PSYCHOLOGICAL MAGNITUDE, RELAXATION OSCILLATORS AND THE DYNAMIC CORE OF CONSCIOUSNESS

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Abstract

This paper attempts to sketch some of the possible relationships between a view of the dynamical brain as a collection of relaxation oscillators at many time and space scales, fundamental concepts of psychophysics, such as psychological magnitude, and a conception of conscious experience based on Tononi and Edelman's dynamic core hypothesis. Construing psychophysics as Fechner seems to have originally intended it, as a way of studying the mind-body problem, I focus here on his inner psychophysics, the relationship between conscious sensations and their brain representations. In this approach, all brain representations are dynamic, that is they are modeled as relaxation oscillators oscillating either at some natural frequency or at some driving frequency imposed by other oscillators coupled to them. The oscillators exist at several scales, from that of the neuron to that of a large scale, across-brain, neural network, the dynamic core of consciousness. The act of perceiving the magnitude of a sensory stimulus in a modality-free way that admits of cross-modality matching is construed as coupling a central (possibly frontal) oscillator to the sensory oscillator(s) representing the stimulus in such a way that the amount of charge flow per unit time (synaptic action density) in the central oscillator matches that in the sensory oscillator(s), the resulting synaptic action density being the modality-free psychological representation of the magnitude of the sensory stimulus. Consciousness of this magnitude, or of the sensation from which it is derived, consists of coupling the central or peripheral oscillator to the dynamic core oscillator. Judgment of this magnitude consists of coupling the dynamic core oscillator to other oscillators (representing active neural networks) that effect verbal or matching responses.

Fechner (1860) construed his psychophysics as a solution to the mind-body problem: how the "insubstantial country of the mind" (Jaynes, 1976) is related to its material substrate, the brain. Believing that this "inner" psychophysics was, at least for the moment, out of empirical reach, he invented "outer" psychophysics to demonstrate that his preferred logarithmic relationship between the magnitude of the simplest conscious experience, a sensation, and its representation in the brain, presumably activity of a group of neurons, was correct. In this paper I speculate freely about the form that an inner psychophysics might take, consistent with many of Fechner's ideas but based on a modern conception of a dynamic brain (see also Ward, 1992, 2001). Perhaps the major conceptual gambit of the paper is to describe the brain in terms of a collection of relaxation oscillators operating at many scales. Before proceeding to some of the implications of this view for psychophysics, I first describe some of the properties of a prototypical relaxation oscillator and indicate how this concept can form the basis of a dynamical model of the brain.

Relaxation Oscillators in the Brain

The relaxation oscillator was first described by van der Pol (1926) in a classic paper. Like all oscillators, this damped, unforced, nonlinear oscillator is described by a differential equation:

$$\frac{d^2v}{dt^2} + \alpha(v^2 - 1)\frac{dv}{dt} + \omega^2 v = 0 \tag{1}$$

where the variable v could stand for the voltage across a resistance in an electrical circuit, for example a neon lamp in parallel with a capacitor, this pair in series with a resistance and a battery. In this equation, the middle term on the left side is the damping term, which opposes the restoring force, $\omega^2 v$, overwhelming it when the voltage becomes large and causing the oscillations. The relationship between α and ω is crucial to the behavior of the oscillator. When $\alpha << \omega$, the oscillator behaves like a linear oscillator with very small amount of damping, generating a very slowly decaying sine wave. When $\alpha = \omega$, the oscillatory behavior becomes less sinusoidal but is still fairly regular. When, however, $\alpha >> \omega$, the oscillation approaches a square wave. In each cycle of the (nearly) square wave, sudden transitions (nearly vertical traces) are preceded by a considerable time period during which the voltage changes only slowly. Van der Pol (1926) called this a “relaxation oscillation” because the slowly changing voltage followed by a rapid voltage change resembles the buildup and release of charge in a capacitor. In this system relaxation, or the time taken for the “memory” of the previous state to decay (or the capacitor to charge), is the important feature, not the restoring force ($\omega^2 v$). Probably the most important feature of a relaxation oscillator for present purposes is that its oscillations easily phase lock with an external driving frequency (forcing), even one that does not correspond to its natural frequency, while maintaining a relatively constant amplitude.

