food stimulus.
(b) When a stereotyped pattern is triggered by a specific stimulus, e.g., a predator-like sound inducing the prey to escape.
(c) When there is a stereotyped reaction to a change in a habitual environmental setting, e.g., the miller who wakes up when the noisy mill stops working.

One role of the limbic system in rodents would be signaling changes among types of behavior. Sokolov and associates tested this hypothesis experimentally, at the neuronal level, focusing on cases B and C above ([8], pp. 226, 233).

An analysis of how habituation works at the ontogenetic scale [18] suggests a possible phylogenetic adaptation for the recognition of a distal stimulus from proximal signals. For example, when we hold a tool with the hand, e.g., a hammer, we first experience touch with the tool, but as we use it we become habituated and the focus of attention turns to the interface between the hammer and the part of the environment that offers a resistance to it, e.g., the nail.

The signals generated internally to the brain are the most proximal stimulus, the ones to which we are phylogenetically most habituated. Is it possible that in the distant evolutionary past, or in some artificial situation, the brain could perceive its own workings? It is possible to amplify a signal from an electrode placed in the scalp, making it possible for the brain to monitor its own activities, a therapeutic practice called “biofeedback” [19,20]. Another example is closing the eyes and pressing the eyeballs with a finger; some phosphorous phantoms can usually be seen, presumably produced by remaining excitatory activity of retinal cells. In both examples, the nervous system perceives a fragment of its own workings, but in normal adaptive situations ancient habituation mechanisms preclude literal brain self-reference. These examples serve to demonstrate that it is not impossible for the brain to perceive parts of itself, hence suggesting that projective intentionality would be generated by habituation mechanisms that block the respective sensation.

Another precursor of this view is Freud. His “Project for a Scientific Psychology” refers to a “dissipation” process that corresponds to our conjecture of allostatic recovery of stability: “Freud defined this as the tendency of neurons to divest themselves completely of the quantities of excitation (endogenous or exogenous) that erupt into the psychical
The primary function of this apparatus would therefore be to reduce to the lowest level possible—ideally a 'level = zero'—the quantity of free energy” [21].

The initial contributions of the Sokolov group have been resumed in current approaches to the projective capabilities of the brain. The Freudian hypothesis, later refined in the concepts of a principle of pleasure and the death drive, has recently been put into perspective in the neuroscientific work of Karl Friston and his colleagues with the Bayesian approach, “Its aim being to avoid too great a variation in the quantity of free energy coming from our sensorial perceptions (both internal and external) on the basis of prediction of sensorial data. This offers an unexpected point of dialog between psychoanalysis and neuroscience centered on an energetics concept of cerebral function.” [21].

The generation of sensations is not explained by homeostasis (the forces that drive the system to stay at the set point) alone, but require reference to another explanatory factor: an “elastic” property that drives the system move to another stable state once a perturbation (stimulus) moved it to a distance from the equilibrium. For instance, in sexual experiences the differences in the stimulation cause a difference in the homeostasis (deviation from the equilibrium) and then, after an excitation threshold is crossed, we feel pleasure (orgasm) as a signal of the return to homeostatic equilibrium. At the homeostatic equilibrium we do not feel pleasure or any other sensation. Therefore, sensations are dynamic temporal patterns experienced in the process of homeostasis deviation and allostatic recovery. This process involves a projective operation in which conscious sensations are generated and attributed to a source of stimulation that is often located externally to the brain [22]. We feel the pain of a tissue lesion in the foot as being located in the foot, not in the brain. Scientifically we know that the sensation of pain is produced in the brain, because the blockage of the signal from the foot to the brain by a local anesthetic abolishes the sensation.

In this approach, sensations have an adaptive function, both internally—to participate in the mechanism of control of brain homeostasis—and externally—to react correctly to the environmental stimulus. For instance, when we feel pain after sticking a finger in a rose thorn, we withdraw the finger and then the homeostasis of the skin tissue is recovered. There are also endocrine, immune and autonomic actions on the physiology (the “psychosomatic effect”) by means of hormones, peptides, modulators, antibodies and other signaling molecules, which can—in flexible systems—change the homeostatic set point and then help us to live with the bad stimulus without becoming severely ill or feeling pain.

