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Research Report

The commissural pathway and cochlear nucleus bushy neurons: An in vivo intracellular investigation

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ABSTRACT

A direct commissural connection formed between cochlear nuclei allows information from the contralateral ear to rapidly influence the processing of the ascending auditory signal. Among the neuronal groups proposed to both receive, and contribute to, commissural input is the bushy cell population in the ventral cochlear nucleus (VCN). In this in vivo electrophysiological study we examine the intracellular recordings of bushy neurons during electrical stimulation of the contralateral cochlear nucleus (CN) for evidence of both their contribution to, and input from commissural projections. Activation of the commissural pathway revealed short-latency fast hyperpolarisation in 19.5% of the 41 bushy neurons examined. The hyperpolarising potentials were small in amplitude, displayed a highly variable time course between neurons, and in some cases were eliminated with injection of depolarising current. There was no indication of antidromic activity, or short-latency excitatory potentials. These results suggest that i) bushy neurons do not contribute projections to the commissural connection, and ii) a small portion of bushy neurons are hyperpolarised following commissural stimulation.

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1. Introduction

The cochlear nucleus (CN), as the first brain centre in the central auditory system, is often regarded as a monaural nucleus, segregating the information received from the cochlea into multiple processing streams to be sent to the assortment of higher auditory centres. However, much evidence now exists to suggest that a commissural connection is present between cochlear nuclei, allowing contralateral information to influence the processing of the ascending auditory signal through the CN (Alibardi, 1998, 2000a,b; Arnott et al., 2004; Babalian et al., 1999, 2002; Cant and Gaston, 1982; Davis, 2005; Doucet and Ryugo, 2006; Joris and Smith, 1998; Mast, 1970, 1973; Needham and Paolini, 2003, 2006; Schofield and Cant, 1996a,b; Shore et al., 1992, 2003; Smith et al., 2005; Wenthold, 1987; Young and Brownell, 1976). This pathway has been implicated in the induction of inhibitory, and occasionally, excitatory effects in neurons throughout the CN (Babalian et

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Abbreviations: AP, action potential; AVCN, anterior ventral cochlear nucleus; BF, best frequency; CN, cochlear nucleus; EPSP, excitatory postsynaptic potential; GBC, globular bushy cell; ISI, interspike interval; P_L, primary-like; P_{LN}, primary-like with notch; PST, poststimulus time; RMP, resting membrane potential; SBC, spherical bushy cell; SR, spontaneous rate; VCN, ventral cochlear nucleus

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al., 1999, 2002; Davis, 2005; Joris and Smith, 1998; Mast, 1970, 1973; Needham and Paolini, 2003, 2006; Shore et al., 2003), and within the ventral cochlear nucleus (VCN) is proposed to principally target the T stellate and bushy cell populations (Alibardi, 2000a; Cant and Gaston, 1982; Schofield and Cant, 1996b).

Physiological evidence of contralaterally-mediated inhibition has been reported for both T stellate and bushy cell populations in intracellular in vitro studies following electrical stimulation of the contralateral auditory nerve (Babalian et al., 1999, 2002). However, the wide range of hyperpolarisation latencies was consistent with transmission via both monosynaptic and polysynaptic pathways. Whilst in vivo intracellular recordings together with stimulation of the contralateral CN have since revealed the monosynaptic nature of commissural input to T stellate neurons (Needham and Paolini, 2003, 2006), a similar in vivo investigation of commissural influences over the bushy cell population has not been undertaken. In addition, although commissural projections are principally proposed to arise from the broadly-tuned glycinergic D stellate (onset) population (Arnott et al., 2004; Doucet et al., 1999; Doucet and Ryugo, 2006; Joris and Smith, 1998; Kolston et al., 1992; Needham and Paolini, 2003, 2006; Schofield and Cant, 1996b; Smith et al., 2005; Wenthold, 1987), anatomical evidence provided by some studies suggests that projections may also originate from bushy neurons (Alibardi, 1998; Shore et al., 1992). Thus, the current study examines the involvement of bushy neurons as both a potential source and target of commissural projections.

