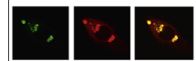


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Research Report

Induction frequency affects cortico-striatal synaptic plasticity with implications for frequency filtering



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ARTICLE INFO

Article history:

Accepted 16 April 2015

Available online 23 April 2015

Keywords:

Frequency filtering

Induction paradigm

Short-term depression (STD)

Long-term depression (LTD)

ABSTRACT

Long-term synaptic depression (LTD) in cortico-striatal circuits is initiated by depolarization of striatal medium spiny neurons through a convergent cortical glutamatergic input. This produces retrograde endocannabinoid signaling to presynaptic cortical terminals and eventually results in long term (>30 min) decreases in glutamate release. These same circuits can also undergo short-term depression (STD) through a less well-defined process in which the magnitude of postsynaptic responses returns to baseline levels within 10 min. Additionally, the cortico-striatal circuit shows characteristics of a GABA_A receptor-dependent low-pass filter, which results in significant attenuation of high frequency cortical inputs. The majority of in vitro studies of LTD have used a 100-Hz induction paradigm and it is unclear whether other frequencies, which may also have physiological relevance, have equivalent ability to induce this form of plasticity. Here we have investigated the effectiveness of a range of induction paradigms in producing LTD in cortico-striatal circuits, and demonstrate that some lower frequency paradigms, with perhaps more physiological relevance, are more effective at inducing LTD. We also show that GABA_A receptor-dependent frequency filtering in this circuit is altered following the induction of LTD and STD suggesting an important role for synaptic depression in signal processing in these circuits.

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1. Introduction

Synaptic plasticity underlies nervous system functions from signal processing to learning and memory (Neves et al., 2008; Song et al., 2000). Short-term changes occurring in presynaptic neurons and in feedback circuits underlie the frequency

dependency and immediate efficacy of transmission of action potentials through neuronal networks, while long-term changes in both the pre- and post-synaptic regions are thought to be the basis of learning and memory (Kreitzer, 2009; Lovinger, 2010). The glutamatergic synapse between layer V cortical projection neurons and medium spiny neurons (MSNs) in the dorsal

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striatum exhibits both of these forms of plasticity. Importantly, cortico-striatal circuits play an important functional role in various forms of associative learning and in modulation of motor behavior (Balleine et al., 2007).

The induction of long-term synaptic depression in cortico-striatal circuits is initiated by convergent glutamatergic (layer V) and dopaminergic (substantia nigra) inputs to MSNs leading to their depolarization and the activation of post-synaptic metabotropic glutamate receptors (mGluRs) and dopamine type-2 receptors (D2Rs). Simultaneous depolarization of MSNs and activation of these receptors leads to the production of endocannabinoids by MSNs, which retrogradely bind pre-synaptic CB1 receptors on glutamatergic terminals leading to long-term decreases in the probability of glutamate release—this phenomenon is characterized as long-term depression (LTD) (Surmeier et al., 2007). Descriptions of this form of LTD in cortico-striatal circuits have been predominantly based upon a high frequency induction paradigm using 3 to 4 trains of 100-Hz stimuli at maximum stimulus intensity (Calabresi et al., 1992). We have previously investigated the role of D2 and CB1 receptors in the induction of LTD following this 100-Hz high frequency stimulus paradigm (Baca et al., 2013) and have confirmed the occurrence of striatal LTD, and the role of both receptors in the LTD induction process.

This 100-Hz high frequency induction paradigm, through repetitive firing of glutamatergic fibers with coincident dopaminergic input, produces an initial post tetanic depression (PTD) followed in some instances by a process referred to here as short-term depression (STD), which is characterized by a return within about 10 min to response amplitudes equivalent to baseline levels prior to the induction paradigm. In other instances, a longer lasting LTD is induced, which is maintained for an excess of 30 min (Lovinger et al., 1993) and is characterized by significantly attenuated response amplitudes (Baca et al., 2013). The dependence of STD and LTD upon the frequency and magnitude of the induction paradigm has not been extensively investigated. One of the few published studies that examined the influence of the stimulus frequency on the induction of LTD in the striatum used a 10-Hz, 5-min stimulus train (Ronesi and Lovinger, 2005) instead of the 100-Hz induction paradigm commonly employed. This form of LTD, unlike that induced with the 100-Hz paradigm, does not appear to depend on post-synaptic depolarization or activation of mGluRs.

