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Research Report

Recent and remote memory recalls modulate different sets of stereotypical interlaminar correlations in Arc/Arg3.1 mRNA expression in cortical areas

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ABSTRACT

Detailed organization of interlaminar relations in neuronal activity underlying recent and remote memory recall is unknown but essential for deciphering interlaminar connections involved in systems-level memory consolidation and permanent information storage. We mapped Arc/Arg3.1 (Arc) mRNA expression, a neuronal activity marker, at multiple rostro-caudal levels of the brain in Wistar rats following a platform search in a water-maze task. Strength of interlaminar correlations in Arc expression and modulation of the strength by memory recall in sensory, motor and association cortical areas were measured at 24 h and 1 month in memory retention. In order to estimate the extent of modular organization in neocortical function underlying memory recall, we studied multiple profiles of interlaminar coupling. At the level of cortical areas, we captured two robust stereotypical laminar patterns for distribution of strong and weak interlaminar correlations. These patterns emerged during both control swimming and navigation, at both retention delays. Within limits of these patterns, we established task-, time- and area-dependent modulations of the Arc correlations. Relative to swimming control, during memory recall, changes in strength of analogous interlaminar relations occurred largely in parallel but recent and remote recall modulated mostly distinct correlations. An effective remote memory recall was accompanied by fewer strengthened correlations as compared to recent recall. Thus, a behavioral experience is accompanied by a well-ordered or stereotypical spatial organization of interlaminar relations in neuronal activity distribution. Interlaminar correlations in Arc expression modulated by recent and remote memory recall could guide future inactivation and detection studies necessary to decipher interlaminar connections involved in systems-level consolidation and to reveal mnemonic plasticity specific to spatial memory.

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Abbreviations: WM, Water maze; WMT, water-maze trained; SW, swimming control; IEG, immediate-early gene; Arc, activity-regulated cytoskeleton associated; Cg1, Cg2, cingulate cortices 1 and 2; RS, retrosplenial; Ins, insular cortices; MO, medial orbital; VO, ventral orbital; DLO, dorso-lateral orbital cortices; Par, parietal association; V1, visual primary; V2M, V2L, secondary medial and lateral cortices; S1, S2, M1, M2, respectively, somatosensory and motor primary and secondary cortices; FrAs, frontal association; Prl, prelimbic; LO, lateral orbital cortices; LEA, lateral entorhinal area; Li, layer i

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1. Introduction

According to both the standard and multiple trace theories of memory the cerebral cortex becomes a depository for remote declarative memories as a result of systems-level consolidation (Nadel and Moscovitch, 1997; Frankland and Bontempi, 2005; Squire and Bayley, 2007). For a spatial memory task such as water-maze (WM) task, the expansion of memory representation into the neocortex occurs within 7–10 days after completion of training on the task (Frankland et al., 2001; Remondes and Schuman, 2004; Teixeira et al., 2006). Interlaminar communication plays a significant role in signal processing in the neocortex (Hirsch and Martinez, 2006). Most likely, structural and functional plasticity underlying remote memories are distributed very sparsely across the neocortex (Kim and Linden, 2007; Matynia et al., 2008; Holtmaat and Svoboda, 2009). Therefore it will be extremely difficult to elucidate roles of various interlaminar connections in long-term memory storage. Identifying candidate connections that could express mnemonic plasticity out of their vast variety would be an important initial step in a guided engram deciphering.

Maps of cortical layer activity during memory recall highlight putative storage sites at the levels of single layers. Comparative analysis of layer activation during recent and remote memory recall helps to monitor layer participation in systems-level memory consolidation. As a next step, we propose that modified interlaminar correlations in neuronal activity during memory recall highlight pairs of cortical layers whose interlaminar connections (at least a subset of them) may express enduring mnemonic plasticity. Changes in the interlaminar correlations during memory activation relatively to behavioral controls would suggest that some interlaminar connections between the two layers most likely express mnemonic plasticity.