In plastic systems, such as brains, the continued changes in homeostatic set points cause irreversible and permanent changes in the functioning of neural tissues, including genetic regulation and differential expression of signals that control the growth of dendrites and axons. This type of process has been proved to be essential to the process of learning and formation of long-term memory [23].

3. Glutamate and Calcium Mechanisms in the Control of Basal Homeostasis

The basal mechanism of homeostasis in the brain is composed of excitatory and inhibitory balancing factors and has a fixed equilibrium set point. Glutamate (Glu) is the main excitatory transmitter in the brain, being largely present in cortico-cortical networks and operating both on excitatory (as pyramidal cortical) and inhibitory neurons (as GABAergic interneurons). The Glu-induced excitation (i.e., membrane depolarization) of interneurons increases their inhibitory action (i.e., GABAergic transmission inducing the flow of chloride ions to hyperpolarize their membrane) on the excitatory ones. Glu transmission is a key component in the balance of excitation and inhibition that is a necessary condition for the operation of information transmission networks that support several brain functions. The temporal process of excitation and inhibition provides the brain with a dynamic mechanism necessary for adequate responses to environmental stimuli and respective adaptive actions.

Glu operates as an information carrier to thalamocortical and cortico-cortical synapses, a role that is crucial for the understanding of perceptual processing in the brain. All perceived information from the environment is carried by neuronal spike trains, which are transduced by Glu at each synapse, reaching the sensory cortex, where they activate
specialized feature detectors. The central nervous system (CNS) constructs integrated scenes, using feature detectors activated by the information patterns carried by a series of neurons by means of spike trains and Glu transmission at each synapse. In the mammalian brain, excitatory sensory signals pass through thalamic relay cells and reach the fourth layer of a column of the sensory cortex, which fires to neurons located in the fifth and sixth layers. These neurons fire back to the thalamus and send the excitatory signal to the superficial layers, where they are horizontally spread to other cortical columns. This excitatory process is soon extinguished by habituation mechanisms, comprising the excitation of thalamic inhibitory interneurons that in turn inhibit the thalamic excitatory neuron soon after, and the neocortical inhibitory interneurons that inhibit the excitatory neurons that excited them [24]. With this mechanism, the excitatory process is conceived as dynamically moving through neocortical columns, composing the flux of thought, containing both unconscious and conscious aspects.

The role of Glu as information carrier in thalamocortical and cortico-cortical synapses is crucial for the understanding of how perceptual learning is possible in the brain. Glu is largely present in cortico-cortical networks, with a central role in the generation of conscious content in normal states, dreams and altered states. This role has been proved in experiments when the Glu NMDA receptor is transiently blocked by doses of an antagonist (ketamine, PCP or MK-801), thus generating perceptual distortions and hallucinations [25].

Spike trains encode information by means of frequency and phase in populations of axons. The CNS constructs episodes from the ensemble of neuron firing patterns received within a temporal period of approximately 2 to 3 s [26]. The concepts of feature-detectors and population-rate coding can be combined in the idea of a sparse population code [27]. In this view, the detection of real-world objects would be made by a cooperative group of neurons, forming a Hebbian cell assembly. A cell assembly is a relatively small neuronal population, located in cortical columns, with strengthened connections elicited by previous learning [28].

Glu membrane receptors control intracellular signaling pathways targeting the dendritic spine, where a molecular device is able to register the relevant afferent patterns, supporting conscious perceptual learning and selective triggering of memory formation, as well as unconscious priming. The mechanism involved in such a recording of sensory patterns has been studied as the early stage of LTP [29]. It involves biological molecular structures and functions, including the system of Glu receptors, and calcium-binding proteins such as calmodulin (CaM) and calmodulin-dependent protein kinase II (CamKII, a protein from the kinase family, having several receptor and effector active sites).

