Bressanone Debates

Vestibular Cognition:

state-of-the-art and future directions

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Abstract

Vestibular information has been traditionally considered as a specialised input for basic orienting behaviours, such as oculo-motor adjustments, postural control and gaze orientation. However, in the past two decades a widespread vestibular network in the human brain has been identified, that goes far beyond the low-level reflex circuits emphasised by earlier work. Because this vestibular cortical network is so widely distributed, it could, in principle, impact multiple neurocognitive functions in health and disease. This paper focuses on the relations between *vestibular input*, *vestibular networks*, and *vestibular interventions* by providing the authors' personal viewpoint on the state-of-the-art of vestibular cognitive neuropsychology, and its potential relevance for neurorehabilitation.

Main Text

The vestibular system is a sensory system which originates with a sophisticated set of sensory transducer organs in the inner ear. It comprises three orthogonal semicircular canals (anterior, posterior and horizontal) that sense rotational acceleration of the head in three-dimensional space, around the yaw, roll, and pitch axes, and two otolith organs (the utricle and saccule) that jointly sense translational acceleration, including the orientation of the head relative to gravity. Traditionally, vestibular information has been considered an essential cue for basic orienting behaviours, such as eye movement control, postural control, balance and orientation. However, a wider vestibular network in the brain has been identified that goes far beyond the traditional, low-level reflex motor circuits. Thus, the vestibular system may play a fundamental, underpinning role in human cognition for at least two reasons. First, vestibular inputs constantly inform the brain about the position and movement of the head in space, and therefore provide a constant backdrop to mental life. Second, the object represented by vestibular signalling is the body itself, rather than any object in the external world. For these reasons, vestibular signals do not give rise to salient, discrete, occasional perceptual contents evoked by particular stimulus objects, in the way that one might see a tree or a cat, hear a word or a scream, or taste an olive. Rather, vestibular signals and vestibular experiences form a ubiquitous background of all one's activities and interactions. The very ubiquity of vestibular signals and projections makes it difficult to isolate exactly *how* a given vestibular input might influence a specific experience or a specific behaviour.

For the neuropsychologist, the vestibular system is not just a distinctive sensory input channel; it is interesting for many other reasons as well. Here we highlight just two. First, the vestibular system has an unusual anatomy, since it comprises both a distinctive combination of a highly-encapsulated brainstem circuitry for reflex orienting responses (Gernandt et al., 1952; Gernandt et al., 1960), and also, in contrast, a highly distributed cortical network (see Lopez et al. 2012; zu Eulenburg et al. 2012 for recent reviews, including more comprehensive bibliographies), whose organising principles remain poorly understood. We will discuss this cortical network in detail below, since it is considered key to the role of vestibular inputs in cognitive neuropsychology and neurorehabilitation. Here we simply note that, although the vestibular cortical network is *defined* by its responsivity to peripheral vestibular inputs, its neuropsychological interest derives from its wide projections, rather than from its modality-specific nature. Second, the vestibular system represents a potential point of therapeutic intervention. Because the vestibular cortical network is so distributed, it could, in principle, produce widespread effects on neurocognitive function in health and disease. This paper accordingly considers the relations among *vestibular inputs*, *vestibular networks*, and *vestibular interventions*. We provide a personal viewpoint on the state-of-the-art of vestibular neuropsychology, and we suggest some general principles for developing the role of vestibular neuropsychological studies.

The first afferent projections of the vestibular nerve are to the vestibular nuclear complex in the brainstem and the cerebellum. The vestibular nuclear complex is the primary processor of vestibular signals and plays a major role in motor reflexes that control eye movements and posture. In particular, the Vestibulo-Ocular Reflex (VOR, Raphan and Cohen, 2002) ensures that the eyes move proportionally to movements of the head, but in the opposite direction, thus stabilising the image on the retina. At the same time, the Vestibulo-Spinal Reflex (VSR, Dichgans and Diener, 1989) regulates the activity of body muscles induced by movements of the head, in order to stabilize posture. The cerebellum plays a key role in the plasticity of these processes, for example by adjusting VOR gain. Importantly, vestibular afferent signals are integrated with somatosensory, proprioceptive and visual input at the levels of both the vestibular nuclei and the cerebellum. In general, these low-level multisensory control pathways have the important role of stabilising the spatial relation between the organism and its environment as it orients and navigates.

