

Intrinsic membrane properties of vertebrate vestibular neurons: Function, development and plasticity

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Abstract

Central vestibular neurons play an important role in the processing of body motion-related multisensory signals and their transformation into motor commands for gaze and posture control. Over recent years, medial vestibular nucleus (MVN) neurons and to a lesser extent other vestibular neurons have been extensively studied *in vivo* and *in vitro*, in a range of species. These studies have begun to reveal how their intrinsic electrophysiological properties may relate to their response patterns, discharge dynamics and computational capabilities. *In vitro* studies indicate that MVN neurons are of two major subtypes (A and B), which differ in their spike shape and after-hyperpolarizations. This reflects differences in particular K^+ conductances present in the two subtypes, which also affect their response dynamics with type A cells having relatively low-frequency dynamics (resembling “tonic” MVN cells *in vivo*) and type B cells having relatively high-frequency dynamics (resembling “kinetic” cells *in vivo*). The presence of more than one functional subtype of vestibular neuron seems to be a ubiquitous feature since vestibular neurons in the chick and frog also subdivide into populations with different, analogous electrophysiological properties. The ratio of type A to type B neurons appears to be plastic, and may be determined by the signal processing requirements of the vestibular system, which are species-variant. The membrane properties and discharge pattern of type A and type B MVN neurons develop largely post-natally, through the expression of the underlying ion channel conductances. The membrane properties of MVN neurons show rapid and long-lasting plastic changes after deafferentation (unilateral labyrinthectomy), which may serve to maintain their level of activity and excitability after the loss of afferent inputs.

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Abbreviations: 2°, second-order; 4-AP, 4-aminopyridine; AHP, after-hyperpolarization; ATD, ascending tract of Deiters; BK, high conductance calcium-dependent potassium channels; CaMKII, calcium/calmodulin-dependent protein kinase II; CV, coefficient of variation; Cx, connexin; DVN, descending vestibular nucleus; FTN, floccular target neurons; HTS, high threshold calcium spikes; Int, abducens internuclear neurons; IO, inferior oblique; IR, inferior rectus; LTD, long-term depression; LTP, long-term potentiation; LR, lateral rectus; LTS, low-threshold calcium spikes; LVN, lateral vestibular nucleus; LVST, lateral vestibulo-spinal tract; MLF, medial longitudinal fascicle; MVN, medial vestibular nucleus; MVST, medial vestibulo-spinal tract; Ncl. III, oculomotor nucleus; Ncl. IV, trochlear nucleus; Ncl. VI, abducens nucleus; NMDA, *N*-methyl-D-aspartate; PC, posterior vertical canal; PH, nucleus prepositus hypoglossi; RMP, resting membrane potential; SK, small conductance calcium-dependent potassium channels; SO, superior oblique; SR superior rectus; SVN, superior vestibular nucleus; Tan, tangential vestibular nucleus; TEA, tetraethylammonium; TTX, tetrodotoxin; UL, unilateral labyrinthectomy

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1. Introduction

For freely moving vertebrates, maintaining their body equilibrium in the gravitational field and being capable of orienting themselves in their environment are fundamental aspects of survival. The accurate control of posture and gaze results from a complex multisensory integration, which transforms and synthesizes multiple internal representations of head and/or body movement obtained through different sensory modalities (visual, vestibular and proprioceptive), into a unique internal frame of reference appropriate for the encoding of motor commands. This sensori-motor transformation requires precise spatial and temporal processing of sensory inputs. Among the key elements involved in this transformation are central vestibular neurons, which receive convergent semicircular canal and otolith inputs from the inner ear, and also proprioceptive and visual signals (Fig. 1A). In addition to spatial and temporal accuracy, the dynamics of the motor output signals that control gaze and posture must be precisely controlled. The motor signals that are relayed to the various extraocular and spinal targets (Fig. 1B) of central vestibular neurons must take into account the different inertial properties of the eyes, ears, neck, limbs and body, and must be able to cover the wide range of frequencies and amplitudes that characterize natural head and body movements.

The process of sensori-motor transformation relies both on the emergent properties of the neuronal networks involved, and on the intrinsic membrane properties of the individual neuronal components. Thus, a detailed knowledge of their electrophysiological properties is essential in understanding how central vestibular neurons process sensory signals to generate appropriate motor commands to control gaze and posture. Depending on their functional roles, different types of central vestibular neuron might be characterized by different sets of membrane properties. In addition, over the past 10 years it has become evident by the efferent connectivity (Fig. 1B) that central vestibular neurons are also essential for the generation of a spatial egocentric map, vegetative reactions and for spatial cognitive function and plasticity involving for instance the hippocampal areas (Berthoz, 1997; Smith, 1997; Cuthbert et al., 2000; Stackman et al., 2002). Therefore, these neurons play a major role both in the internal coding of space in the brain and in the motor control of gaze and posture. Both processes require the maintenance of a stable, internal representation of self-motion by the brain, in a continually changing internal and external environment. Indeed the complex transformation of sensory signals performed by central vestibular neurons must be constantly modified, for example in response to ageing-related deterioration or pathology of the inner ear or the motor apparatus, and in order to adapt to excessive natural

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