

A ROLE FOR MATERNAL PHYSIOLOGICAL STATE IN PRESERVING AUDITORY CORTICAL PLASTICITY FOR SALIENT INFANT CALLS

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Abstract—A growing interest in sensory system plasticity in the natural context of motherhood has created the need to investigate how intrinsic physiological state (e.g., hormonal, motivational, etc.) interacts with sensory experience to drive adaptive cortical plasticity for behaviorally relevant stimuli. Using a maternal mouse model of auditory cortical inhibitory plasticity for ultrasonic pup calls, we examined the role of pup care versus maternal physiological state in the long-term retention of this plasticity. Very recent experience caring for pups by Early Cocarers, which are virgins, produced stronger call-evoked lateral-band inhibition in auditory cortex. However, this plasticity was absent when measured post-weaning in Cocarers, even though it was present at the same time point in Mothers, whose pup experience occurred under a maternal physiological state. A two-alternative choice phonotaxis task revealed that the same animal groups (Early Cocarers and Mothers) demonstrating stronger lateral-band inhibition also preferred pup calls over a neutral sound, a correlation consistent with the hypothesis that this inhibitory mechanism may play a mnemonic role and is engaged to process sounds that are particularly salient. Our electrophysiological data hint at a possible mechanism through which the maternal physiological state may act to preserve the cortical plasticity: selectively suppressing detrimental spontaneous activity in neurons that are responsive to calls, an effect observed only in Mothers. Taken together, the maternal physiological state during the care of pups may help maintain the memory trace of behaviorally salient infant cues within core auditory cortex, poten-

tially ensuring a more rapid induction of future maternal behavior. © 2013 IBRO. Published by Elsevier Ltd. All rights reserved.

Key words: inhibitory plasticity, maternal behavior, vocalization, auditory cortex, sensory plasticity, spontaneous rate.

INTRODUCTION

An individual's internal state impacts ongoing perception and cortical processing of sensory stimuli (Gandelman, 1983; Parlee, 1983; Critchley and Rolls, 1996; Steinmetz et al., 2000; Supèr et al., 2003; Balçetis and Dunning, 2006; Niell and Stryker, 2010). Since such states are often mediated by neurochemical mechanisms that also contribute to experience-dependent cortical plasticity (Gu, 2002), the neural correlates of sensory memories acquired under distinct states are likely also different. Yet the neurobiological connection between internal states and sensory memories is not fully understood, particularly at the level of sensory cortex, where neural traces of sensory experience can be found (Weinberger, 2004; Ivanova et al., 2011). For example, a putative cortical signature of associative learning is sensory map plasticity, and internal factors like motivation during learning can affect the relative magnitude of this plasticity (Rutkowski and Weinberger, 2005). However, learned behaviors can persist in the absence of sensory map expansion (Reed et al., 2011), and other forms of neural plasticity may also contribute to the longer term memory trace of a sensory experience (Polley et al., 2004; Schnupp et al., 2006; Razak et al., 2008). Inhibitory plasticity is one such experience-dependent mechanism that has gained recent attention (Pallas et al., 2006; Galindo-Leon et al., 2009; Woodin and Maffei, 2011), though little is known about how internal states affect its long-term expression. Developing an understanding of how intrinsic factors influence forms of cortical plasticity can shed new light on how our sensory systems shape the inputs that lead to each individual's unique interpretation of the external world from prior experience.

Neuroplasticity during motherhood provides an opportune natural system in which to explore this question. Motherhood is associated with long-term behavioral (Fleming et al., 1994; Kinsley et al., 1999; Lambert et al., 2005; Pawluski et al., 2006) and neurophysiological (Fleming and Korsmit, 1996; Kinsley et al., 2006; Swain et al., 2007; Kim et al., 2010)

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Abbreviations: A1, primary auditory field; AAF, anterior auditory field; ABRs, Auditory Brainstem Responses; BF, best frequency; CC, correlation coefficient; FIR, Finite Impulse Response; LFP, local field potential; LSD, least significant difference; PSTH, peri-stimulus time histogram; RMS, root mean square; SU, single unit; UF, ultrasound field.

changes, including plasticity in inhibitory systems (Maguire and Mody, 2008; Maguire et al., 2009). Dramatic hormonal changes accompany pregnancy and parturition, and the degree to which this intrinsic maternal hormonal environment contributes to adaptive plasticity for infant care has been of long-standing interest (Terkel and Rosenblatt, 1972; Bridges, 1984; Fleming and Sarker, 1990; Maguire and Mody, 2009). Such questions now extend to sensory systems, given recent findings of sensory cortical plasticity during motherhood (Xerri et al., 1994; Liu et al., 2006; Rosset et al., 2006; Liu and Schreiner, 2007; Kim et al., 2010; Cohen et al., 2011). However, much less is known about how physiological state and experience might combine to establish and maintain functionally adaptive cortical plasticity.

