Neural Networks 24 (2011) 1062–1073

Contents lists available at SciVerse ScienceDirect

Neural Networks

journal homepage: www.elsevier.com/locate/neunet

Persistent storage capability impairs decision making in a biophysical network model

Dominic Standage [a,b,*], Martin Paré [a,b,c]

[a] Canadian Institutes of Health Research Group in Sensory-Motor Integration, Queen's University, Canada
[b] Department of Physiology, Queen's University, Canada
[c] Department of Psychology, Queen's University, Canada

ARTICLE INFO

Article history:
Received 18 March 2010
Received in revised form 21 February 2011
Accepted 11 May 2011

Keywords:
Decision making
Persistent mnemonic activity
Network model
NMDA receptor
Working memory
Posterior parietal cortex
Lateral intraparietal area

ABSTRACT

Two long-standing questions in neuroscience concern the mechanisms underlying our abilities to make decisions and to store goal-relevant information in memory for seconds at a time. Recent experimental and theoretical advances suggest that NMDA receptors at intrinsic cortical synapses play an important role in both these functions. The long NMDA time constant is suggested to support persistent mnemonic activity by maintaining excitatory drive after the removal of a stimulus and to enable the slow integration of afferent information in the service of decisions. These findings have led to the hypothesis that the local circuit mechanisms underlying decisions must also furnish persistent storage of information. We use a local circuit cortical model of spiking neurons to test this hypothesis, controlling intrinsic drive by scaling NMDA conductance strength. Our simulations provide further evidence that persistent storage and decision making are supported by common mechanisms, but under biophysically realistic parameters, our model demonstrates that the processing requirements of persistent storage and decision making may be incompatible at the local circuit level. Parameters supporting persistent storage lead to strong dynamics that are at odds with slow integration, whereas weaker dynamics furnish the speed–accuracy trade-off common to psychometric data and decision theory.

1. Introduction

The length and variability of the time needed to discriminate visual stimuli and the susceptibility of this behaviour to errors indicate that decisions intervene between sensory and motor processing (see Schall, 2001, for review). The eye movement system has been invaluable as a model of decision making and experiments on non-human primates show that decisions can be decoded from neural activity in several cortical regions, including the lateral intraparietal area (LIP) of posterior parietal cortex (PPC) (Roitman & Shadlen, 2002; Thomas & Paré, 2007) and the frontal eye fields (FEF) (Schall & Hanes, 1993) and dorsolateral region of pre-frontal cortex (PFC) (Hasegawa, Matsumoto, & Mikami, 2000).

Abstract mathematical models have long provided phenomenological explanations of decision making. Sequential sampling models assume that decision making involves an integration process, where evidence is integrated until a threshold is reached (see Smith & Ratcliff, 2004). Because neural processing is noisy and evidence may be incomplete or ambiguous, integration is slower than the sampling rate, so decisions are based on an average of the evidence and not on momentary fluctuations in processing (see Bogacz, 2007). Several models have addressed the neural mechanisms underlying such a process (Usher & McClelland, 2001; Wang, 2002; Wong & Wang, 2006). The underlying premise of these models is that a discrete population of pyramidal neurons is selective for each decision option, and that competition between these populations is provided by a common pool of inhibitory interneurons. Activity in each stimulus-selective population therefore comes at the expense of the other(s), providing a natural means of selection that scales with the number of decision options. Under constraints with biophysical correlates, mutual inhibition instantiates a calculation of the difference between the evidence favouring each option in two-choice tasks, a process known to optimize speed and accuracy with respect to one another with independent sequential samples (see Bogacz, Brown, Moehlis, Holmes, & Cohen, 2006). Consistent with cortical processing (Douglas & Martin, 2004, 2007), intrinsic (recurrent) activity is crucial to these models, where the time constant of integration depends on a balance between the passive leakage of information and the amplification of information by recurrent activity (Usher & McClelland, 2001).

