



Review article

Vertigo and the processing of vestibular information: A review in the context of predictive coding



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ABSTRACT

This article investigates the processing of vestibular information by interpreting current experimental knowledge in the framework of predictive coding. We demonstrate that this theoretical framework give us insights into several important questions regarding specific properties of the vestibular system. Particularly, we discuss why the vestibular network is more spatially distributed than other sensory networks, why a mismatch in the vestibular system is more clinically disturbing than in other sensory systems, why the vestibular system is only marginally affected by most cerebral lesions, and whether there is a primary vestibular cortex. The use of predictive coding as a theoretical framework further points to some problems with the current interpretation of results that are gained from vestibular stimulation studies. In particular, we argue that cortical responses of vestibular stimuli cannot be interpreted in the same way as responses of other sensory modalities. Finally, we discuss the implications of the new insights, hypotheses and problems that were identified in this review on further directions of research of vestibular information processing.

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1. Introduction

The vestibular sense responds to a change in head position by measuring head movements in relation to gravity. In terms of measuring and forwarding this information to the brain for processing, it is probably one of the simplest forms of sensory input and is not even included amongst the five traditional senses. However, vestibular information plays a critical role on sensorimotor control and perception as this information codes three-dimensional head positions. These effects constitute the basis for our spatial frame of reference and are important for maintaining erect human posture (Berthoz, 2000).

Aside from its importance, the vestibular sense has some specific features that differ from all other senses. For example, all other sensory systems have a primary cortex while its existence in the vestibular system is disputed (Lopez and Blanke, 2011; zu Eulenburg et al., 2012). Furthermore, there is no other sense where a peripheral lesion to the receptor causes similar substantial physical complaints and a subjective feeling of sickness (vertigo and dizziness). A central lesion, however, causes comparatively little functional impairment even in areas that are central for vestibular information processing (Baier et al., 2013).

Up until now, no clear concept has emerged to interpret the cerebral processing of vestibular information that accounts for these differences. This article endeavors to interpret vestibular processing and its known differences to other sensory systems by interpreting current experimental knowledge in the framework of a contemporary theory on brain function. Predictive coding is currently the leading theory on the processing of sensory information (Friston, 2005; Rao and Ballard, 1999). The theory is based on two central ideas: first, that the brain constructs an explanation of the world based on our sensory experience and second, that sensory perception relies on predictions instead of detailed information. The main task in processing sensory information is therefore to identify unpredicted (new) information. For auditory, somatosensory and visual systems, interpreting current experimental knowledge within the framework of predictive coding may deliver additional insights into the systems' functioning (Rao and Ballard, 1999; Stefanics et al., 2014; Winkler et al., 2012). However, there is currently no such interpretation available for the processing of vestibular information.

We review the current knowledge of the anatomy, function, and connectivity of the vestibular system. Based on this information, we attempt to capture the diverse anatomical and physiological attributes of the vestibular system within the framework of predictive coding. We demonstrate that this theory can account for a remarkable range of issues specific to the processing of vestibular information. We discuss reasons of and explanations for the differences between the vestibular system and other sensory systems. In the end, we outline future challenges and possible research directions in vestibular science derived from our conception in this review.

2. Brain areas involved in vestibular processing

Today there are at least ten cortical areas known to be involved in the processing of vestibular information. These areas together with their thalamo-cortical, cortico-cortical and cortico-thalamo-

cortical connections form a very complex network. Here, we will review the anatomical and functional properties of this vestibular network. We will limit our review to properties that are relevant for the understanding and interpretation of vestibular processing (for a more detailed review about the anatomy of the vestibular network see the excellent review by Lopez (Lopez and Blanke, 2011)).

2.1. The parieto-insular vestibular cortex (PIVC)

Reliable data on the localization of brain structures involved in the processing of vestibular information was first gained from animal experiments. Walzl and Mountcastle were the first to describe a cortical area that was involved in the processing of vestibular information (Walzl and Mountcastle, 1949). They demonstrated evoked potentials of the anterior supra-sylvian sulcus after stimulation of the vestibular nerve in cats (Walzl and Mountcastle, 1949). This finding has been confirmed by multiple other studies (Kempinsky, 1951; Mickle and Ades, 1952, 1954), and a similar finding was also demonstrated in dogs (Beritashvili, 1965).

In macaque and squirrel monkeys, a cortical area that was responsive to vestibular input was found adjacent to the posterior insula and was termed "parietal insular vestibular cortex" (PIVC) (Grusser et al., 1990a,b; Guldin et al., 1992). It is difficult to compare the spatial locations of vestibular areas between cats and monkeys because only primates have developed a temporal lobe with an operculum. However, in 1973, Pandya and Snides suggested that the retroinsular parietal area in primates corresponds to the vestibular cortex in the supra-sylvian sulcus of cats (Pandya and Sanides, 1973). Today, the correspondence of these areas is well accepted, as multiple studies have demonstrated similarity in the responsiveness of PIVC neurons between cats and monkeys (Chen et al., 2010; Lopez and Blanke, 2011). Through the use of different methods of vestibular stimulation (caloric and galvanic) and different imaging modalities (fMRI and PET), studies in humans have also confirmed the retro-insular location of the PIVC and its functional importance for the processing of vestibular information (Bense et al., 2001; Bottini et al., 2001, 1994; Bucher et al., 1998; Dieterich et al., 2003; Klingner et al., 2012; Lobel et al., 1998; Stephan et al., 2005). Some of these studies have also found an involvement of the anterior insular in vestibular processing (Bense et al., 2001; Bottini et al., 2001; Dieterich et al., 2003; Stephan et al., 2005), suggesting an influence of vestibular signals on various aspects of interoception and bodily awareness (Trousseau et al., 2004). However, the PIVC in the retro-insular regions is considered the core location of the vestibular network and has been suggested as a "distinct and unique vestibular cortex" (zu Eulenburg et al., 2012).

2.2. The postcentral gyrus

The postcentral gyrus contains mainly neurons dedicated for the processing of general somatic sensation. This gyrus can be divided into four areas: 3b, 3a, 1 and 2. In primates, the vestibular part of area2 (area2v) was the first cortical area that was identified to be involved in the processing of vestibular information (Fredrickson et al., 1966). This area is located at the posterior border of area2 (Schwarz et al., 1973; Schwarz and Fredrickson, 1971). Area2v was found to overlap with the receptive field of the contralateral median nerve (Fredrickson et al., 1966). The responsiveness

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