THE ROYAL SOCIETY

The labile brain. II. Transients, complexity and selection

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The successive expression of neuronal transients is related to dynamic correlations and, as shown in this paper, to dynamic instability. Dynamic instability is a form of complexity, typical of neuronal systems, which may be crucial for adaptive brain function from two perspectives. The first is from the point of view of neuronal selection and self-organizing systems: if selective mechanisms underpin the emergence of adaptive neuronal responses then dynamic instability is, itself, necessarily adaptive. This is because dynamic instability is the source of diversity on which selection acts and is therefore subject to selective pressure. In short, the emergence of order, through selection, depends almost paradoxically on the instabilities that characterize the diversity of brain dynamics. The second perspective is provided by information theory.

Keywords: neuronal transients; complexity; functional integration; neural codes; selection; self-organization

1. INTRODUCTION

This paper reviews the notion of complexity and how it relates to transients and dynamic instabilities in neuronal systems. In §2, it relates neuronal transients to nonlinear dynamical concepts such as intermittency, itinerancy and dynamic instability. This section introduces the distinction between different sorts of complexity (type I and II), which is useful when considering complexity and diversity in relation to selective mechanisms that may operate in the brain. After considering the genesis of complexity, §3 addresses the role of asynchronous or nonlinear coupling. The strengths of connections, among simulated populations, are manipulated to induce changes in (i) the nature of the coupling and (ii) the complexity of the ensuing dynamics. This allows the relative contributions of synchronous and asynchronous coupling to complexity to be characterized. In brief, we will show that complexity and nonlinear coupling go hand in hand, presiding in regimes of sparse connectivity. The importance of complexity for self-organization (Kelso 1995) and the selective consolidation of synaptic connections in terms of neuronal selection (Edelman 1993) are introduced in §4. In this section it is suggested that selective mechanisms of a high order are sufficient to explain why the brain expresses complicated dynamics.

2. A DYNAMICAL PERSPECTIVE

(a) *Complexity*

In this section we consider transients in relation to the complexity of the dynamics that they generate. Complexity is itself a complex field with numerous definitions and perspectives (Horgan 1995). Generally, complexity refers to something in the behaviour of a system that is not ordered or predictable nor chaotic or random but something in between that reflects an underlying order that, is itself, inherently unstable or labile. There are two distinct approaches to complexity: those that derive from information theory and those that come from the field of deterministic chaos in nonlinear systems. The former approaches are based on some measure of the entropy of the system (e.g. Morgera 1985) and can be related to algorithmic complexity (framed in terms of the minimum length of an algorithm required to generate an observed time-series). More recently, entropy-based complexity measures have been proposed that try to capture the balance between integration among different neuronal systems and the preservation of information that is unique to them. Functional segregation requires the dynamics of each area to be distinct, in terms of their intrinsic activity and responses to input. Functional integration, on the other hand, requires segregated areas to influence each other in a way that facilitates coherent integration. It has been proposed that the resolution of this dialectic, between the preservation of regionally specific dynamics and global coherence, is a hallmark of complexity (Tononi *et al.* 1994; Friston *et al.* 1995). A measure of this complexity, based on the theory of stochastic processes and information theory, is found in Tononi *et al.* (1994).

In this paper we are concerned with the second approach to complexity, namely that predicated explicitly on nonlinear dynamic systems. Within this class there is another dichotomy that distinguishes between dimensional complexity in chaotic systems and dynamic instability (Kelso 1995) associated with self-organizing and pattern-forming systems. Dimensional complexity is a measure (the correlation dimension) that reflects the degree of chaos in terms of the average local behaviour of

Received 2 September 1998 *Accepted* 8 June 1999