



## Research paper

## Influence of inter-field communication on neuronal response synchrony across auditory cortex

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## ABSTRACT

Sensory information is encoded by cortical neurons in the form of synaptic discharge time and rate level. These neuronal codes generate response patterns across cell assemblies that are crucial to various cognitive functions. Despite pivotal information about structural and cognitive factors involved in the generation of synchronous neuronal responses such as stimulus context, attention, age, cortical depth, sensory experience, and receptive field properties, the influence of cortico-cortical connectivity on the emergence of neuronal response patterns is poorly understood. The present investigation assesses the role of cortico-cortical connectivity in the modulation of neuronal discharge synchrony across auditory cortex cell-assemblies. Acute single-unit recording techniques in combination with reversible cooling deactivation procedures were used in the domestic cat (*Felis catus*). Recording electrodes were positioned across primary and non-primary auditory fields and neuronal activity was measured before, during, and after synaptic deactivation of adjacent cortical regions in the presence of acoustic stimulation. Cross-correlation functions of simultaneously recorded units were generated and changes in response synchrony levels across cooling conditions were measured. Data analyses revealed significant decreases in response time coincidences between cortical neurons during periods of cortical deactivation. Collectively, the results of the present investigation demonstrate that cortical neurons participate in the modulation of response synchrony levels across neuronal assemblies of primary and non-primary auditory fields.

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## 1. Introduction

Networks of cortico-cortical connections have been implicated in the modulation of signal transmission between primary and non-primary auditory cortical fields [for review see (Hackett, 2011)]. In particular, functional assessments of inter-field communication in

feline and primate models, have shown that deactivation of auditory cortical fields can weaken the response rate of cells in nearby acoustic-responsive areas (Rauschecker et al., 1997; Carrasco and Lomber, 2009a,b; 2010). In light of these findings and mounting evidence demonstrating that neuronal response coincidences across cortical modules is crucial to sensory signal decoding (deCharms and Merzenich, 1996) and cognitive function [for reviews see (Singer, 1999; Uhlhaas and Singer, 2006)], the present investigation examined the influence of several known cortico-cortical pathways on the regulation of neuronal response synchrony.

Stimulus context (Singer, 1999), attention level (Singer, 1999), age (Eggermont, 1992), cortical depth (Eggermont, 1992), neuronal separation (Eggermont, 1992, 2000), sensory experience (Kilgard et al., 2007), and receptive field properties (Engel et al., 1990; Nelson et al., 1992; Brosch et al., 1995; Brosch and Schreiner, 1999; Brosch et al., 2002; Eggermont, 2006), have all been found to influence response synchrony levels. Despite these reports, it remains unclear how known inter-field circuits in auditory cortex

**Abbreviations:** A, anterior; AAF, anterior auditory field; aes, anterior ectosylvian sulcus; AI, primary auditory cortex; AII, second auditory cortex; D, dorsal; dPE, dorsal posterior ectosylvian area; DZ, dorsal zone of auditory cortex; IN, insular region; iPE, intermediate posterior ectosylvian area; FAES, auditory field of the anterior ectosylvian sulcus; P, posterior; PAF, posterior auditory field; pes, posterior ectosylvian sulcus; ss, suprasylvian sulcus; T, temporal region; V, ventral; VAF, ventral auditory field; VPAF, ventral posterior auditory field; vPE, ventral posterior ectosylvian area

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participate in the modulation of neuronal response patterns [cat: (Imig and Reale, 1980; Bowman and Olson, 1988; Clarey and Irvine, 1990; Rouiller et al., 1991; Winer and Lee, 2007; Lee and Winer, 2008b) monkey: (Fitzpatrick and Imig, 1980; Morel et al., 1993; Hackett et al., 1998, 1999; Kaas and Hackett, 2000; de la Mothe et al., 2012) rodent: (Budinger et al., 2000; Thomas and Lopez, 2003)]. This unresolved question has hindered the advancement of our understanding of information processing across acoustically responsive cortical regions. Consequently, in an attempt to expand current models of cortico-cortical functionality, we measured the effects of primary and non-primary auditory cortex silencing on the level of neuronal response discharge time coincidences across various auditory areas.

The well-described network of inter-field projections in cat auditory cortex offers a unique opportunity to study the role of cortico-cortical connections on neuronal synchronization (Imig and Reale, 1980; Bowman and Olson, 1988; Clarey and Irvine, 1990; Rouiller et al., 1991; Lee and Winer, 2008b). Based on established pathways of connectivity between primary and non-primary auditory fields (Lee and Winer, 2008b) and evidence of their role in neuronal response rate modulation (Carrasco and Lomber, 2009a,b; 2010); we hypothesized that deactivation of primary auditory cortex (AI) should disrupt response synchrony levels across clusters of second auditory cortex (AII) and posterior auditory cortex (PAF) neurons, and deactivation of AII neurons should result in discharge synchrony changes between AI cell-assemblies. Collectively, our results supported the proposed hypothesis by demonstrating that inter-field cortical networks can modulate the magnitude of neuronal response synchrony in various fields of auditory cortex.

