How do specializations of vestibular hair cells and primary afferent neurons shape vestibular signals?

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Head movements deflect the mechanosensitive hair bundles of vestibular hair cells, evoking electrical signals. The hair cells transmit the signals across synaptic contacts with fibers of the eighth nerve, which carry the signals to the brain. The signals contribute to our sense of orientation in space and drive reflexes that move the eyes, head and body to compensate for head movements. Without such compensatory reflexes, the visual world would move with every step you take. Indeed, damage to vestibular hair cells and afferents may be a significant cause of balance and mobility defects in patients, especially the elderly. Understanding vestibular dysfunction requires analysis of the mechanisms underlying normal function of the vestibular hair cells and neurons.

Vestibular organs of higher vertebrates – mammals, birds and reptiles – have several special properties that make them interesting from a neurobiological perspective. First, they have central and peripheral zones that are anatomically and physiologically distinct. (In the otolith organs, the analogous zones are called the striola and extrastriola.) In response to sinusoidal head movements, vestibular afferents from central/striolar zones have gains that rise with frequency and phases that lead the stimulus, whereas afferents from peripheral/extrastriolar zones tend to show less filtering. Other measures such as mutual information density reveal other differences in stimulus processing between the two zones. These differences may reflect between-zone differences at all levels of stimulus processing, including differences in: otoconial and gel layers of the accessory structures; hair bundles; electrical properties of hair cells; synaptic transmission; morphology of the afferent terminals; and intrinsic electrical properties and calcium binding proteins of the afferent neurons. Central/striolar afferent neurons also have the largest diameters and therefore the fastest conduction velocities.

A second special property of the vestibular organs of higher vertebrates is the presence of a unique receptor: the type I hair cell. Type I hair cells were first recognized anatomically by the form of the afferent ending (Wersäll 1955). For most hair cells, eighth-nerve fibers contact hair cells with small, button-shaped (bouton) nerve endings. For the type I hair cell, in contrast, the nerve ending is an elaborate, cup-shaped structure (calyx) that wraps much of the cell. More recently it has become clear that type I hair cells also have a distinctive set of ion channels which shape their receptor potentials (reviewed in Eatock and Lysakowski 2006). In birds and reptiles, type I cells and calyx endings are confined to central zones; in mammals, type I cells and calyx endings are found everywhere in the sensory epithelium, but differ anatomically between zones. The restriction of type I hair cells to higher vertebrates suggests that they serve specific roles in compensating the head movements of reptiles and their descendants. Unlike fish and amphibians, these animals have necks that permit independent head movements, which may be as a result relatively large and/or fast.

A third special property of the vestibular system in all species, but especially mammals, is the wide range in regularity of firing of vestibular afferent neurons. Vestibular afferents from the central/striolar zones tend to have highly irregular inter-spike intervals; in this property, they resemble auditory afferents. Vestibular afferents from the periphery/extrastriola, in contrast, have highly regular inter-spike intervals. This difference may influence the encoding properties of neurons innervating the two zones (Sadeghi et al. 2007). Regularity differences may reflect the detailed morphology of synaptic endings and terminal branches and the intrinsic ion channel properties of the afferent fibers (reviewed in Eatock et al. 2008).

In summary, the vestibular organs of higher vertebrates, including humans, have distinct zones. Afferents emanating from the central/striolar zones favor higher frequency head motions, have more irregular inter-spike intervals, and convey signals at greater speeds than peripheral/extrastriolar afferents. Such properties may specialize the central and striolar zones for fast motion signals and may arise through multiple specializations of accessory structures, hair cells and afferent neurons. Understanding the separate roles of central and peripheral zones has clinical relevance, given evidence that afferent signals from central and striolar zones are the most vulnerable to ototoxic insult (Wersäll 1981) and deterioration with aging (Leonard and Kevetter 2007).

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