This mechanism operates in dendritic spines distributed over the whole neocortex. In the sensory cortex, exogenous patterns transmitted through thalamocortical glutamatergic projections are received and processed by post-synaptic mechanisms. Activation of Glu receptors combined with voltage-dependent calcium channels (VDCCs) converge to the dendritic spine, where they control CaM/CaMKII signaling mechanisms. Glu released from the pre-synaptic neuron’s axon terminal is spread in synaptic space and binds to three different kinds of receptors (AMPA, NMDA and metabotropic Glu receptors–MetGR) located at the post-synaptic neuron membrane. The three kinds of receptors activate signal-transduction pathways that converge into the dendritic spine [30].

Calcium cations (Ca$$^{++}$$) are largely employed biological ions with a flexible electronic structure able to encode information. CaM and CamKII have several receptor and effector active sites, where Ca$$^{++}$$ ions entering through NMDA and VDCCs are trapped. The ions trapped in CaM are transferred to the kinase and trigger regulatory functions. The informational state of CaM/CaMKII is dependent on the interaction with the Ca$$^{++}$$ population passing through NMDA and VDCCs. In normal cases, most of Ca$$^{++}$$ entry is made through the NMDA channel, which is considered to be a coincidence-detector for both bottom-up (sensory afferent) and top-down (previously learned) patterns [31]. Because of this condition, the NMDA channel assures the reliability of perception in regard to stimuli since it is opened to Ca$$^{++}$$ entry only if endogenous and afferent pulses reach the NMDA.
receptor together. When VDCCs (which are not coincidence detectors) assume the main role in glutamatergic transmission, perceptual distortions and hallucinations may occur.

The multimeric structure of CamKII, having binding sites for Ca\(^{++}\) and phosphatases that participate in the phosphorylation of other proteins, constitutes a micro computing device able to read quantized information from incoming Ca\(^{++}\), to process this information, and to activate other proteins according to the results of the information processing. The multimeric structure of CaMKII contains four sites that bind to CaM, determining the conformational state of the kinase and the resulting phosphorylation functions [24]. Such a micro computing device uses quantum information encoded in the electronic configuration of the ions. Besides binding with CaMKII, Ca\(^{++}\)-activated CaM can trigger other signaling pathways in the cell, some of them exerting feedback control on the state of the membrane and others reaching the nucleus and inducing the formation of long-term memory.

The above signaling pathways can be related to cognitive processes that depend on the glutamatergic mechanisms responsible for perceptual learning. For instance, one of the key proteins present in the converging Glu receptor pathways is DARPP-32, which is found, among other places, in the striatum, controlling thalamocortical glutamatergic and cholinergic neurons with the participation of dopaminergic modulation [32]. Striatal signals processed by such converging molecular pathways convey information to the cortex as an “efferent copy” or “corollary discharge” (i.e., signals sent from motor to perceptual areas when a voluntary action is initiated). DARPP-32 activity, as a converging route for intra-neuronal dopaminergic and Glu-activated signal transduction pathways, has been related to schizophrenia, possibly participating in the generation of its positive, negative and cognitive symptoms. An explanation for the role of DARPP-32, and for the cognitive deficits that occur when its respective signaling pathways are disturbed, is that the “efferent copy” would have the role of reinforcing perceived patterns, increasing their chance to form long-term memories.

4. Synaptic Plasticity and Homeorhesis

The instantiation of information patterns in neural tissue and computational processes using these patterns correspond to the process of sequential excitation and inhibition of cortical columns [24,33,34]. At the level of each column, the homeostatic set point is previously established by long-term memory macromolecular mechanisms that establish the “weight” or “strength” of connections that define the basal type of state (resting electrical potential). During the lifetime experience of an individual, changes in the production and release of neurotransmitters [35,36], resulting in differential concentrations at the synapse, can change the set point. These changes correspond to homeorhetic processes, moving the system beyond the simpler homeostasis of excitation and inhibition. Together with the homeorhetic process, the flexible or plastic reaction of the system to the changes in the set point can elicit a response that is experienced as a sensation or feeling of having learned something new and having knowledge of it. In the case of a complete process of learning, acquiring knowledge and becoming aware of it by means of the “feeling of knowing”, the whole process can be considered allostatic.