Biophysically based models predict that NMDA receptors (NMDAR) at intrinsic synapses onto pyramidal neurons provide

---

[*] Corresponding address: Department of Physiology, Queen's University, Botterell Hall, Room 453, 18 Stuart Street, K7L 4K9 Kingston, Ontario, Canada. Tel.: +1 613 533 3256; fax: +1 613 533 6880.

E-mail address: standage@biomed.queensu.ca (D. Standage).

0893-6080/$ – see front matter © 2011 Elsevier Ltd. All rights reserved.
doi:10.1016/j.neunet.2011.05.004

an important mechanism underlying the integration of evidence, where their long time constant enables the slow buildup of evidence (Wang, 2002; Wong & Wang, 2006). It is widely believed that intrinsic synapses also provide a mechanism for persistent mnemonic activity following the extinction of a stimulus, though this mechanism is just one of a number of mechanisms hypothesized to support persistent mnemonic activity (see the Discussion). Such activity is extensively correlated with working memory, the active retention of information for use in cognitive tasks (Goldman-Rakic, 1995; Wang, 2001). In this regard, NMDARs are hypothesized to provide an excitatory plateau (Fransén & Lansner, 1995; Lisman, Fellous, & Wang, 1998) while limiting network oscillations (Durstewitz, Seamans, & Sejnowski, 2000; Wang, 1999), a hypothesis supported by observations that injection of NMDA blockers in PFC impairs working memory (Aura & Riekkinen, 1999; Dudkin, Kruchinin, & Chueva, 1997). Because persistent mnemonic activity has been recorded in cortices correlated with perceptual decisions, including PFC (Funahashi, Bruce, & Goldman-Rakic, 1989; Fuster, 1973), FEF (Bruce & Goldberg, 1985) and PPC (Gnadt & Andersen, 1988), it has been proposed that intrinsic excitation strong enough to support persistent mnemonic activity is a property of decision circuits (Wang, 2002, 2008; Wong & Wang, 2006), similar in principle to suggestions that persistent storage (PS) capability may be required for coordinate transformations in PPC (Salinas & Sejnowski, 2001).

To address the hypothesis that decision making relies on local circuit PS capability (Wang, 2002, 2008; Wong & Wang, 2006), we model a decision-correlated circuit in LIP with a spiking implementation (Ardid, Wang, & Compte, 2007; Compte, Brunel, Goldman-Rakic, & Wang, 2000; Furman & Wang, 2008; Gutkin, Laing, Colby, Chow, & Ermentrout, 2001; Ma, Beck, Latham, & Pouget, 2006) of a local circuit model widely used in population and firing rate simulations of cortical circuits (Douglas & Martin, 2007; Pouget, Dayan, & Zemel, 2000; Wilson & Cowan, 1973), including visuospatial maps in PFC (Camperi & Wang, 1998), PPC (Standage, Trappenberg, & Klein, 2005) and frontoparietal cortex (Cisek, 2006). A spiking implementation provides synaptic resolution, enabling the manipulation of intrinsic NMDARs. Unlike earlier models with discrete stimulus-selective neural populations (Usher & McClelland, 2001; Wang, 2002), the model assumes a columnar organization where the strength of intercolumnar pyramidal interactions decreases with axial distance (see Abeles, 1991; Goldman-Rakic, 1995; White, 1989). Combined with unstructured or more broadly tuned synapses onto inhibitory interneurons, this synaptic profile creates centre-surround activity in which pyramidal neurons support each other locally via intrinsic projections and inhibit each other distally via interneurons. This family of networks is often used to model persistent mnemonic activity in visuospatial working memory tasks (Camperi & Wang, 1998; Trappenberg & Standage, 2005), where intrinsic excitation must be sufficiently strong for a selective population to drive itself over a memory interval, necessitating strong inhibition to limit the spread of excitation. These constraints lead to strong intrinsic dynamics that naturally cater to choice selection in decision making tasks, but are potentially at odds with the slow, simultaneous buildup of activity seen in decision-related cortices in multiple-choice tasks (see Schall, 2001).