Neurons display relaxation oscillations par excellence: they fire an action potential when the voltage across the cell membrane in the trigger zone of the soma exceeds a threshold, and then “gradually” build back up again, usually under the influence of input from other neurons, until the threshold is crossed again and then they fire another spike, and so forth. Hodgkin and Huxley (1952) proposed a mathematical model of this process based on action potentials in the squid giant axon. This model, consisting of four first-order differential equations, is not easy to solve or to analyze. Fortunately, FitzHugh (1961) noticed that neural action potentials can be described as relaxation oscillations similar to those described by van der Pol (1926). He created a model of neuron dynamics based on a special case of Equation 1 ($\omega = 1$) plus some additional terms, including a forcing input, and showed how it mimicked the behavior of the Hodgkin-Huxley equations. The resulting equations were also studied by Nagumo, Arimoto and Yoshizawa (1962) and are now called the FitzHugh-Nagumo model of the neuron.

The FitzHugh-Nagumo neuron model equations are

$$\frac{dv}{dt} = \alpha(w + v - v^3/3 + z) \tag{2}$$

$$\frac{dw}{dt} = -(v - a + bw)/\alpha \tag{3}$$

where v is a voltage across the neuron’s cell membrane that represents a fast, excitation process, w is a voltage that represents a slower, recovery process, z is the forcing term representing input from other neurons, α is the damping constant (greater than $\omega = 1$ so that the system shows relaxation oscillations), and a and b are constants that affect the recovery rate. Since 1961 the FitzHugh-Nagumo model of the neuron has been used in many applications in biophysics. In many of these, stochastic (noise) forcing is added to the "fast" Equation 2 and deterministic, usually sinusoidal, forcing, replacing z in Equation 2, is added to the "slow" Equation 3 (e.g., Longtin, 1993). This represents the usual case that neural noise fluctuates at a much faster time scale, one comparable to spike duration, than does a neural signal, which can fluctuate at a timescale comparable to recovery duration. Longtin (1993) showed that these modified FitzHugh-Nagumo equations behave much like neurons, in particular generating action-potential-like oscillations, including bursts, at frequencies characteristic of neurons. In further papers he showed how the equations' behavior can be synchronized to periodic forcing (Longtin, 1995a) and demonstrate stochastic phase locking (Longtin, 1995b).

The dynamics of the brain are probably most apparent at the scale of the individual neurons and their connections to other neurons. At one time these relationships were thought to be adequately modeled by the influence of neurons on each other's firing rates. This influence reflects *rate coding* by neurons, that is, representing the presence of a trigger feature by an increase or decrease in firing rate. Recently, however, the idea that the *timing* of a neuron's action potentials is influenced by the timing of its inputs from other neurons has gained credence (see Singer, 1993). *Synchronization* of neural activity is considered to be important to the way the brain's state evolves in time and for the way in which it generates cognitive and behavioral states. It has been suggested that synchronization is the mechanism by which the coding of necessary relations between neural activity in anatomically-separated but functionally-related brain areas is accomplished (the *binding problem* - Singer, 1999). Of course, synchronization is particularly easy for relaxation oscillators, including in the form of FitzHugh-Nagumo model neurons, which are easily entrained by forcing inputs.