In vivo studies have shown that long term potentiation (LTP) is induced in striatal circuits with sustained focal 5-Hz stimulation of 500–1000 pulses (Charpier et al., 1999), but similar in vivo conditions for LTD induction have not been clearly established. It is known that layer V cortical inputs to striatal MSNs contain regular spiking (RS) and intrinsic bursting (IB) cells. In vivo measurements have shown that the mean frequency of spikes for IB cell burst firing is ~77 Hz and it is less for RS cells (Degenetais et al., 2002), so inputs from IB cells may provide high frequency input to striatal MSNs. Intra-somatic current injection of between 100 and 400 pA into patch-clamped dopamine D1- or D2 receptor-expressing MSNs reveals firing rates that are less than about 15 Hz for D1 MSNs and less than about 25 Hz for D2 MSNs, indicating that D2 MSNs are more excitable than D1 MSNs (Gertler et al., 2008). Recently, in vivo recordings of striatal MSNs showed baseline firing rates of ~4.5 Hz for

these neurons (Jin et al., 2014). During a task in which mice learned rapid action sequences by pressing a lever, it was found that MSNs fell into two populations one that demonstrated increases in baseline firing rates ranging from ~10–20 and another that showed decreases in firing rates below ~2 Hz (Jin et al., 2014). While the relationship of these rapid action sequence tasks to striatal plasticity has not been established, it does suggest the probable range of firing frequencies of MSNs during baseline and task-specific conditions. To better understand the role of long-term synaptic plasticity in cortical inputs to striatal MSNs, it is important to characterize the effectiveness of physiologically-relevant frequencies in the induction of STD and LTD. We therefore explored the relationship of the magnitude or occurrence of LTD and STD to the frequency and magnitude of the input stimulus when delivered at frequencies between 10 Hz and 100 Hz.

Following such an induction paradigm, the resulting LTD or STD in MSNs would be expected to affect subsequent transmission of information through the cortico-striatal circuit. We have previously demonstrated low-pass filter characteristics of layer V glutamatergic inputs to MSNs in the striatum (Jelinek and Partridge, 2012) and provided evidence that GABAergic feedback mechanisms underlie these characteristics. We have also previously shown differential filtering characteristics within the CA3, CA1, and dentate gyrus of the hippocampus (Scullin and Partridge, 2012), indicating that filter properties are a local property of specific brain regions. If this low-pass filtering and synaptic plasticity are a characteristic feature of the cortico-striatal circuitry, it is an interesting and important question to examine how these phenomena may interact. In this study, we have extended our previous findings to investigate the effect of the induction of LTD or STD in cortico-striatal synapses on the inherent low-pass filter characteristics of the striatal circuit.

2. Results

2.1. Comparison of frequency paradigms and LTD induction

Extracellular field excitatory postsynaptic potential (fEPSP) population spike (PS) amplitudes were measured in the medial portion of the dorsal striatum in coronal slices of P21–P28 C57/BL6 mice. To characterize the role of the frequency and magnitude of the input stimulus on the induction of synaptic depression, six distinct induction paradigms, which are outlined in Table 1, were used (see Section 4 for details).

The low frequency continuous stimuli induction paradigms (#1 and #2) were included in order to make comparisons with previous data (Lerner and Kreitzer, 2012; Kreitzer and Malenka, 2005; Ronesi and Lovinger, 2005), which suggest that there may be different mechanisms involved in the induction of STD or LTD at this frequency. The 400 stimuli induction paradigms (#3, #4, and #5) were included in order to assess the influence of the frequency with a fixed number of total stimulus pulses. Both half maximum and maximum stimulus intensities (stimulus current inputs to obtain half maximum or maximum PS outputs) were used in several of the induction paradigms in order to determine the influence of the magnitude of the stimulus on the induction of STD or LTD.

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