In addition, researchers have identified a tentacular ascending vestibular network that goes far beyond the classical brainstem circuits for sensorimotor postural and oculomotor reflexes, with which the vestibular system is traditionally identified. Electrophysiological studies in non-human primates described a widespread vestibular cortical and subcortical network whose core area is the Parieto-Insular-Vestibular Cortex (PIVC) (Guldin and Grüsser 1998; Angelaki and Cullen 2008; Shinder and Taube 2010; Lopez and Blanke 2011; Gu 2018). This area lies in the posterior parietal operculum extending into the posterior insular lobe. Similarly, many cortical and subcortical areas show an increased haemodynamic response when the vestibular system is experimentally activated by thermal or electrical vestibular stimulation in humans (Fasold et al., 2002; Eickhoff et al, 2006; Frank and Greenlee, 2018). Neuroimaging studies (fMRI, PET and EEG) suggest that this network is bilateral, even for unilateral vestibular stimulation. It includes the posterior parietal operculum, the secondary somatosensory cortex, the inferior parietal cortex, the superior temporal cortex, the posterior insula and the premotor cortex (Bottini et al., 1994; Bottini et al., 1995; Bottini et al., 2001; Brandt and Dieterich 1999; Suzuki et al., 2001; De Waele et al., 2001; Dieterich et al., 2003; Eickhoff et al. 2006; Lopez and Blanke 2011; Lopez et al. 2012; zu Eulenburg et al. 2012). Cortical electrical stimulation studies in humans identified the areas immediately above and below the Sylvian fissure, including the parietal operculum, as the core of this vestibular network (Kahane et al., 2003; Mazzola et al., 2014). Uniquely among the sensory modalities, vestibular inputs do not project to any *primary* unimodal cortex, analogous to visual V1, somatosensory S1 or auditory A1. Instead, vestibular signals project to areas traditionally labelled with respect to *other* functions, such as visual, somatosensory, motor, memory-related or affective.

This basic neuroanatomical knowledge makes useful predictions regarding the effects of artificial vestibular stimulation on behaviour and cognition. In essence, the distinctive anatomical connectivity of the vestibular cortical network suggests that vestibular inputs should have pervasive, modulatory influence on multiple neurocognitive functions. Based on the neurophysiological features of the subcortical and cortical networks activated by vestibular stimulation, we hypothesised that the vestibular system is involved in at least three main domains of function (Figure 1). First, an *autonomic domain* which includes pathways for the integration of information regarding ongoing processes relative to the current physiological condition of the body, including adjusting blood pressure, pain, heart rate, and respiration

