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Combination sensitivity and processing of communication calls in the inferior colliculus of the Moustached Bat *Pteronotus parnellii*

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ABSTRACT

Many animals use complex communication calls in social behaviors. In some species we know the features in the calls that elicit particular behaviors, but we do not understand how the auditory system encodes the calls. Nor do we understand the mechanisms underlying neural selectivity to calls. Our studies of the auditory midbrain of the Moustached Bat *Pteronotus parnellii* have revealed a neural mechanism important for generating selective responses to calls. Neurons that integrate information across different frequencies show selectivity to communication calls. "Combination sensitivity" may be a common mechanism for encoding complex sounds because it is also important for encoding echolocation signals.

Key words: auditory system, inferior colliculus, communication calls, bat.

INTRODUCTION

Many animals use acoustically complex communication calls in social interactions with conspecifics. The acoustic properties and functional importance of species-specific vocalizations have been studied in a variety of animals. For example, the importance of acoustic communication is well illustrated by the ability of mothers to recognize their own offspring in a variety of species (bats: Balcombe and McCracken 1992; fur seal: Insley 2000, Mathevon et al. 2004; penguins: Jouventin and Aubin 2002, Aubin 2004; sheep: Searby and Jouventin 2003). However, we have very little understanding of how communication sounds are processed in the auditory midbrain, particularly in mammalian species. The inferior colliculus (IC) is the main auditory midbrain nucleus, and almost all auditory information from lower centers converges in the IC (Brunso-Bechtold et al. 1981, Casseday et al. 2002). It is also the first site in the ascending auditory pathway where neurons with spectral integration properties emerge (Portfors and Wenstrup 2001, Wenstrup and Leroy 2001). Because of these features, the IC is a prime site to examine neural processing of complex sounds such as communication sounds.

Bats represent a model system for studying auditory processing of complex sounds because of their high reliance on echolocation for orientation and foraging (Griffin 1986). Because of this, most studies have focused on how the auditory system encodes and represents echolocation signals. What is often neglected is that bats also emit a rich repertoire of communication calls that are spectrally and temporally complex. Considering that bats likely evolved from a non-echolocating ancestor that used acoustic signals for communication, it is our hypothesis that similar neural mechanisms underlie

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the processing of echolocation and communication calls in the auditory midbrain. In this short communication, we outline the features of a certain type of neural response property, combination sensitivity, and discuss how this response may underlie processing of echolocation signals and communication signals in the IC of the Moustached Bat *Pteronotus parnellii.*

COMBINATION SENSITIVITY AND PROCESSING ECHOLOCATION SIGNALS

There are many combination-sensitive neurons in the IC of the Moustached Bat. These neurons integrate spectral and temporal information in complex sounds, and the majority of research has focused on how these neurons integrate elements in the echolocation signal of that species (Mittmann and Wenstrup 1995, Portfors and Wenstrup 1999). Combination-sensitive neurons respond in a facilitatory or inhibitory manner to combinations of distinct spectral elements in the echolocation signal as long as the elements occur in a specific temporal order. The Moustached Bat echolocation signal has a fundamental frequency in the 24-31 kHz range and consists of a constant frequency component (20-30 ms) followed by a brief (3-4 ms) frequency modulated (FM) down sweep. The characteristic frequency and temporal tuning of one type of combination-sensitive neuron, the so-called "FM-FM" neuron, provides an indication that this neuron type is involved in analysis of target distance information (Portfors and Wenstrup 1999). These neurons are tuned in frequency to one of the higher harmonic FM bands in the sonar signal (FM2, FM3 or FM4) and are facilitated by a second sound in the frequency band of the first harmonic FM (FM1) of the sonar call, providing that the two sounds occur in a specific temporal relation. In particular, the higher harmonic FM signal must occur after the FM1 signal. The time delay that elicits the best response (best delay) ranges between 1 and 20 ms (Portfors and Wenstrup 1999). These best delays correspond to the behavioral range of echolocation (Kick 1982). In frequency bands that represent the echolocation signal, over 70% of the neurons show either facilitatory or inhibitory combination sensitivity (Portfors and Wenstrup 1999) suggesting that combination sensitivity is a common response feature in the IC of the Moustached Bat, at least in the regions involved in processing echolocation signals. In the sections below, we provide evidence for combination-sensitive neurons in "non-sonar" frequency regions in the IC and suggest that these neurons may be involved in processing communication sounds.