Modular organization is a core postulate in theories for neocortical function and intelligence (Creutzfeldt, 1977; Mountcastle, 1997; Hawkins, 2004). There could be multiple spatial scales for modular organization (Rockland and Ichinohe, 2004). Microcircuitries across the entire neocortex are characterized by a number of common elements and patterns in structural and functional organization (Silberberg et al., 2002; Mountcastle, 2003; Thomson and Bannister, 2003; Hirsch and Martinez, 2006; Markram, 2006) and gene expression (Lein et al., 2007). This type of consistent organization has been termed stereotypy (Silberberg et al., 2002). Although participation of neocortical modules in systems-level consolidation has been proposed in theoretical models (McClelland et al., 1995), experimental evidence about the extent of modular or stereotypical organization in laminar activity representing memory recall is very limited. Stereotypical and well-ordered organization of interlaminar activity would be essential for deciphering sparsely distributed memory engram. Stereotypical organization of memory related activity could facilitate detection of enduring storage correlates by pointing at most common putative storage sites/connections across the entire cortex.

Arc/Arg3.1 is an effector immediate early gene (IEG) encoding an activity-regulated cytoskeleton-associated (Arc) and a synaptic protein expressed by cortical excitatory neurons following strong synaptic activity and behavioral experiences (Link et al., 1995; Lyford et al., 1995; Guzowski et al., 2000; Vazdarjanova et al., 2006). We used Arc mRNA expression as a molecular marker for neuronal activity induced by water-maze (WM) memory recall in the hippocampus (Gusev et al., 2005). Arc has been implicated in Hebbian and homeostatic neuronal plasticity, memory consolidation, and experience-dependent changes in sensory representations (Guzowski et al., 2000; Plath et al., 2006; Rial Verde et al., 2006; Shepherd et al., 2006; Wang et al., 2006). Thus Arc mRNA may also serve as an indicator of excitatory neurons undergoing plasticity processes underlying information storage. In line with studies employing IEG mapping (Tagawa et al., 2005; Zhang et al., 2005), we use Arc induction as a marker of brain regions in which neuronal genomic activation occurs during memory tests. This genomic activation may not directly reflect the number of spikes fired by neurons. With this consideration, we will further refer to genomic activation of neurons as to neuronal activity.

We now map pairs of cortical layers that display changes in Arc expression correlations after recent or remote WM memory recall. A correlation approach is more sensitive in discovery of subtle changes in the brain activity when compared to isolated analyses of total frequency or temporal structure of spike activity (Baeg et al., 2007), and expression of immediate early genes (IEGs) (Poirier et al., 2008). Correlation analyses of action potentials trains, EEG, MEG, and fMRI across the brain areas revealed the candidate brain mechanisms such as synchronization and small-world network operation and elucidated the narrow range of changes in brain activity upon switch from one task to another (Singer, 1999; Salinas and Sejnowski, 2001; Fries, 2005; Bassett et al., 2006; Sporns and Honey, 2006; Bullmore and Sporns, 2009).

Modulated Arc correlations highlight the pairs of cortical layers whose interlaminar connections between excitatory neurons could be altered and represent memory storage. The correlation analysis is as an extension of our previous studies of Arc mRNA expression levels in the hippocampus (Gusev et al., 2005) and the neocortex (Gusev and Gubin, 2010). We now examine the hypothesis that distribution patterns for weak and strong pairwise correlations in Arc laminar expression are stereotypical across various cortical areas during varied behaviors. We further measured modulation of the Arc correlations by recent and remote memory recall. We propose that a set of the stereotypical pairwise correlations in neuronal activity distribution (or an interlaminar functional connectome) measured at the level of an anatomical area represents function of a new type of cortical modules. The maps for pairs of cortical layers with modulated interlaminar correlations in Arc expression following memory recall can guide future inactivation and detection studies necessary to decipher anatomical interlaminar circuits involved in systems-level consolidation and to reveal mnemonic plasticity specific to spatial memory storage.

2. Results

2.1. *Rats recall a hidden platform position without decline 1 month after training*

We represent here a description of behavioral data originally published in our hippocampal and neocortical mapping studies (Gusev et al., 2005; Gusev and Gubin, 2010).

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