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Research Report

Environmental enrichment alters neuronal processing in the nucleus accumbens core during appetitive conditioning

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ABSTRACT

Although the core region of the nucleus accumbens (NAcc) has been implicated in motor control and the acquisition of appetitive learning, these processes are altered by environmental experience. To assess how environment influences neuronal processing in NAcc core, we recorded single-unit activity during acquisition of an appetitive learning task in which rats reared in an environmentally enriched condition (EC) learned the operant response (nosepoke into a lit hole) for sucrose reinforcement faster than rats reared in an isolated condition (IC). In the first training session, even before the emergence of learning differences, core neurons were more likely to respond (increase or decrease activity) during the operant and consummatory responses in EC than IC rats. By the third training session, when learning differences emerged, EC neurons continued to be more responsive than IC neurons, but in very different ways: the response shifted to the cues that signaled trial onset (1900 Hz tone and green LED) and reward availability (4500 Hz tone and yellow LED). Cue-related responding, moreover, was dominated by neuronal excitations. In contrast, post-acquisition recordings revealed no EC-IC differences. Collectively, these results suggest that core neurons are initially more responsive to discrete, goal-directed movements in EC rats, but as learning materializes, the neuronal response shifts to the cues that predict these movements. Thus, environmental experience alters core neuronal processing of both motor- and sensory-related events but at different stages over the course of learning.

1. Introduction

Anatomical, pharmacological, and electrophysiological investigations have long established that the nucleus accumbens (NAcc), a brain region found in ventral striatum, is involved in the regulation of adaptive, goal-directed activity, such as feeding (Heffner et al., 1980), drinking (Young et al., 1992), and sex (Fiorino et al., 1997; Mas et al., 1990). Accumulating data suggest that the NAcc, in particular, plays an important role in flexible approach of appetitive stimuli (Ikemoto and Panksepp, 1999; Mogenson and Nielsen, 1984; Wood et al., 2004; Wood and Rebec, 2004). Examination of the anatomical underpinnings of these behaviors reveals functional differences between the core and shell subregions. For example, shell is more sensitive to novel circumstances and more involved in visceral and motivational mechanisms (Carlezon and Wise, 1996; Maldonado-Irizarry et al., 1995; Rebec et al., 1997a,b), while core is involved specifically in motor control and

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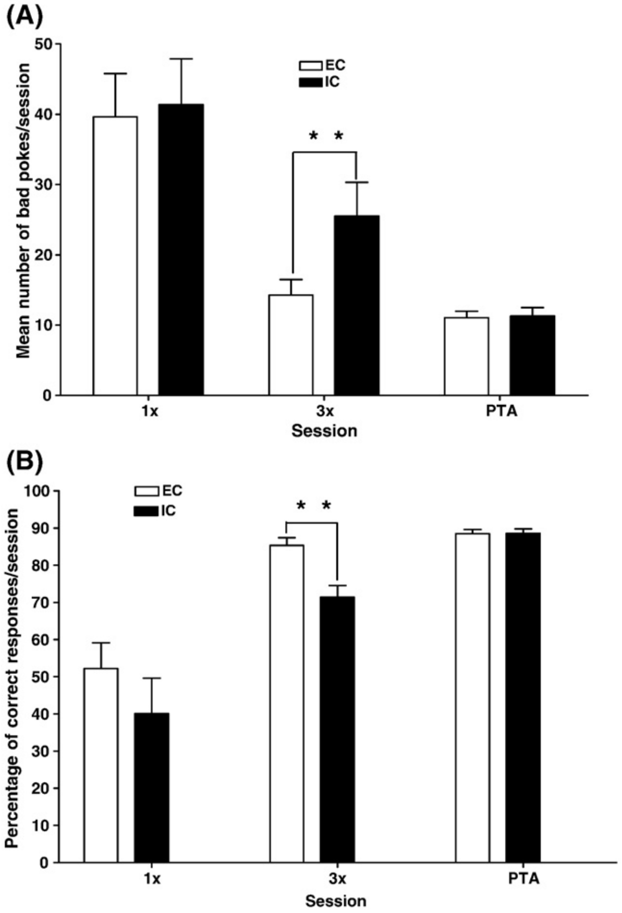