Nunez (2000) proposed a dynamical theory of the relationship between brain activity and EEG recordings in which neurons act like relaxation oscillators, producing standing and traveling waves of cortical activity that influence global and local oscillations and cognitive and behavioral states, even consciousness. The relevant general principles of the theory are: (1) brain state is described by physiologically-based control parameters that depend on neuro-modulatory action; (2) neural networks operate in a background of standing waves of synaptic action - oscillatory changes in the number of active synapses; (3) excitatory and inhibitory synaptic action density (number of active synapses per unit brain volume) and action potential density are treated as macroscopic field variables; (4) cognitive and overt behavior depend on the levels of these variables in various brain regions. Nunez (2000) collapses the multiple scales of dynamics described by the theory to two prominent scales of oscillations and their interaction. *Local oscillations* in synaptic action density are the result of interactions between neurons in relatively small functionally segregated areas of the brain, connected in neural networks through both excitatory and inhibitory connections. Such oscillations could be taken, for example, to represent the response of a sensory system to a stimulus. *Global oscillations* are composed of interactions between such local regions, with longer communication delays caused by the longer axonal pathways, and possibly multiple intervening synapses, involved. Such oscillations could be taken to represent "higher" processing of sensory stimuli. Under some conditions it is possible to derive simple expressions for local and global activity and their interaction. In one such case, a set of five second order differential equations can be obtained, each one a relaxation oscillator:

$$\frac{d^2Z}{dt^2} - \varepsilon(1 - Z^2)\frac{dZ}{dt} + [k_n^2 - (1+\varepsilon)Z^2]Z = 0 \qquad (4)$$

Here Z stands for the synaptic action density (like voltage in the van der Pol Equation 1), ε is the damping parameter, and $[k_n^2 - (1+ \varepsilon)Z^2]Z$ is the restoring force term. Numerical solutions to one set of such equations exhibit both local (faster) and global (slower) oscillations that resemble prominent EEG waves such as theta and gamma, which are associated with information processing by the brain. It has been suggested that gamma (approximately 40 Hz) and theta (approximately 6-7 Hz) oscillations in the brain reflect the processes that give rise to working memory (Lisman, & Idiart, 1995). In this theory, one “rehearsal” of all working memory “slots” takes place during every (global) theta cycle, rehearsal of each item taking place at the (local) gamma frequency, about 40 Hz or one item every 25 msec, the maximum rate at which short-term memory can be “scanned.” Therefore, about 7±2 items (≈40/6) can be retained in working, or short-term, memory. In the service of confirming their model, Lisman and Idiart (1995) published plots of embedded oscillations recorded from both human auditory cortex and from rat hippocampus that look remarkably like those exhibited by Nunez (2000). Thus, it seems useful to describe the brain as a coupled system of relaxation oscillators, from individual neurons (e.g., FitzHugh-Nagumo neurons) to local neural networks, to large scale networks of networks. At each level, the dynamics can be modeled as a relaxation oscillator or as a coupled system of such oscillators. Such a model would naturally represent brain dynamics; the challenge is to relate those dynamics to more conventional descriptions of structural and functional properties, in the present case to psychophysical concepts.

The Dynamic Core of Consciousness

Another modern development that would have intrigued Fechner concerns the neural correlates of conscious experience. An important discovery is that changes in conscious awareness, such as alternations in which of two binocularly rivaling stimuli is seen, are accompanied by a change in the *synchrony* of the firing of the various neurons representing the stimuli. For example, Tononi, et al. (1998) reported that when humans are conscious of a particular one of rivaling visual grating stimuli, there is widespread coherence between MEG measurements at various brain sites and the MEG measurements of the activity of the neurons in visual cortex responding to the seen grating; such coherence is lacking for the unseen grating (*coherence* is related to the square of the correlation coefficient between two time series. Tononi and Edelman (1998) suggested that both *differentiation* (a large number of possible states) and *integration* (widespread coherence resulting in a particular one of those states) are fundamental aspects of conscious experience. They suggest that both are achieved by the emergence of a *dynamic core*, that is, “...a large cluster of neuronal groups that together constitute, on a time scale of hundreds of milliseconds, a unified neural process of high complexity...” (Tononi & Edelman, 1998, p. 1849). In this proposal, parallel processing in the brain is integrated in consciousness, with various aspects of the current sensory and cognitive processing constituting the dynamic core, and thus being “in consciousness,” while other aspects of simultaneously occurring processing are outside the dynamic core, and thus are outside of consciousness. Neural synchrony, possibly constituted of the global oscillations described by Nunez (2000), across widespread areas of the brain would be the “force” that binds various neural activity into the dynamic core, with unsynchronized activity continuing outside of awareness (with often significant consequences, as ideas “pop” into our minds, problem solutions “just appear,” and our bodies react in unpredicted ways to unperceived stimuli). The plausibility of this view has been demonstrated by a large-scale (65,000 integrate-and-fire neurons, similar to FitzHugh-Nagumo neurons, and 5 million connections) simulation of thalamocortical circuits in the brain (Lumer, Edelman & Tononi, 1997). When this simulated neural network was simulated with continuous input, multilevel synchronous oscillations at roughly 50 Hz emerged. These oscillations were not programmed into the simulation in any way, they simply occurred as a consequence of the interactions between the neural activity in the various simulated brain areas in response to the stimulus input.