(Yates, 1992; Yates and Miller, 1998; Yates et al., 2011; McGeoch et al., 2008; Yamamoto et al., 2005; Ferrè et al., 2013). These effects would be mediated by vestibular projections to subcortical structures including the brainstem, hypothalamus and fastigial nucleus of the cerebellum, and to cortical regions including the anterior cingulate cortex and limbic system (Yates, 1996; Yates 1992). Second, a *sensorimotor domain* which includes pathways for the sensory integration of vestibular, visual, proprioceptive and somatosensory information and for modulation of motor responses (Karnath, 1994; Ferrè et al., 2011; Ferrè et al., 2012; Ferrè et al., 2015; Fitzpatrick et al., 1999; Bresciani et al., 2002; Rode et al., 1998; Schmidt et al., 2013). These effects would be mediated by the strong vestibular projections to the parietal cortex, operculum and insula (Bottini et al., 1995; Bottini et al. 2005). Third, a *cognitive domain* which includes pathways for regulation of decision making, attention, emotion and other higher cognitive functions (Hitier et al., 2014; Smith and Zheng, 2013; Geminiani and Bottini, 1992; Cappa et al., 1987; Bisiach et al., 1991; Rode at al., 1992; Rode et al., 1998; Vallar et al., 1990; Utz et al., 2011; Ferrè et al., 2013; Wilkinson et al., 2008; Smith et al., 2010; Preuss et al., 2014a; Preuss et al., 2014b; Pavlidou et al., 2018; Lopez et al., 2012; Mast et al., 2006; Smith et al., 2010; Bächtold et al., 2001; McKay et al., 2013; Lenggenhager et al., 2008). These effects would be primarily mediated by vestibular projections to the frontal lobes (Lopez et al. 2012; zu Eulenburg et al. 2012). We thus view the vestibular system's interactions with cognition as a logical consequence of the functional neuroanatomy of the vestibular projections. That is, the overlap between cortical areas subserving a given cognitive function and the areas activated by artificial vestibular stimulation (Lopez et al. 2012; zu Eulenburg et al., 2012) should allow specific predictions about behaviour, given the three-way relation between stimulation, functional anatomy and cognitive performance.

But what is the functional architecture of vestibular cognition? Although evidence suggests a vestibular contribution to autonomic, sensorimotor and cognitive domains, the observed effects of vestibular stimulation could be explained by either of two alternative architectures. First, vestibular signals could provide general tonic input to basic circuits for autonomic control on which all other cerebral functions depend. Vestibular inputs would target the autonomic domain primarily, while sensorimotor and cognitive functions would be only indirectly affected, to the extent that they require normal homeostatic and autonomic functioning as a background condition (Figure 1). Alternatively, vestibular signals might project by independent pathways to multiple areas each subserving a distinct function (Figure 1). Importantly, these two models lead to opposite empirical predictions. According to the "enabling" model, effects of the vestibular signals on sensorimotor and cognitive functions must be correlated between autonomic and sensorimotor functions, and between autonomic and cognitive functions, since the effects of vestibular input on the latter two domains depend on the former. Conversely, the "independent projections" model predicts that vestibular signals could have independent and uncorrelated effects between autonomic, sensorimotor and cognitive domains. Is it possible to differentiate experimentally between the "enabling" model and the "independent projections" model? In our view, systematic data on the effects of vestibular stimulations, together with patterns of correlation across measures of different domains, could potentially support or reject models of the cognitive neuroanatomy of vestibular cognition. Importantly, distinguishing which model is correct for the vestibular network may not be possible from the estimated effect sizes for the reported modulations of each domain – it may additionally require correlations between measures of various functional domains. Since the vast majority of vestibular stimulation studies to date focus on a single outcome variable, this constitutes a limitation in current understanding of the vestibular network (see below).