The formation of cognitive contents (“representations”) in conscious episodes comprises a deviation from the basal family of states and returning to the same type of state (homeostasis, in elastic processes) or reaching another stability region (homeorhesis, in flexible and plastic processes). A representation corresponds to a pattern of active connections [37] in neuronal networks, leading to a temporal pattern of neuron firing that communicates the result to other neurons in charge of controlling muscles and glands, thus generating behavioral patterns. These excitations are not static, but under a physiological dynamic process of habituation and response to novelties that perturb the system and drive it away from homeostatic equilibrium. Neural assemblies activated at one moment are inhibited in the next moment, while the chain of excitations move along neocortical tissues radially connected with the thalamus [34]. The temporal chain of thought corresponds to a series of excitations and inhibitions moving along neocortical tissue. The control is
the response of the system (using Sokolov’s terminology, it is the orientation of the system that supports the process of adaptation to the changing environment), directing the dynamics of connections back to the synaptic basal level of activity determined by long-term potentiation or to another stability region, by means of changes in the concentration of neuromodulators.

The dynamics of spiking neurons and their patterns of connectivity in cortical tissue have the characteristics of complex dynamical systems, in which the trajectory moves through a rich landscape containing many attractors (see [38,39]). Changes in axonal signaling (spike trains) and resulting changes in the strength or weight of synaptic connections can compose an allostatic process, because of flexible or plastic changes in neuromodulation [35], leading the system to occupy new regions of the state space and constructively building on the new experiences. After the allostatic process, synaptic homeostasis is guided by another set point or region in the system's state space. In experiential terms, this type of learning process is accompanied by the “feeling of knowing” something new. This feeling is, in the proposed framework, an experiential correlate of the cognitive allostatic process.

5. Neuron-Astrocyte Interactions

Glutamatergic synapses are mostly “tripartite” (composed of two neurons and one astrocyte). The Glu released by the presynaptic neuron reaches both the postsynaptic neuron and the astrocyte. By binding to the NMDA and AMPA receptors of the postsynaptic neuron, Glu induces membrane depolarization, and the opening of NMDA channels to fast calcium currents. This excitation decays in around 150 ms [24] but can be sustained by gliotransmission (Glu released by the astrocyte, binding to extrasynaptic NMDA receptors), producing slow calcium currents through NMDA receptors. The second input of calcium may activate the path of calmodulin and its kinase (CaMKII), which phosphorylates or dephosphorylates AMPA receptors and thus induces synaptic potentiation or depression.

When the animal is awake, the astrocytic network is pre-activated by adrenergic, purinergic and cholinergic mechanisms, facilitating the generation of calcium waves at the time when Glu transmission occurs. In the astrocyte, the induction of local calcium waves by means of excitatory transmission generates intercellular, global waves that broadcast information to many other parts of the brain [3,4].

While in the “Neuron Doctrine” (formulated by Ramon y Cajal) neurons were considered the functional units of the mind, in the new emerging model of neuro-astroglial interactions the tripartite synapse becomes the functional unit, constituting the basis for psycho-physiological processes. Neural networks are mostly responsible for cognitive processes (such as the formation of representations and logical operations in processes of perception, attention, action, learning and memory formation), whereas the astrocyte network performs an appreciation of the information carried by the neural network, putatively by means of intercellular, global calcium waves. Based on the appreciation, the astrocyte network modulates neuronal activity, reinforcing the patterns of information that have positive valence for the individual, and weakening those with negative valence. These complex neuron-astrocyte interactions can elicit flexible and plastic processes mediated by signals between the two types of cell populations [3]. From neurons to astrocytes, several transmitters can be used, while from astrocytes to neurons—besides the release of gliotransmitters by means of transporters and vesicles—experimental research has revealed a central role of potassium ion concentrations controlled by the astrocyte [40].