FACILITATORY COMBINATION SENSITIVITY AND SELECTIVITY TO COMMUNICATION CALLS

The first suggestion that combination-sensitive neurons may be involved in processing sounds other than echolocation signals came from a study by Leroy and Wenstrup (2000) in which they showed that some neurons in the IC of the Moustached Bat were facilitated or inhibited by combinations of frequencies outside of the sonar frequency ranges. For example, some neurons were facilitated or inhibited by combinations of pure tones that had frequencies in the 10-23 kHz and 33-47 kHz bands. More recently, Portfors and Wenstrup (2002) studied neurons in the frequency bands between 15 and 59 kHz and found that over fifty percent of the neurons in this region of the IC had complex frequency tuning that included multiple excitatory frequency response areas and facilitatory combination sensitivity. Further, some neurons showed combination-sensitive facilitation to more than two different frequency sounds (Portfors and Wenstrup 2002). These complex frequency-tuning characteristics suggest that some neurons in the IC may be well suited for the analysis of the bat's communication calls.

The Moustached Bat has a rich repertoire of spectrally and temporally complex communication calls (Kanwal et al. 1994). We have examined selectivity of IC neurons to fourteen different communication calls and tested whether combination sensitivity could explain selective responses. In these experiments we inserted a micropipette electrode into the IC of the awake, restrained Moustached Bat and recorded responses of single neurons to pure

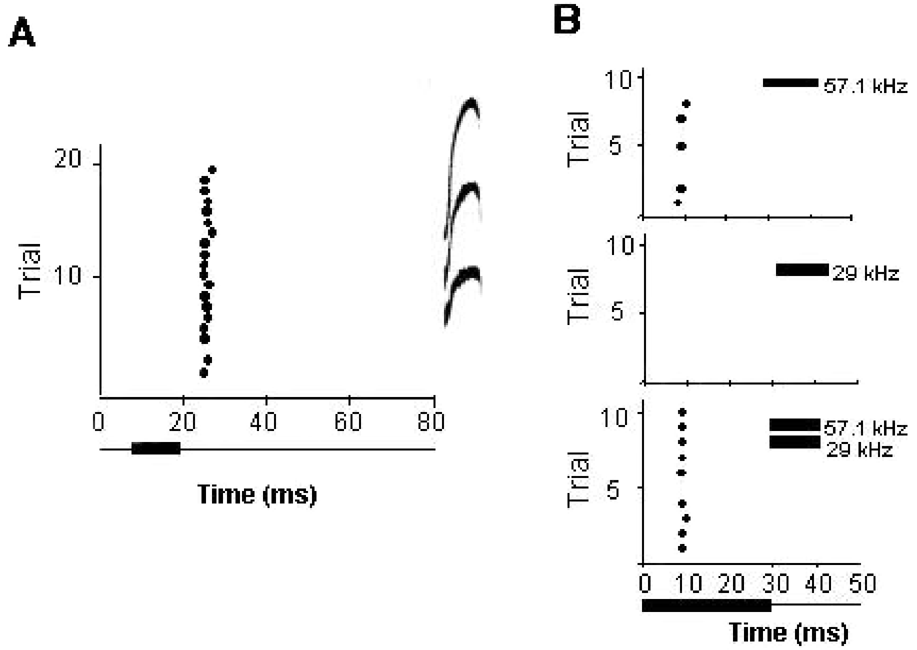

Fig. 1 – Responses of a single neuron in the IC to a communication call and tone stimuli. The single unit shown here responded to only one of fourteen different communication calls. A: Raster plot of the neuron's response to its preferred vocalization (three-harmonic, upward frequency modulated sweep call is shown in the insert). Twenty emissions of the call were presented to the single unit. B: Raster plots showing combination-sensitive response of the neuron. The neuron responded in a facilitatory manner to the combination of the 57 kHz and 29 kHz tones. Ten emissions of the stimuli were presented. Black bars under raster plots indicate onset time and duration of stimulus.