Implications for Psychophysics

In the view of the dynamic brain adumbrated above, a sensory stimulus is represented by synchronous firing in a group of (sensory) neurons. Conscious awareness of the stimulus occurs when the widespread networks of the dynamic core become synchronous with the network that represents the stimulus. A plausible candidate for the macroscopic field variable that would represent the magnitude of the sensory stimulus would be the synaptic action density (in units of charge flow) associated with the representing sensory network. For example, a pure tone excites a group of neurons in primary auditory cortex that includes at least those tuned to the tone's frequency, and probably many others at nearby frequencies if it is more intense than about 30 dB. The more intense the tone, the more neurons, with characteristic frequencies farther from the tone frequency, join the group, all firing at their maximum rate (saturated) except for those with the furthest away characteristic frequencies. The total number of active synapses in this group would represent the tone's intensity. However, the synaptic action density in that network represents local, modality-specific, encodings. It is not directly comparable to that in local networks of other sensory modalities (re cross-modality matching), or in a form that could be mapped to numbers (magnitude estimation). Therefore, it would be necessary to create a modality-free representation of the magnitude of any sensory stimulus. One way to do this would be by bringing its sensory representation into synchrony with a common central inhibitory network, that, possibly via other oscillating networks, would recruit neurons into the network until the sensory input was canceled. The synaptic action density of the canceling network would be the modality-independent psychological magnitude of the sensory stimulus, abstracted from its peripheral representation. A report of this magnitude could be made either by adjusting input from another modality until the same central magnitude was achieved (cross-modality matching), or by recruiting other, cognitive representations, say of numbers or of categories, that would in turn control verbal or key-press responses (magnitude estimation). Although directly experiencing the sensory stimulus, by synchronizing the dynamic core with its neural representation, would include an experience of its sensory magnitude, the actually reported psychological magnitude necessarily would be controlled by the canceling central oscillator.

This suggestion resembles that of Ward (1991) regarding a modality-independent representation of psychological magnitude. However, embedding it in the context of relaxation oscillators emphasizes different aspects. First, all such representations fluctuate over time, especially over scales of seconds to hours. Relaxation oscillators have chaotic parameter regimes and these are in the region of parameter values that make sense physiologically. Moreover, such fluctuations also are characterized by "colored" noise (noise whose power spectrum is proportional to $1/f^{\alpha}$), which arises from processes that cause fluctuations at several, widely spread time scales whose influence on future states decays exponentially. These properties of sensory and cognitive representations by relaxation oscillators imply that those representations will be fuzzy (imprecise-Ward, 1979), that regardless of technique there will be an irreducible core of noisiness associated with measurement of these representations, and that series of psychophysical judgments of such fuzzy representations will be correlated in particular ways. But perhaps most importantly, this approach emphasizes the relevance of psychophysics to the study of consciousness, because our techniques are uniquely suited to probing the dynamic core through precise first-person reports of phenomenological experience (cf. Overgaard, 2001). Psychophysical laws of the future will refer to properties of the dynamic core of consciousness other than its ability to abstract psychological magnitude from sensory representations. Perhaps then, finally, Fechner’s program will be fully realized.

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