

## NEUROSCIENCE FOREFRONT REVIEW

# RESOLVING THE ACTIVE VERSUS PASSIVE CONUNDRUM FOR HEAD DIRECTION CELLS

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**Abstract**—Head direction (HD) cells have been identified in a number of limbic system structures. These cells encode the animal's perceived directional heading in the horizontal plane and are dependent on an intact vestibular system. Previous studies have reported that the responses of vestibular neurons within the vestibular nuclei are markedly attenuated when an animal makes a volitional head turn compared to passive rotation. This finding presents a conundrum in that if vestibular responses are suppressed during an active head turn how is a vestibular signal propagated forward to drive and update the HD signal? This review identifies and discusses four possible mechanisms that could resolve this problem. These mechanisms are: (1) the ascending vestibular signal is generated by more than just vestibular-only neurons, (2) not all vestibular-only neurons contributing to the HD pathway have firing rates that are attenuated by active head turns, (3) the ascending pathway may be spared from the affects of the attenuation in that the HD system receives information from other vestibular brainstem sites that do not include vestibular-only cells, and (4) the ascending signal is affected by the inhibited vestibular signal during an active head turn, but the HD circuit compensates and uses the altered signal to accurately update the current HD. Future studies will be needed to decipher which of these possibilities is correct. © 2014 IBRO. Published by Elsevier Ltd. All rights reserved.

**Key words:** head direction, navigation, passive movement, self-motion, spatial orientation, vestibular.

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## INTRODUCTION

Accurate navigation requires knowledge of both location and directional heading. Neurophysiological studies have identified three major cell types representing this kind of information. Place cells, found throughout the three major areas of the hippocampus, discharge in relation to the animal's specific location within the environment (O'Keefe and Dostrovsky, 1971). Different place cells represent different locations, such that the summed activity of place cells collectively defines the animal's perceived location. Grid cells fire at multiple locations in a regular, repeating hexagonal grid pattern throughout the environment and are found primarily in the entorhinal cortex, but have also been observed in the pre- and parasubiculum (Hafting et al., 2005; Boccara et al., 2010). The third cell type, head direction (HD) cells, are found primarily in the classic Papez circuit, and discharge as a function of the animal's HD in the horizontal plane, independent of the animal's location and on-going behavior (Taube et al., 1990a). Each HD cell is tuned to a particular orientation with the environment and is referred to as the cell's preferred firing direction. Other spatial cells, which combine various aspects of these three basic spatial cell types, have also been reported in hippocampal-related structures, including place × HD cells (Cacucci et al., 2004), border cells (Lever et al., 2009), which fire along a portion of a border in an enclosed environment, and conjunctive grid × HD cells (Sargolini et al., 2006). The spatial correlates of all these cells respond to landmark cues, such that rotation of a landmark in a cue-controlled environment leads to a corresponding shift of the spatial cell's firing pattern. Thus, a place cell's place field, a HD cell's preferred firing direction, and the orientation of the grid cell firing pattern

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**Abbreviations:** AHV, angular head velocity; CW, clockwise; CCW, counterclockwise; DTN, dorsal tegmental nucleus; HD, head direction; NPH, nucleus prepositus; PGRNd, paragigantocellular reticular nucleus, dorsal part; SGN, supragenual nucleus.

all shift a similar amount when a prominent landmark cue is rotated relative to the environment. These cell types also receive and are affected by information about the animal's self-motion through the environment. These self-motion (idiothetic) cues include information from vestibular, visual, proprioceptive, and motor efference systems. Both landmark and self-motion information are normally in register with one another as an animal moves through its environment. Motor and proprioceptive information have in particular been shown to be important for updating the HD signal as an animal moves from a familiar environment to a novel one that contains unfamiliar landmarks (Stackman et al., 2003; Yoder et al., 2011). In contrast to updating the orientation of the HD signal's preferred firing direction relative to landmarks, vestibular information is critical for generating the HD signal, as disruption of vestibular system inputs to the HD network completely disrupts the HD signal in both cortical and sub-cortical areas. Further, vestibular information allows the HD system to update the perceived orientation without constantly assessing the external environment as is necessary for processing landmark information. Although previous studies have indicated that passive rotation of an animal lowers and in some cases attenuates HD cell responses, more recent work that has recorded HD cells in rats with their heads and bodies immobile, has shown that passive back-and-forth yaw rotation of the animal's head in the horizontal plane does not reduce cell firing at the cell's preferred direction (Shinder and Taube, 2011a).