tones and communication calls. Sounds were presented through a speaker located 10 cm away and 25 degrees toward the contralateral ear. All sounds were presented at a range of intensities up to 80 dB-SPL. The major finding is that a neuron's response to communication calls was not well predicted by its response to single tones but was well predicted by its combination-sensitive response. Figure 1 shows an example of a neuron that only responded to one call (a multi-harmonic, upward frequency modulated sweep; Fig. 1A) regardless of intensity. This selectivity could not be explained by the neuron's response to single tones (excitatory frequency response area) but could be explained by the neuron's combination-sensitive facilitatory response to pairs of tones. The neuron responded weakly to tones at and near 57 kHz and was facilitated when a tone in that frequency was presented simultaneously with a second tone around 29 kHz (Fig. 1B). The communication call to which this neuron responded had energy in both the 57 kHz and 29 kHz bandwidths and these frequency components overlapped in time (Fig. 1A). The important characteristics of this neuron were the weak response to the high frequency tone and the robust facilitatory response to the combination of the two tones. These features caused the neuron to respond poorly or not at all to vocalizations that had energy in only one of the frequency bands and to respond well to vocalizations with energy in at least two of the frequency bands as long as the spectral components of the vocalization were in the proper temporal relationship. Thus, the combination-sensitive properties of some neurons in the IC of the Moustached Bat make these neurons selective to particular communication calls.

INHIBITORY COMBINATION SENSITIVITY AND SELECTIVITY TO COMMUNICATION CALLS

Inhibition is another mechanism for creating selectivity. Klug et al. (2002) tested selectivity of neurons in the IC of the Mexican Free-tailed Bat *Tadarida brasiliensis* to ten different communication calls and found that most neurons showed selective responses to a subset of the vocalizations even though some of the other vocalizations had energy in the excitatory frequency response area of the neuron. Using iontophoresis of bicuculline (a GABA receptor antagonist) onto the selective neurons, they showed that blocking inhibition decreased the selectivity of the neurons. In their study, however, it was not clear what range of frequencies was important for creating the selectivity.

In our studies of selectivity and combination-sensitivity in the Moustached Bat IC, we used a two-tone paradigm to determine the frequency tuning of the inhibitory combination-sensitive responses. Combination-sensitive inhibition occurs when the excitatory response of the neuron is inhibited by a second frequency signal that is at least one octave above or below the frequency that elicits the neuron's best response. Combination-sensitive inhibition presents an interesting mechanism for suppressing a neuron's response to a variety of stimuli, thereby creating selectivity. For example, a neuron with a best frequency of response of 50 kHz would be expected to respond to all communication sounds with energy in that frequency range. However, if the neuron was also inhibited by a second sound in the 18-25 kHz range, it would not respond to any calls that had energy in both of the frequency ranges. This type of inhibitory combination sensitivity is common in the IC of the Moustached Bat and seems to play an important role in creating selectivity to certain communication calls.

CONCLUDING COMMENTS

In this short communication we have briefly described how facilitatory and inhibitory combination sensitivity may underlie the selectivity to communication calls of some neurons in the IC of the Moustached Bat. Many questions remain regarding the processing and representation of communication calls in the auditory system. For example, it is not clear whether combination sensitivity underlies processing of communication calls in other mammals. We have recent evidence that some neurons in the Laboratory Mouse *Mus musculus* IC show combination-sensitive facilitation and/or inhibition, but we do not know if these neurons are involved in processing communication calls (Portfors 2003). However, considering that many of the spectral and temporal features of combination-sensitive neurons in Laboratory Mouse IC are similar to those in Moustached Bat IC, it seems likely that combination sensitivity is a common neural mechanism in mammals for generating selectivity in neurons involved in processing complex sounds.