The bushy cell population, typically divided into spherical and globular bushy cells (SBCs and GBCs respectively), is distinguished from other CN neurons in that it receives its afferent input via the endbulbs of Held, the large, secure endings of the auditory nerve (Brawer and Morest, 1975; Cant and Morest, 1979b; Rouiller et al., 1986; Ryugo and Sento, 1991; Sento and Ryugo, 1989). As afforded by their unique morphology and specific complement of membrane currents, these neurons are also renowned for their short time constant and low temporal summation (Manis and Marx, 1991; Oertel, 1983; Rothman and Manis, 2003a,b,c; Wu and Oertel, 1984). Together these properties provide the bushy neuron with the ability to faithfully reproduce, or even enhance, the temporal information contained within the signal of the auditory nerve (Joris et al., 1994; Pal et al., 2004, 2005; Rothman et al., 1993; Rothman and Manis, 2003a,b,c). Whilst these neurons respond to best frequency (BF) tones with a primary-like (P_L) or primary-like with notch (P_{LN}) pattern of activity as observed in the poststimulus time (PST) histogram (Pfeiffer, 1966; Rhode et al., 1983; Rouiller and Ryugo, 1984; Smith and Rhode, 1987), intracellularly the unique properties of the bushy neuron are reflected in a distinctive array of fast synaptic potentials, comprising both excitatory postsynaptic potentials (EPSPs) and action potentials (APs) (Feng et al., 1994; Ostapoff et al., 1994; Paolini et al., 1997; Rouiller and Ryugo, 1984; Smith and Rhode, 1987). Here we examine the intracellular activity of such neurons recorded in vivo during electrical stimulation of the contralateral CN to investigate both the nature of the commissural input to the bushy cell population, and, through the presence of antidromic activity, the contribution of their projections to the contralateral pathway.

2. Results

These results were gathered over a period of 3 years in conjunction with studies examining the role of the stellate cell populations in the commissural pathway (see Needham and Paolini, 2003, 2006; Paolini et al., 2004). The intracellular recordings presented here are proposed to represent the activity of the VCN's bushy cell population due to their intracellular profile observed in response to BF tones and/or noise (Section 2.1). Although the cellular origin of such activity was not identified morphologically given the constraints of intracellular recording in our experimental approach, we have proposed that these recordings most likely represent the activity of the globular bushy cell population on the basis of the location of electrode placement within the CN (Section 2.2).

2.1. *Intracellular Profile*

Intracellular recordings were obtained from 41 neurons displaying the distinct pattern of bushy cell activity—an assortment of fast synaptic potentials of variable amplitude, comprising both APs and EPSPs (Fig. 1). As seen in both the single (Fig. 1A) and averaged intracellular profile (Fig. 1A, inset) of one such neuron, the bushy cell response displayed a well-timed first spike and vigorous firing at stimulus onset before settling to more sustained levels of firing for the remainder of the tone, accompanied by a short period of post-tone hyperpolarisation at stimulus offset. The overall pattern of activity in the PST histogram (Fig. 1B, upper) and level of irregularity observed in the interspike interval (ISI) histogram (Fig. 1B, lower) of this neuron were both consistent with a P_L-type response. Indeed, correlation of the intracellular profile with either P_L or P_{LN} activity was possible in 17 neurons (13 P_L; four P_{LN}). However, it is important to note that difficulty differentiating APs from EPSPs in the intracellular profile (APs and EPSPs could be differentiated in less than 25% of cases: see also Smith and Rhode, 1987) suggest that the PST and ISI histograms provide only a guide to response pattern and cannot be used as a reliable means of classification alone.

Where BF tones could not be presented due to the limited time-frame over which stable intracellular recordings were possible, identification was made on the basis of the intracellular response to noise (the search stimulus; Figs. 1C–E). Like the response to tones, these intracellular profiles each exhibited a combination of fast EPSPs and APs. Indeed, as shown in Fig. 1C, noise-evoked activity closely matched that displayed by the same neuron during BF tone presentation (Fig. 1A). This profile was distinct from the responses observed in our extensive sample of intracellular recordings from chopper and onset neurons, the other major cell types found in the VCN (as shown in Needham and Paolini, 2006; Paolini et al., 2004, 2005).

Another feature common to many bushy neurons was the presence of a high spontaneous rate (SR) in the absence of auditory stimuli (Figs. 1F–G). As shown in the single intracellular profile (Fig. 1F, black trace), spontaneous activity comprised a combination of EPSPs (demonstrating little temporal summation) as well as APs. Interestingly, when averaged over a larger period of time (Fig. 1F, grey trace) the high levels of excitatory

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