In simulated visuospatial tasks, we control the network's intrinsic drive by scaling NMDA conductance at intrinsic synapses onto pyramidal neurons. In a simulated visuospatial working memory task, we determine values of this parameter that support (and do not support) PS. In a simulated two-choice visual search task, we measure the decision making abilities of the network for a range of values of this parameter. Our decision making task has no memory component, so there is no *a priori* requirement of local circuit PS capability for task completion. Under parameters consistent with biophysical data, we find that parameters supporting PS lead to intrinsic dynamics too strong for slow integration of evidence, amplifying momentary fluctuations and leading to hasty, inaccurate decisions. The model is a much more accurate decision maker under parameters that do not support PS. Indeed, the best decision making network is far from the PS regime (Fig. 2). In this case, the network enacts a speed–accuracy trade-off with increasing task difficulty (eg. Palmer, Huk, & Shadlen, 2005), simulated reaction times and their distributions are consistent with those of psychophysical experiments, and simulated neural data are consistent with neural recordings in LIP during visual search tasks. This finding is different from that of earlier studies, but the mechanisms underlying it are much the same. Intrinsic processing fosters a balance between leakage and amplification of accumulated evidence (Usher & McClelland, 2001) that corresponds to a given NMDAR conductance strength (Wang, 2008). Under our parameters, the balance that best supports the task is outside the PS regime.

Our results fit with a distributed framework in which no single microcircuit is responsible for all aspects of a decision task, but where different functions (e.g. integration of evidence and choice selection) are mediated by different circuits (Beck et al., 2008). Our results further speak to the functions of decision-related cortical regions in distributed circuitry. For example, the prediction that decision circuits in LIP are characterized by weak intrinsic dynamics is consistent with reports that LIP represents the relative importance of items in the visual field (Goldberg, Bisley, Powell, & Gottlieb, 2006; Serences & Yantis, 2006), a function for which categorical dynamics are not well suited. The difference between our findings and those of earlier studies is explained by consideration of the network's time constant of integration, optimization of which is parameter dependent. We thus do not claim that PS capability cannot be a property of local circuits mediating decision processes, but under biophysically realistic parameters, we demonstrate the potential incompatibility of persistent mnemonic activity and decision making in the same local circuit at the same time.

2. Materials and methods

We simulated a decision circuit in LIP with a fully connected recurrent network of leaky integrate-and-fire neurons (Tuckwell, 1988) with 1000 pyramidal neurons and 250 interneurons, depicted in Fig. 1(A). Intrinsic (recurrent) activity from pyramidal cells was mediated by AMPA and NMDA conductances and from interneurons by GABA conductances (Fig. 1(B)). The strength or *weight* of pyramidal-to-pyramidal synapses was thus scaled by a decreasing function of spatial location (see Abeles, 1991; Goldman-Rakic, 1995; White, 1989), added to a baseline weight (Ardid et al., 2007; Compte et al., 2000; Tegnér, Compte, & Wang, 2002) (Fig. 1(C)). Combined with unstructured synapses between pyramidal cells and inhibitory interneurons, this synaptic profile creates a centre-surround network where pyramidal neurons support each other locally via intrinsic projections and inhibit each other distally via interneurons. In simulated visuospatial working memory and visual discrimination tasks, stimuli were simulated by Poisson spike trains where spike rates were drawn from a normal distribution and the mean corresponded to the centre of a Gaussian receptive field, depicted in Fig. 1(A) for the discrimination task. Spike response adaptation among upstream, visually responsive neurons was mimicked by a decaying function of input rate (Trappenberg, Dorris, Munoz, & Klein, 2001; Wong, Huk, Shadlen, & Wang, 2007) with a 40 ms (Thomas & Paré, 2007) response delay (Fig. 1(D)). These selective inputs were superimposed on non-selective Poisson input spikes that lead to background spike