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RESUMO

Muitos animais usam gritos de comunicação complexos nos seus comportamentos sociais. Sabemos em algumas espécies quais parâmetros dos gritos estimulam determinados comportamentos, mas não entendemos como o sistema auditivo codifica os gritos. Tampouco entendemos os mecanismos subjacentes à seletividade neural aos gritos. Nossos estudos do mesencéfalo auditivo do morcego *Pteronotus parnellii* revelaram um mecanismo neural importante para produzir respostas seletivas aos gritos. Neurônios que integram informação proveniente de várias freqüências diversas mostram seletividade a gritos de comunicação. "Sensibilidade a combinações" de freqüências pode ser um mecanismo comum para codificar sons complexos, já que é importante também para codificar sinais de ecolocação.

Palavras-chave: sistema auditivo, colículo inferior, gritos de comunicação, morcego.

REFERENCES

AUBIN T. 2004. Penguins and their noisy world. An Acad Bras Cienc 76: 279-283.

BALCOMBE JP AND MCCRACKEN GF. 1992. Vocal recognition in Mexican Free-tailed Bats: do pups recognize mothers? Anim Behav 43: 79-87.

BRUNSO-BECHTOLD JK, THOMPSON GC AND MASTERTON RB. 1981. HRP study of the organization of auditory afferents ascending to central nucleus of inferior colliculus of cat. J Comp Neurol 197: 705-722.

CASSEDAY JH, FREMOUW T AND COVEY E. 2002. The inferior colliculus: A hub for the central auditory system. In: OERTEL D et al. (Eds), Integrative functions in the mammalian auditory pathway. New York: Springer Verlag, p. 238-318.

GRIFFIN DR. 1986. Listening in the dark. Ithaca, NY: Cornell University Press.

INSLEY SJ. 2000. Long-term vocal recognition in the Northern Fur Seal. Nature 406: 404-405.

JOUVENTIN P AND AUBIN T. 2002. Acoustic systems are adapted to breeding ecologies: individual recognition in nesting penguins. Anim Behav 64: 747-757.

KANWAL JS, MATSUMURA S, OHLEMILLER K AND SUGA N. 1994. Analysis of acoustic elements and syntax in communication sounds emitted by Mustached Bats. J Acoust Soc Am 96: 1229-1254.

KICK SA. 1982. Target detection by the echolocating bat, *Eptesicus fuscus*. J Comp Physiol 145: 431-435.

KLUG A, BAUER EE, HANSON JT, HURLEY L, MEITZEN J AND POLLAK GD. 2002. Response selectivity for species-specific calls in the inferior colliculus of Mexican Free-tailed Bats is generated by inhibition. J Neurophysiol 88: 1941-1954.

LEROY SA AND WENSTRUP JJ. 2000. Spectral integration in the inferior colliculus of the Mustached Bat. J Neurosci 20: 8533-8541.

MATHEVON N, CHARRIER I AND AUBIN T. 2004. A memory like a fur seal female: long-lasting recognition of pup's voice by mothers. An Acad Bras Cienc 76: 237-241.

MITTMANN DH AND WENSTRUP JJ. 1995. Combination-sensitive neurons in the inferior colliculus. Hear Res 90: 185-191.

PORTFORS CV. 2003. Spectral and temporal response properties of single neurons in the inferior colliculus of the mouse. Daytona Beach, Florida, USA: Assoc Res Otolaryngol Abstr, p. 175.

PORTFORS CV AND WENSTRUP JJ. 1999. Delay-tuned neurons in the inferior colliculus of the Mustached Bat: Implications for analyses of target distance. J Neurophysiol 82: 1326-1338.

PORTFORS CV AND WENSTRUP JJ. 2001. Responses to combinations of tones in the nuclei of the lateral lemniscus. JARO 2: 104-117.

PORTFORS CV AND WENSTRUP JJ. 2002. Excitatory and facilitatory frequency response areas in the inferior colliculus of the Mustached Bat. Hear Res 168: 131-138.

SEARBY A AND JOUVENTIN P. 2003. Mother-lamb acoustic recognition in sheep: frequency coding. Proc R Soc Lond B 270: 1765-1771.

WENSTRUP JJ AND LEROY SA. 2001. Spectral integration in the inferior colliculus: role of glycinergic inhibition in response facilitation. J Neurosci 21: RC124 (1-6).