The physiology of the peripheral vestibular system: the birth of a field

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This essay looks at the historical significance of three APS classic papers that are freely available online:


With this trilogy, Fernández and Goldberg (2–4) provided the first complete characterization of the physiology of the mammalian peripheral otolith system, which senses linear accelerations, including gravity and the inertial motion of the head in space. This treatise, which even to date represents the most comprehensive and thorough investigation of the spatial and temporal properties of primary otolith afferents, followed just a few years after the same authors had provided a similarly thorough characterization of the other type of vestibular sensor, the semicircular canals, which sense angular movements (1, 6, 7). Combined, these papers constituted the seed for an explosion of quantitative studies on the properties of neurons in the central nervous system that detect and coordinate movement.

During the 40s and 50s, pioneering work by Lowenstein and Wersall (11) demonstrated the relationship between the physiology of vestibular nerve fibers and the distribution of spatial directions (morphological polarization) of hair bundles in the vestibular and lateral line organs. Although the function of the semicircular canals was established relatively early (10, 12), the complexity of the morphological polarization of the otolith organs, the utricle and the saccule (8), had delayed our understanding of the system. Furthermore, whether the saccule had an equilibrium or vibratory function remained a central question of uncertainty. A few years before the featured trilogy, Fernández et al. (5) tested and verified the hypothesis that primary otolith afferents could be characterized by spatially tuned properties, that is, a functional polarization corresponding to the direction with which gravity must be aligned to elicit the maximum firing rate modulation. Yet, before the Fernández and Goldberg studies in 1976, little was known about the physiology of these neurons, as all previous studies had almost entirely dealt with primary otolith afferent responses to static tilts (5, 9) rather than dynamic linear accelerations.

With these three papers (2–4), Fernández and Goldberg set the stage for vestibular system sensory function and launched a plethora of related quantitative studies during the decades to follow. In contrast to earlier work, in the 1976 experiments the authors used centrifugal forces to provide the linear acceleration stimulus activating primary otolith afferents. Aside from being precisely controlled, this stimulation also allowed for the first time a systematic manipulation of both acceleration magnitude and time course as a stimulus source to the otolith organs. These heroic experiments required hours of cell isolation, as in all units the direction of functional polarization (i.e., direction of max-
but also the cellular components responsible for these properties. The first of these papers (2) describes the adaptive properties and response asymmetries of the neurons. It also provides the first direct and convincing evidence that the saccule in mammals responds to linear accelerations. The second paper (3) characterizes the directional selectivities and input/output relationships for stimuli up to 5 G (with 1 G corresponding to the force of gravity). The paper concludes convincingly that shearing forces parallel to the cell’s functional polarization were effective in changing firing rate, whereas orthogonal compression forces were ineffective in eliciting a response from the afferents. It also established that, within the range of accelerations typically experienced in normal life, otolith afferent responses operate linearly, although some saturation was observed in inhibitory directions of motion. The most important contribution was in the third paper (4), which described the response properties of primary otolith afferents to sinusoidal linear acceleration stimuli and provided the first quantification of the neurons’ response dynamics using system analyses techniques. A range of responses were described, with the most regularly firing afferents with thin axons having tonic-like dynamics and the most irregularly firing, thick afferents being characterized by phasic response properties. Such a difference in temporal properties has fueled numerous studies over the past 30 years in trying to understand not only the functional significance of this distributed representation of linear acceleration sensors but also the cellular components responsible for these properties.

During the past three decades, César Fernández (Fig. 1) and Jay Goldberg (Fig. 2) continued to provide outstanding morphological and physiological characterizations of the peripheral vestibular system. Fernández’s last seminal papers appeared in the Journal of Neurophysiology in 1995, a few years before his death in December of 1999, just shy of his 90th birthday in May 2000. Jay Goldberg, a Professor at the University of Chicago, remains a very active researcher of vestibular function, his interests now being more focused on synaptic and cellular physiology of receptors and peripheral innervation as they pertain to our understanding of sensory transduction. Recent works continue to provide important insights and significant understanding into the properties of the peripheral vestibular system, extending these original scientific contributions by Fernández and Goldberg that remain truly classic seminal works. Their findings cemented the solid foundation on which the future of modern vestibular processing and information coding has been based. Their work adds to the long tradition of the American Physiological Society in providing the foundation for important new areas of knowledge.

REFERENCES