The functions of integration and appreciation of information are closely related because the lived experience intrinsically contains an appraisal, by assigning positive, neutral or negative valence to certain aspects of the experience. The astrogial network participates in both processes of integration and appreciation of information patterns processed in a distributed manner in the thalamocortical system, interacting with somatic processes by means of signaling via blood flow and cerebral fluid, and uses the results to modulate the
neuronal network, thus participating in processes of perception, attention, learning, training of semantic and episodic memory, emotion, consciousness and control of behavior [3,4].

As the astrocyte is in contact with blood and cerebrospinal fluid (while neurons are not), it receives the signals that come in the flow, forming a continuously updated reference of the state of the body in the world. The intracellular astrocyte signaling generate small calcium waves that interfere with each other in the whole astroglial network, resulting in larger waves built by means of constructive interference. The intrinsic patterns of the larger waves, to be studied experimentally, were proposed to correspond to the first-person experienced feelings [4].

Astrocytes are not connected to sensory transducers or muscle and endocrine effectors. All sensation and perception, as well as all actions in the world, begin with neurons; the results of neuronal processes (information patterns embodied in local electromagnetic fields) reach the astrocytes and induce the larger waves (see the ‘domino’ and ‘carousel’ effects [3]). The larger waves in the astrocyte network require a coordinating action from neurons:
(a) Local EM fields are formed by active neuronal assemblies.
(b) Neuronal large-scale synchronization occurs in theta to gamma frequencies (not delta; synchronization in the slowest frequencies imply unconsciousness).
(c) There are chemical and ephaptic (magnetic) transmissions of information from the neuronal local fields to astroglial waves; and
(d) There is an interference of the smaller waves, leading to the formation of the larger ones in the astroglial network.

6. The Hydro-Ionic Wave and Allostasis

The neuro-astroglial interaction model has theoretical resources to address not only the cognitive representation of emotions, but also the lived experience of conscious sensations by whole biological individuals. Amplitude-modulated ionic waves in astrocytes and extracellular fluid are regarded as the carriers of the sensory affective or emotional response to a perturbation of homeostasis. The elicited process may be allostatic, leading the system to stable states far from homeostatic equilibrium. In this regard, the “Endogenous Feedback Network” hypothesis [41] advanced the idea that conscious feeling involves the interaction of neuronal and astroglial networks, the first responsible for the processing of information and the constructing of representations, while the second would be responsible for the lived, direct experience of feeling.

The concept of allostasis, in this context, is co-extensive to learning and memory [42] processes at cellular and tissue scales, as treated in computational modelling. In neurobiological language, authors refer to processes of reciprocal modulation [3,43], regulation [44] and control [45] of neurons and astrocytes, generating as a result the phenomenon of neural plasticity [14,46]. This process is more intense during the development stages [47] and persists during the whole life of biological individuals, determining processes of health and disease [48]. The connection with cognitive learning, i.e., the formation of new memories, can be exemplified by neurophysiological studies of neuron-astrocyte interactions in the hippocampus [49,50].

The temporal process in which neurons activate calcium waves in astrocytes and these waves modulate neurons in the following time interval is the following (see also the “carousel effect” concept advanced in [3]): A given neural microstate generates both the EEG signal and changes in the previously existing standing calcium wave in astrocytes, by means of the release of transmitters [43]. In the next moment, the calcium wave modulates the following microstate, reinforcing patterns with systemic positive valence, and depressing patterns with systemic negative valence. The second microstate generates both the next EEG register and the changes in the existing calcium wave, and so on. Although the scalp EEG does not measure the calcium wave directly, the modulatory function exerted by the wave is implicit in the temporal evolution of the registered electromagnetic signal.
7. Summary of Concepts

Based on the above considerations, I summarize the concepts of homeostasis, homeorhesis, allostasis, elasticity, flexibility and plasticity used in this paper:

(a) Homeostasis: A physiological (temporal) process in which the system has a fixed point or region of equilibrium, and returns to this point or region after a perturbation.

