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Research Report

Neuronal correlates to consciousness. The “Hall of Mirrors” metaphor describing consciousness as an epiphenomenon of multiple dynamic mosaics of cortical functional modules

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ABSTRACT

Humans share the common intuition of a self that has access to an inner ‘theater of mind’ (Baars, 2003). The problem is how this internal theater is formed. Moving from Cook’s view (Cook, 2008), we propose that the ‘sentience’ present in single excitable cells is integrated into units of neurons and glial cells transiently assembled into “functional modules” (FMs) organized as systems of encased networks (from cell networks to molecular networks). In line with Hebb’s proposal of ‘cell assemblies’, FMs can be linked to form higher-order mosaics by means of reverberating circuits. Brain-level subjective awareness results from the binding phenomenon that coordinates several FM mosaics. Thus, consciousness may be thought as the global result of integrative processes taking place at different levels of miniaturization in plastic mosaics. On the basis of these neurobiological data and speculations and of the evidence of ‘mirror neurons’ the ‘Hall of Mirrors’ is proposed as a significant metaphor of consciousness.

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1. Introduction

Humans seem to share a common intuition of a ‘self’ that has access to conscious sensations, inner speech, images and thoughts (self-consciousness). This intuition may be

metaphorically described as a “theater of mind” (Baars et al., 2003), and conscious events can be defined as those brain activities a subject can accurately report in optimal conditions (Baars et al., 2003). Once the assumption of a chemico-physical basis of consciousness has been accepted, we are

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² Dedicated to Professor Angelo Pierangeli (1932–2010) and to Professor Pasquale Montagna (1950–2010), University of Bologna.

confronted with the question of how brain activity leads to conscious experiences, i.e., what are the neuronal correlates of consciousness (NCC). As Chalmers emphasizes, the search for NCCs is the cornerstone of the recent resurgence of the science of consciousness (Chalmers, 2000). NCCs have become important in the wake of the enthusiasm generated by neuro-imaging techniques, which correlate specific cognitive tasks with the activation of restricted brain areas, making the relationships between psychology and neurobiology more realistic and fruitful (Monti et al., 2010). This research effort allowed to show that conscious perceptual processing involves the sequential activation of cortical networks at several brain locations with the onset of oscillatory synchronous activity (Gray et al., 1989a, 1989b). Hence, studies on consciousness must explore both a temporal and spatial dimension.

As far as the temporal dimension of conscious events is concerned, Pöppel and Logothetis (1986) investigated reaction times to visual stimuli, and proposed that perceptual processing operates in basic units of 30 ms, while conscious episodes composing the “conscious present” can be extended to periods of 2 or 3 s (Pöppel, 1994). Studies in humans based on the event-related potential (ERP) paradigm allow an estimate of the temporal dynamics of conscious perceptual processing. ERP measures the temporal location of brain events correlated with conscious processing evoked by stimulus presentation. These studies indicate that the ERP P300 and N400 components are related to working memory and/or attention functions that probably involve conscious processing (Coull, 1998; Knight, 1997). The corresponding brain events occur from 300 to 400 ms after stimulus presentation. According to Pereira and Furlan (2009), these data suggest that 200 ms can be a good estimation of the minimum temporal duration from stimuli presentation to the formation of a conscious percept.

Therefore, the neuronal activity required to support conscious processing would need to be sustained from 200 ms to 2/3 s. Consistently, studies on subliminal perception (Murphy and Zajonc, 1993) reveal that a visual stimulus presented for only 5 ms and followed by a mask is not consciously perceived, although it may have unconscious priming effects. This implies that a threshold input firing for perceptual consciousness has not been reached (Pereira and Furlan, 2010).

Since such an appropriate temporal dynamics (from 200 ms to 2/3 s) of conscious events is the result of processes linking a large network of brain systems (Buzsáki, 2007; Laureys, 2005), it follows that the spatial dimension (i.e. the brain’s morpho-functional organization) is a key feature to consider in order to derive deductions on the communication modes involved in brain integrative processes leading to conscious percepts.

In the present review aspects of the brain’s morpho-functional organization corresponding to increasing levels of integration will be addressed (also based on data and hypotheses proposed by our group). In particular, the following issues and their relevance for consciousness formation will be analyzed:

1. Recent findings on the special features of neurons and astrocytes (Agnati et al., 1995; Allman et al., 2005; Pereira and Furlan, 2010; Premack, 2007) and the possible existence

- of a proto-consciousness phenomenon founded on the mechanism of cell ‘sentience’ (Cook, 2008; Sevush, 2006);
2. The Volume and Wiring Transmission (VT, WT) modes of communication processes in the brain (Agnati et al., 2005a, 2010a) will be briefly examined since they are the fundamental neurobiological mechanisms that allow the dynamic formation of cell assemblies and the integration of their activity.
3. The concept of mosaics of computational elements will be introduced (Agnati et al., 1982, 1990, 2007a, 2008). In particular, the cellular mosaic (Functional Module, FM) formed by neuron–astroglial interactions will be analyzed and proposed to be capable of a first-level integrative sentience;
4. Mechanisms for large-scale integration of FMs into mosaics of higher-order leading to the formation of the neuronal correlates of consciousness allowing the integration of different percepts will be analyzed from the neurobiological perspective.

Finally, these aspects will be used to propose a new interpretative metaphor of consciousness, namely the brain as a ‘Hall of Mirrors’.

2. Special features of neurons and astrocytes in the human brain

A neurobiological approach to the human capacity for auto-reflection should start at the lower level to clarify the fundamental question of what neural substrates make a human being human (DeFelipe et al., 2002). Plainly, these investigations focused on the amount of neurons and synaptic contacts, the presence of some type of special neurons, the properties of astrocytes and, of major potential interest, a comparison of possible specific features in some transmitter-identified neuronal systems such as monoamine systems (for details see Fuxe et al., 2010).

2.1. Neuronal aspects specific to the human brain

Let us start by examining some data on the peculiarities of neurons present in the human brain.

2.1.1. Quantitative evaluations of neural and synaptic densities
A crucial quantitative difference in neuronal density (neurons/mm³ in layers I–VI) distinguishes the human brain from other species. Neuronal density in the cerebral cortex is lower in humans (24186/mm³) than in rats (54483/mm³) and mice (120315/mm³), whereas the number of synapses per neuron is higher in humans (29807) than in rats (18018) and mice (21133) (DeFelipe et al., 2002). The number of dendritic spines of basal dendrites of layer III pyramidal neurons also differs in mouse and human temporal cortex. The mean number (mean±SEM) of spines per 10 μm segment is 10.9±0.5 for cells in temporal cortex of mice and 14.2±0.4 with respect to the temporal cortex of humans (Benavides-Piccione et al., 2002). Study of the size of spine heads revealed that the mean area in the temporal cortex of mice was smaller than in humans (mean±SEM: 0.37±0.01 μm² and 0.59±0.01 μm², respectively) and the spine necks in the temporal cortex of

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