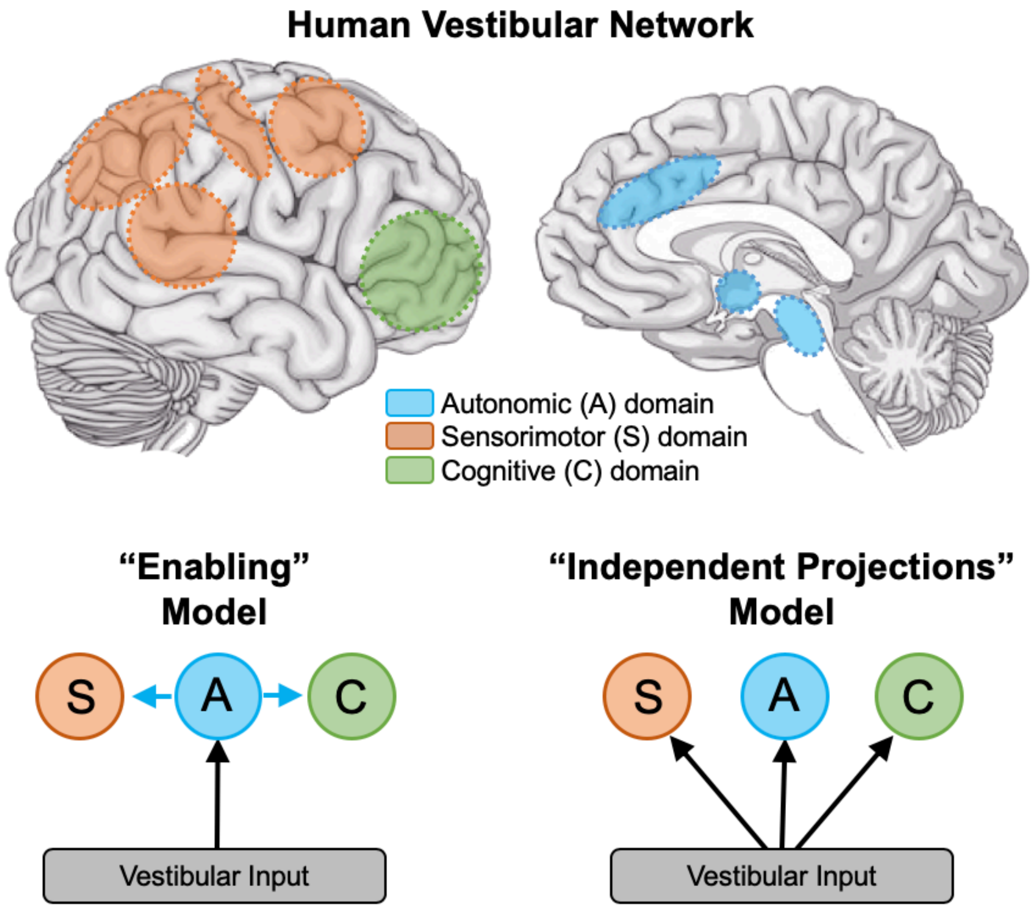

Figure 1. Human vestibular network and functional architectures of vestibular cognition.

Based on its neuroanatomical features, the vestibular system may contribute to at least three main functional domains: (1) an autonomic domain (A) which includes pathways for the integration of information regarding ongoing processes relative to the current physiological condition of the body, including adjusting blood pressure, heart rate, and respiration; (2) a sensorimotor domain (S) which includes pathways for the sensory integration of vestibular, visual, proprioceptive and somatosensory information and for modulation of motor responses; (3) a cognitive domain (C) which includes pathways for regulation of decision making, attention, emotion and other higher cognitive functions. We hypothesised two alternative functional architectures for vestibular cognition. In the "Enabling" Model, vestibular signals provide general tonic input, which underpins autonomic regulation, and on which all other cerebral functions depend. Alternatively, the "Independent Projections" Model implies that vestibular signals project to multiple areas, each subserving a distinct function.

We used this division into three separate domains of vestibular modulation to capture a representative, though clearly not systematic, sample of recent vestibular stimulation studies. Our selection focussed on papers that have been widely cited, that tested a diversity of autonomic, sensorimotor and cognitive functions, and that used different methods to stimulate the vestibular organs (Table 1). Importantly, we have ignored those studies within the peripheral vestibular neurology tradition that deliver vestibular stimulation with the aim of evoking vestibular reflex responses (Colebatch, 2001). Instead, we have focussed on studies in the neuropsychological tradition that use vestibular stimulation to modulate other, non-reflex functions. We have also excluded some studies which did not provide sufficient details to estimate the effect sizes of the reported results.