(b) Homeorhesis: A physiological (temporal) process in which perturbations destroy the system’s previous fixed point or region and drives it to an unstable region of the state space.

(c) Allostasis: A physiological (temporal) process in which the system moves away from the basal equilibrium point or region, crosses an unstable phase and then achieves a new stable point or region, driven by an adaptive response based on tissue waves that may be related to conscious sensations.

(d) Elasticity: A property of homeostatic systems returning to equilibrium after a perturbation.

(e) Flexibility: A property of homeorhetic systems responding to perturbations alternating between equilibrium points or regions. It implies a diversity of attractors.

(f) Plasticity: A property of allostatic systems creating new attractors far from equilibrium, on the basis of internal and external (adaptive) interactions. The creation of new attractors implies a psycho-physical learning process and formation of long-term memory and, therefore, a degree of cognitive and enactive processing together with the experiencing of basic sensations.

8. Concluding Remarks

The dynamics of the generation of sensations in neural tissues, in elastic, flexible and plastic systems, can be illustrated by the exchange of potential and kinetic energy in the movement of a pendulum. At one point there is only potential energy, and at another point there is only kinetic energy; between them, there are all possible combinations of both, on a continuum. The same reasoning applies to neural systems. During slow-wave sleep, there are only potential sensations and during wakefulness there are moments when we are making the most of our potentialities [34].

The circadian rhythm in chronobiology concerns these oscillations experienced across the 24-h period. In addition, there are faster oscillations that happen at every moment, and several combinations of potential and actual consciousness, from dreaming (in which a maximum of conscious control in realized in lucid dreaming) to varied experiences in wakefulness, from empty minds to mindfulness. The brain process is continuous, but there are three relevant differences between the dynamics of the pendulum analogy and the functioning of neural tissues [34]:

(a) The existence of a ‘switch’ between unconscious sleep and wakefulness, but not in the movement of the pendulum. However, the existence of a ‘switch’ does not mean that non-consciousness and consciousness compose a binary structure. The ‘switch’ is a point on a continuum, such as the transition from liquid to gaseous water at 100 degrees centigrade; although there is a phase transition, it does not imply a discontinuity in the temporal process. For the first-person perspective of the biological individual, sensations are felt only when the system crosses this threshold.

(b) The “state of pure potentiality” of the pendulum is just a point on a continuum, whereas this point practically does not exist for conscious living systems; it exists only for our corpses when we are completely dead, because even when we are alive and not conscious there is some degree of basal activity.

(c) A fixed point of equilibrium exists only in artificial devices such as thermostats, not in living systems. Indeed, even for a perfect gas in a closed container, the equilibrium modes (the ‘Maxwellian equilibrium’) are active, consisting, as they do, of Brownian motion. The conscious system is always active, therefore the basal/equilibrium state is a class of states changing within a region of the state space of the system. A stimulus
impinging on the system changes the regimen or mode of activity, but the system is already active.

In sum, the dynamic physiological processes that generate sensations and feelings are composed of three phases [34]:

1. A dynamical baseline that embodies the structural potentialities of the system. The structure and the derived dynamics, together with the existing boundary conditions, determine if the system is sentient (capable of feeling) or not. A thermostat is not sentient because the equilibrium is defined—by the engineer who designed it—as a set point.

2. An unstable phase in which a stimulus (internal or external to the system) drives the trajectory away from homeostatic equilibrium and generates a response (the hydro-ionic wave) that supports a qualitative experience (sensation) in the first-person perspective of the system. If the process moves to an adaptive resolution, the experienced sensation is more likely to be pleasant; if not, it is likely to be unpleasant.

3. The recovery of stability, when the system returns to the homeostatic equilibrium class of states (elastic systems) or moves to another class of states (attractor region of the state space, in flexible and plastic systems).

To account for both the physiological processes discussed in this paper, and the psychological processes experienced by the individual, I have proposed [34] the distinction of sentiomics (objective study of dynamical patterns involved in the generation of sensations, feelings and emotions, in the third-person perspective) and qualiomics (the study of feeling experiences in the first-person perspective).

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