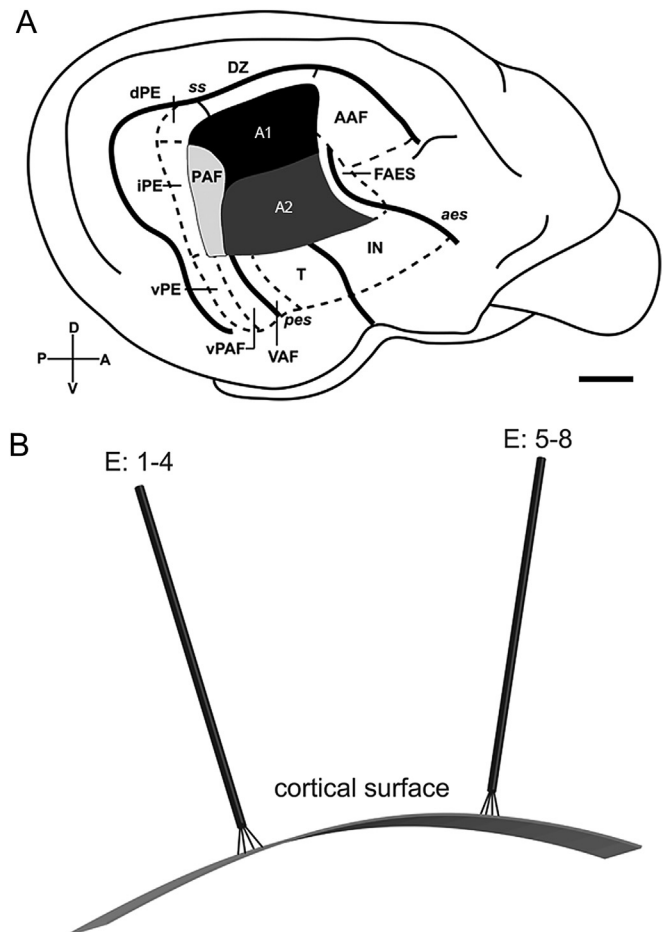
## 2. Materials and methods

### 2.1. Overview

Extracellular responses to acoustic signals were recorded from the right auditory cortex of 15 adult (>6 months) cats (*Felis catus*). Animals were housed in an “enriched” colony where social interactions, toys, and periods of acoustic and visual stimulation via a television set were available. Experimental procedures followed US National Research Council’s *Guidelines for the Care and Use of Mammals in Neuroscience and Behavioral Research* (2003), Canadian Council on Animal Care’s *Guide to the Care and Use of Experimental Animals* guidelines (Olfert et al., 1993), and were approved by the University of Western Ontario Animal Use Subcommittee of the University Council on Animal Care. Experimental techniques and earlier exploration of the data presented have been described in previous publications (Carrasco and Lomber, 2009a,b; 2010).

### 2.2. Preparation

After a 24-h fast, an initial dose of sodium pentobarbital (25 mg/kg i.v.) was used to induce general anesthesia (Cheung et al., 2001). Constant levels of anesthesia were maintained with supplemental doses of sodium pentobarbital administered based on blood oxygenation and electrocardiogram information. Body temperature was monitored and maintained at 37 °C with a water-filled heating system (Gaymar, model T/pump). Respiration was assisted by tracheal intubation and breathing secretions were reduced by administration of atropine (0.03 mg/kg s.c.) on a 12-h schedule. Animals were hydrated with an infusion pump supplying 2.5% dextrose/half-strength lactated Ringer’s solution (12 ml/kg/h i.v.). Cornea desiccation was prevented by applying ophthalmic ointment (Neosporin). The head was fixed by palato-orbital restraints and blunt (nonrupture) ear bars in a stereotaxic frame (David Kopf



**Fig. 1.** (A) Schematic view of cat auditory cortex. Highlighted regions represent cortical fields examined in the present study. Scale bar = 0.5 cm. (B) Illustration of electrode arrays positioning during recording periods. Sulci are indicated by italics and thick black lines. For abbreviations, see List.

Instruments, model 1530). A midline incision was made in the scalp, and the right temporalis muscle was removed from its origin and reflected laterally. Craniotomy and durotomy procedures were conducted over areas AI and AII, or AI and PAF (Fig. 1). Silicone oil was applied to the exposed pial surface to prevent tissue desiccation and dexamethasone (1.0 mg/kg i.v.), was used to decrease the risk of edema. A head-holder was attached to the frontal bone of the skull to hold and maintain head position while permitting access to auditory cortex. Ear bars and palato-orbital restraints were removed to eliminate pressure points on the animal. A photograph of cortical tissue was used to document the location of electrode penetrations in reference to cerebral vasculature.

### 2.3. Recording procedures

Extracellular activity was measured simultaneously from multiple cortical locations with parylene-coated tungsten microelectrodes arranged in  $2 \times 1$  or  $2 \times 2$  configurations and with impedances between 1 and 2 M $\Omega$  at 1000 Hz (FHC). Electrodes were placed approximately orthogonal to the cortical surface and lowered  $\sim 1200 \mu\text{m}$ . Independent micromanipulators (David Kopf Instruments) were used to lower two electrode arrays into cortex enabling the simultaneous recording of four to eight cortical locations. While electrodes within an array were separated by  $\sim 150 \mu\text{m}$ , the space between electrode arrays was dictated by the closest distance two carriers could be positioned before colliding

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