Our survey identified many interesting links between vestibular processing and wider neurocognitive functions. However, it also suggested that the existing literature on vestibular interventions is unsystematic in several ways. First, the vestibular stimulation applied varies dramatically across studies. Caloric Vestibular Stimulation (CVS) and Galvanic Vestibular Stimulation (GVS) have dominated. However, these techniques are physiologically very different: while CVS (applied with cold water/air) leads to a relatively selective stimulation of the semicircular canals, GVS stimulates all vestibular end organs. Accordingly, physiological and behavioural effects of CVS are very different from that of GVS (e.g., CVS induces a horizontal nystagmus, while GVS evokes a torsional nystagmus). There are differences not only between different types of stimulation, but even between studies that use a single stimulation type. In particular, the duration, intensity and parameters of CVS and GVS studies are highly variable. In addition, sample size, the nature of participant groups, and behavioural outcome measures are also highly heterogeneous across studies. Control conditions, testing a function predicted to be unaffected by vestibular stimulation, are rare. No study, to our knowledge, has reported correlations between the effects of well-controlled vestibular stimulation on autonomic, sensorimotor, and cognitive domains assessed in the same participants. As a result, non-specific accounts, including mediation by autonomic function, often cannot be excluded. Direct replications are rare in this literature. Reporting standards vary widely: in some cases we could identify a single test which allowed the effect size of vestibular stimulation to be estimated, but in other cases we could not derive a clear estimate of effect size, and were only able to offer a subjective opinion about the size or importance of an effect.

Table 1. A representative sample of vestibular interventions studies in the autonomic, sensorimotor and cognitive domains.

Reference	Target function/construct	Group	Vestibular Stimulation	Effect Size Estimates	Present authors' personal estimate of scientific importance: minor/important/extremely important
			Autonomic Domain		
Cui et al. 1997	Sympathetic Responses	Healthy	CVS	-	Important
Yates et al. 1999	Cardiovascular Regulation	Healthy	CVS	-	Important
Yamamoto et al. 2005	Autonomic Responses	Healthy	GVS	-	Important
McGeogh et al. 2008	Post-stroke Pain	Neurological	CVS	*d*= 0.70, Strong	
Ferrè et al. 2011	Pain Processing	Healthy	CVS	*d*= 1.94, Strong	
			Sensorimotor Domain		
Rode et al. 1998	Motor impairment	Neurological	CVS	*d*= 0.86, Strong	-
Fitzpatrick et al. 1999	Motor control	Healthy	GVS	*d*= 0.51, Medium	-
Bresciani et al. 2002	Motor control	Healthy	GVS	$\eta 2_p$= 0.9 Strong	-
Bottini et al. 2005	Hemianaesthesia	Neurological	CVS	*d*= 3.02, Strong	-
Ferrè et al. 2011	Somatosensory perception	Healthy	CVS	*d*= 0.98, Strong	-
Schmidt et al. 2013	Position Sense	Neurological	GVS	$\eta 2_p$= 0.09 Strong	-
			Cognitive Domain		
Cappa et al. 1987	Visuo-Spatial Neglect	Neurological	CVS	*d*= 2.68 Strong	-
Geminiani et al. 1992	Representational Neglect	Neurological	CVS	*d*= 1.73, Strong	-
Mast et al. 2006	Mental Imagery	Healthy	CVS	*d*= 4.78 Strong	-
Wilkinson et al. 2008	Memory	Healthy	GVS	*d*= 0.50 Medium	-
Lopez et al. 2011	Bodily Awareness	Healthy	CVS	*d*= 0.79 Strong	-
Utz et al. 2011	Visuo-Spatial Neglect	Neurological	GVS	*d*= 0.53 Medium	-
Ferrè et al. 2013	Visuo-spatial Attention	Healthy	GVS	d= 2.1 Strong	-
Preuss et al. 2014	Decision Making	Healthy	CVS	*d*= 0.41 Weak	-
Preuss et al. 2014	Emotion Control	Healthy	CVS	*d*= 1.14 Strong	-
Pavlidou et al. 2018	Perspective Taking	Healthy	GVS	$\eta 2_p$= 0.2 Strong	-

This survey leads us to propose a systematic approach to studying the vestibular cortical network, and its potential for neuropsychological intervention. A first step involves identifying *double dissociations* between cognitive functions (i.e. which cognitive functions are not influenced by vestibular inputs, as well as which functions are affected). Second, patterns of correlation among modulations of different tests would be informative about functional architecture, but are not yet available, to our knowledge. In the absence of richer information, we can only attempt informal interpretations of representative effect sizes in each domain. Taken as a whole, this exercise offers modest support for vestibular modulation of autonomic function, strong support for vestibular modulation of sensorimotor function, and strong support for vestibular modulation of cognitive function.