We investigate maternal sensory plasticity in a mouse model of acoustic communication between offspring and adult females. Mouse pups emit bouts of ultrasonic whistles that are recognized as behaviorally relevant to mothers but not pup-naïve virgins (Ehret et al., 1987; Ehret and Koch, 1989). Neural correlates for this behavioral difference have been demonstrated in the auditory cortex of both anesthetized (Liu et al., 2006; Liu and Schreiner, 2007; Cohen et al., 2011) and awake, head-restrained animals (Galindo-Leon et al., 2009). In particular, after weaning pups, awake mothers show a stronger single unit (SU) pup call-evoked inhibition compared to virgins, an effect hypothesized to improve the functional detection of pup calls (Galindo-Leon et al., 2009). Rather than a reflection of the maternal physiological state, this long-term inhibitory cortical plasticity could simply be a result of experience with pups. We tested that possibility here using SU recordings in cocaring females, which are virgin mice that raise pups with a littermate mother. Importantly, cocarers do not undergo the same physiological changes as mothers, although they still behaviorally recognize pup ultrasounds after sufficient pup care experience (Ehret et al., 1987).

EXPERIMENTAL PROCEDURES

All surgical and experimental procedures were approved by the Emory University Institutional Animal Care and Use Committee. Experiments were carried out on adult CBA/CaJ female mice, all between 14 and 24 weeks old. Animals were housed under a reversed light cycle (14-h light/10-h dark), had access to food and water *ad libitum*, and were tested during their dark cycle. In the course of our study, distinct Animal Groups were used: Mothers, which were studied after weaning their pups at postnatal day P21; Virgins, which had no adult contact with pups and no breeding experience; Cocarers, which were adult virgins given the same full term (21 postnatal days) of experience caring for pups as a Mother (but without the physiological changes due to pregnancy, parturition and lactation) and studied after pups were weaned; and Early Cocarers, which were adult virgins with experience caring for pups with a Mother at least through postnatal day P6, and studied between P6 and

P11. In the subsequent text, these terms when capitalized refer to our specific study groups; when not capitalized, they refer to generic animals of their respective types.

All Mothers, Cocarers and Early Cocarers used in electrophysiological studies were screened to check that they would successfully retrieve scattered pups in the home cage over a 10-min period on P5 or P6 (retrieval screening for behavioral studies described below). This ensured that our animals not only had some minimum baseline of experience with ultrasonically vocalizing pups – verified by an ultrasound detector (U30, Ultra Sound Advice, London, United Kingdom) – but also showed comparable levels of maternal responsiveness.

Electrophysiological recordings

A head post surgery under isoflurane anesthesia was performed on animals a few days before chronic, restrained electrophysiological recordings began. During surgery, a stereotaxically targeted grid of small recording holes covering core auditory cortex was marked with India ink on the skull for later opening (~150- μ m diameter) before each recording session. Animals were given 2–3 days recovery before electrophysiological recording sessions began, at which point their weight and activity levels appeared normal. Before each day's recording session, animals were very briefly re-anesthetized with isoflurane and placed in the nose clamp of the stereotax so that small holes (about 150 microns diameter) could be drilled with an insect needle held by a pin vise (Fine Science Tools, Foster City, CA, USA) through the holes defined by the grid. Two to three hours after recovering from this brief procedure, the mouse was handled for 10 to 15 min to reduce stress and then prepared for electrophysiology recordings by placing them into a two-piece (top and bottom halves), plastic tube (~3-cm diameter) lined with soft foam. The animal's head post was affixed into a stationary metal bar while its restraint tube was suspended by rubber bands. This helped to ensure that any animal movement would not place torque on the head post, and to minimize any movement-related recording artifacts. If an animal did not acclimate well to the restraint, it was removed; no recordings were collected under sedation. Further details on the methods for head post implantation and lesions for electrophysiological studies may be found in (Galindo-Leon et al., 2009).

Electrophysiological recordings were performed on a vibration isolation table (TMC 63-533, Peabody, MA, USA) in a 9'-4" \times 10'-6" double wall anechoic chamber (IAC, Bronx, NY, USA) using 6 M Ω tungsten electrodes (FHC, Bowdoin, ME, USA), targeting the ultrasound field (UF), primary auditory field (A1), and the anterior auditory field (AAF) in the left auditory cortex (Galindo-Leon et al., 2009). An electrode was advanced using a hydraulic microdrive (FHC), while monitoring the activity on a computer speaker. A reference depth was established at the dural surface by listening for a change in the electrode channel noise level, and all SU and local field potential (LFP) recordings were located

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