Fig. 1 – (A) Mean number of bad pokes in EC and IC rats during the first training session (1×), the third training session (3×), and post-training acquisition (PTA) recording sessions. As indicated (*), IC rats performed significantly more bad pokes than EC rats during 3× ($p<.01$), although no differences were observed during 1× or PTA. (B) Percentage of correct responses in EC and IC rats during 1×, 3×, and PTA. As indicated (*), EC rats exhibited a significantly higher percentage of correct responses than IC rats during 3× ($p<.05$) although no differences were observed during 1× or PTA.

learning of appetitive behavioral responses (Kelley et al., 1997; Maldonado-Irizarry and Kelley, 1995b; Smith-Roe and Kelley, 2000).

Other research shows that rats reared in an environmentally enriched (EC) or isolated condition (IC) exhibit clear behavioral and physiological differences. For example, in addition to enhanced learning capacity (for review, see Renner and Rosenzweig, 1987), EC rats exhibit reduced reward-seeking behavior (Bardo et al., 2001; Lamden and Rose, 1979; Rose and Lamden, 1983; Rose et al., 1985, 1986; van der Harst et al., 2003) and altered structure and function of the NAcc (Bowling et al., 1993; Wood et al., 2005) relative to IC littermates. To assess the impact of differential environmental experience on learning and reward-seeking behavior, we recently analyzed the behavioral performance of EC and IC rats during acquisition of a discriminative learning task for sucrose reinforcement (Wood et al., 2006). Because of reduced discriminative responding to the operant stimulus, IC rats acquired an appetitive learning task more slowly than EC rats. Our working hypothesis is that this learning difference occurs in conjunction with differential responsiveness of NAcc core neurons to individual task events as learning progresses. To test this prediction, we recorded single-unit activity in EC and IC rats during and after task acquisition.

2. Results

2.1. *Operant performance*

Training in our discriminative learning task was provided in three successive approximations or phases (see Section 4). Briefly, in phase one, animals learned that sucrose was available from a spout; this availability temporally corresponded with a feeder cue. In phase two, nosepokes were required to elicit this feeder cue (sucrose availability). In the third and final phase of training, a discriminative nosepoke to one of these two nosepoke holes (correct response) was required for the activation of the feeder cue.

As we observed in previous work (Wood et al., 2006), EC rats ($n=21$) acquired this discriminative behavioral response (phase-three training) more rapidly than IC rats ($n=17$). Because EC-IC behavioral differences were evident by the third session in this training phase, our analyses during acquisition of this discriminative learning response focused on the first and third sessions.

Although both groups performed comparably in the first session, by the third session EC relative to IC rats made significantly fewer bad pokes ($t=3.30$; $p<0.01$; see Fig. 1A) and had a significantly higher percentage of correct responses ($t=3.60$; $p<0.01$; see Fig. 1B). Thus, as we observed in previous work (Wood et al., 2006), third-session performance revealed a critical EC-IC behavioral difference. This difference was no longer evident in the post-training acquisition (PTA) session, indicating that with additional training IC rats can match EC performance.

2.2. *Electrophysiology*

During task acquisition (first and third training sessions) and PTA, we discriminated and recorded a total of 271 neurons in NAcc core in EC and IC rats (see Fig. 2). In both groups, similar proportions of neurons were identified during each session (see Table 1), and spike waveforms ranged between 0.6 and 1.2 ms in duration and 300 and 500 μV in amplitude. Signal-to-noise ratios of discriminated waveforms typically ranged between 3 and 4:1. Pre-trial baselines were similar in EC and IC rats, typically averaging between 2–3 spikes/s in each case.

2.3. *Unit responses during task acquisition*

During the first training session, roughly half of core neurons in EC rats exhibited phasic firing changes (excitations or inhibitions) during the nosepoke response to the lit hole (47%) and during sucrose consumption (47%), while significantly fewer neurons responded to these events (16%, $\chi 2=8.39$; $p<0.01$; 22%, $\chi 2=6.69$; $p<0.01$, respectively) in IC rats (see Fig. 3). In the