Ways forward: a suggested research pipeline for vestibular studies

Our informal survey suggests that the research field has been largely driven by isolated findings of behavioural modulations, rather than *a priori* by neurophysiological or neuroanatomical models. This may be both a cause and a consequence of publication bias. As a result of these problems, no comprehensive view of vestibular effects on neurocognitive function has emerged, because no systematic research programme of testing and quantifying such effects appears to have been conducted. Therefore, we propose a research pipeline that could form the basis of such a programme. This pipeline could have at least three distinct benefits: (1) identification of research priorities, and systematic guidance of research projects, capable of meeting current research standards, (2) improved scientific understanding of the mechanism of vestibular effects, and (3) generating a scientific evidence base of potential clinical benefits.

In this section, we therefore sketch the outlines of a vestibular research pipeline designed to deliver knowledge and impact on neuropsychological rehabilitation.

Step 1: Identify the sensory pathway involved in the intervention, by driving the pathway in feedforward fashion with appropriate peripheral vestibular stimulation. This implies well-controlled stimulation techniques, an intact peripheral receptor surface, and suitable measures of the effects of the intervention, such as a behavioural modulation. Measures of vestibular reflex responses to the intervention may be particularly valuable as an indicator of effective stimulation, independent of the target neuropsychological domain.

Step 2: Identify the brain areas activated by such stimulation, for example by neuroimaging techniques. Independently confirm that these areas are indeed driven by vestibular input, rather than merely correlating with vestibular stimulation (e.g., by further neuroimaging studies showing altered patterns of activation in these areas in patients with peripheral vestibular lesions). This step demonstrates that the vestibular input to the pathways identified in steps 1 and 2 has an important causal role.

Step 3: Use existing knowledge of cognitive functional neuroanatomy to interpret the core functions of the areas activated by vestibular stimulation (bearing in mind that the activated areas may not be primarily vestibular). Assess whether vestibular stimulations modulate these functions, e.g., by significantly affecting scores on established tests of these functions.

Step 4: Estimate effect sizes for a known vestibular input on the target cerebral functions, in order to identify targets where therapeutic vestibular stimulation is likely to have strongest effects.

Step 5: Consider whether any modulation reflects possible non-specific, enabling effects of vestibular input, or rather reflects specific signals that directly modulate a target set of cerebral functions. This step implies measuring the effects of vestibular stimulation on multiple outcome measures, and testing correlations between the effects of vestibular stimulation on these measures, as well as mean effect sizes.

Step 6: Predict likely effect of vestibular stimulations on specific cognitive functions in specific neuropsychological syndromes, and thus generate targeted interventional or rehabilitative strategies.

Step 7: Disseminate the results not only when there is a positive change in behaviour, but also if vestibular stimulation made symptoms worse, or produced no effect. All types of observations are equally valuable to improve our understanding of the functional architecture of the vestibular system.

Conclusion

In the past two decades a vestibular network in the brain has been identified, that goes far beyond the traditional, low-level reflex circuits for gaze orientation and postural control. Knowledge of this vestibular cortical network has been driven primarily by neuroimaging studies in humans. The vestibular cortical network has been linked to a surprising range of cerebral functions, from autonomic regulation and sensorimotor control to the highest levels of perception and consciousness. However, in our view, we still lack a clear understanding of the vestibular functional architecture. Vestibular research has tended to generate unstructured data on multiple vestibular effects without theories or explicit computational models of the mechanisms underlying these effects. Here we have suggested a research pipeline that could inform the development of a systematic vestibular cognition research programme.

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