Studies have also shown that signals conveying information about the animal's angular head velocity (AHV) are an important component in generating the HD signal. AHV information is an ideal signal for updating the HD response to reflect the change in the animal's current perceived orientation following any head movement. Cells within the dorsal tegmental nucleus (DTN), which receive inputs from the vestibular system and project to the HD cell network, predominantly contain neural correlates related to the animal's AHV, although a few HD cells have been identified there (Bassett and Taube, 2001; Sharp et al., 2001b). Moreover, lesions of the DTN disrupt the HD signal throughout the HD cell network (Bassett et al., 2007). The origins of the AHV signal could come from a combination of vestibular and motor efference inputs, although it is generally believed that vestibular inputs play the major role because (1) HD cell responses are not impaired in the absence of head movements, which occur as a result of full head and body restraint, and (2) the presence of an anatomical circuit between the vestibular system and the nuclei involved in generating the HD signal.

During the past decade, several studies have recorded from vestibular nucleus neurons in head-free behaving monkeys. These studies have shown an important property – namely that responses in some types of vestibular neurons are attenuated or substantially depressed when the monkey makes an active head turn. In one type of vestibular nuclei neuron, passive rotation of the head elicits classic firing rate responses that are correlated primarily with AHV, and

are therefore likely candidates as the source of the AHV signal to the HD system. These cells are known as vestibular-only neurons. But responses from these same neurons are substantially diminished when the monkey makes an active head turn (McCrea et al., 1999; Roy and Cullen, 2001, 2004). If the firing of these vestibular-only neurons is attenuated during actively generated head turns, then these vestibular responses would be 'turned off' when the animal is in a freely-moving condition and making active head movements. Taken in conjunction with the fact that a vestibular signal is necessary for generating the HD signal, these findings result in a conundrum (Cullen and Roy, 2004). If the vestibular nuclei cells become quiescent during an active head turn, then how does the vestibular system and the associated ascending AHV signal enable the HD network to generate the HD signal during an active head turn? This review discusses this issue and tries to resolve the conundrum. We present four possible mechanisms that may resolve this issue, each of which are not mutually exclusive. First, it is possible that the ascending vestibular signal is created by more than just vestibular-only neurons. Second, it is possible that not all vestibular-only neurons contributing to the HD pathway have firing rates that are equally and severely attenuated by active head turns. Third, the ascending pathway may be partially spared from the effects of the attenuation, in that the HD system might receive information from vestibular brainstem sites that do not include the vestibular-only cells. Finally, we consider the possibility that the ascending signal is affected by the inhibited (or altered) vestibular signal during an active head turn, but the HD circuit compensates and uses the altered signal to accurately update the current HD.

## THE HD CELL NETWORK AND SIGNAL GENERATION

The HD signal has been identified in a number of interconnected areas that form a major part of the Papez circuit, including the DTN, lateral mammillary nuclei, anterodorsal thalamus, postsubiculum, and entorhinal cortex (Sharp et al., 2001a; Taube, 2007). Although HD cells have been found in other brain areas (e.g., dorsal striatum, retrosplenial cortex, and medial pre-central cortex), the HD signal in these other areas is thought to be dependent on the pathway through the Papez circuit. Previous work has established that the HD cell signal is most likely generated subcortically – either within the DTN or in its connections with the lateral mammillary nuclei. The vestibular system and its associated nuclei play a critical role in the generation of the HD signal. Permanent neurotoxic lesions of the vestibular labyrinth (Stackman and Taube, 1997), inactivation of the vestibular hair cells (Stackman et al., 2002), or occlusion of the semicircular canals (Muir et al., 2009) have all effectively disrupted direction-specific firing in HD cells. Therefore, the ascending pathway from the vestibular nuclei, which contains sensory information about the animal's AHV and translational head acceleration, is critical for the formation of the HD signal. Vestibular inputs that

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