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NEUROSCIENCE FOREFRONT REVIEW

DYNAMIC INTERHEMISPHERIC COMPETITION AND VESTIBULO-CORTICAL CONTROL IN HUMANS; A THEORETICAL PROPOSITION

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Abstract—Neuroscientific research has made a concerted effort to determine cortical localization using various functional imaging techniques. This approach has undoubtedly yielded important novel anatomical knowledge, albeit at times contradictory, regarding the structural organization of the vestibular cortex. Unfortunately however, this knowledge has not translated to our understanding regarding how neural mechanisms control vestibular function. Based upon recent functional imaging, lesion and neuro-physiological data that have demonstrated (i) the close behavioral and neuro-anatomical relationship between cortical processing of vestibular and spatial attention signals, and (ii) that inducing interhemispheric competition can in-turn strongly modulate vestibular function akin to that observed in cortical lesion patients, I herewith propose the hypothesis that vestibular cortical processing is controlled, as per for spatial attention, via dynamic interhemispheric competition. In the first half of this review I discuss previous key findings in the field of vestibular neuroscience that can be reinterpreted to support the role of interhemispheric competition for the control of high-level vestibular functions. Contrastingly, in the second half of this review, I present previous findings that show how disrupting interhemispheric interactions can modulate the brainstem-mediated vestibulo-ocular reflex (VOR). I conclude by speculating why interhemispheric competition induces correlated biases at the cortical and brainstem level respectively. Specifically, I propose that brainstem-mediated vestibulo-spatial and vestibulo-temporal transformations, in addition to coding for head displacement, underpin a generalized cortical magnitude estimation system which the CNS uses to construct dynamic spatio-temporal maps of the physical world,

in-turn ensuring spatial orientation. © 2017 Published by Elsevier Ltd on behalf of IBRO.

Key words: vestibular cortex, spatial orientation, vestibular cognition, VOR, handedness, dynamic interhemispheric competition.

	Contents	10
		11
Background		00 12
Interhemispheric competition		00 13
Influences of dynamic interhemispheric competition upon higher order vestibular functions		14
Spatial orientation and self-motion perception		00 15
Verticality perception		00 16
Postural control		00 17
Disorders of the perception of self		00 18
Cognition		00 19
Numerical cognition		00 20
Relationship between spatial neglect and vestibular mechanisms		00 21
Influences of dynamic inter-hemispheric competition upon lower-order vestibular functions		00 22
Effects of higher order visual stimuli such as binocular rivalry and visuo-spatial attentional tasks upon the VOR		00 23
Probing more directly the role of interhemispheric competition for inducing asymmetrical VOR modulation during the experience of binocular rivalry		00 24
Electro-cortical modulation of the VOR		00 25
Is lateralization of the vestibular cortex more pronounced in left handers?		00 26
Functional significance of VOR modulation		00 27
Concluding remarks		00 28
References		00 29

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Abbreviations: cTBS, continuous theta burst stimulation; MNL, mental number line; PET, positron emission tomography; PIVC, posterior insular vestibular cortex; PPC, over the posterior parietal cortex; rTMS, repetitive transcranial magnetic stimulation; SNARC, spatial numerical association response code effect; SPV, slow phase velocity; SSA, subjective straight ahead; tDCS, trans-cranial direct current stimulation; TPJ, tempo-parietal junction; VIP, ventral intraparietal area; VOR, vestibular-ocular reflex; VSM, velocity storage mechanism.

BACKGROUND

Historically reviewing the vestibular neuroscientific literature suggests that insights illuminating the cortical processing that underpins vertigo have been made since at least the 1940s. Arguably the earliest evidence was provided by Hallpike and Colleagues who demonstrate that cortical lesions can impact upon vestibular nystagmus (Fitzgerald and Hallpike, 1942) and this work was closely followed by that of the noted neurosurgeon Wilder Penfield that demonstrated direct

focal cortical stimulation can induce sensations of dizziness (i.e. ranging from rocking to spinning vertigo) (Penfield, 1957). However, it was not until the 1980s that the first empirical data from animal studies arose which demonstrated cortical involvement for vestibular functions by demonstrating neuronal discharging in the visual associative cortex during whole-body rotations in cats (Becker et al., 1979; Deecke et al., 1979; Mergner, 1979; Mergner et al., 1981; Vanni-Mercier and Magnin, 1982a,b). Further, this work was followed by studies in primates in the 1980s and early 90s which identified a large vestibular network that was distributed between the parieto-temporal cortex, the retro-insular and the prefrontal cortex and moreover this network was found to be directly connected to the vestibular nuclei complex (Ventre and Faugier-Grimaud, 1986, 1988; Faugier-Grimaud and Ventre, 1989; Akbarian et al., 1993, 1994). Indeed it could be argued that precisely these primate data and the desire to identify the human-analog of the posterior insular vestibular cortex (PIVC) inspired and drove researchers to undertake human studies in order to identifying the neural correlates of vestibular signals, which began in earnest in the mid-90s.

Neuroscientific research in humans over the past two decades has focused considerable effort to determine cortical localization of vestibular functions, in the main via implementing various functional imaging techniques (Bottini et al., 1994; Suzuki et al., 2001; Fasold et al., 2002; Dieterich et al., 2003). This search has proven difficult in part owing to the fact that vestibular signals induce widespread cortical activations (Brandt and Dieterich, 1999; Dieterich et al., 2003; Guldin and Grüsser 1996; Guldin and Grüsser 1998; Suzuki et al., 2001). In an attempt to reconcile these previous disparate findings from the imaging data two recent comprehensive meta-analysis studies have been performed independently, which have both implicated the cytoarchitectonic area OP2 within the parietal operculum as a key node for vestibular processing. Further, these meta-analyses have suggested that hemispheric dominance for vestibular function occurs in the non-dominant (i.e. with respect to language) hemisphere (i.e. right hemisphere in right handers) (Lopez et al., 2012; Zu Eulenburg et al., 2012), a notion initially proposed in a seminal paper by Dieterich and colleagues on the basis of a positron emission tomography (PET) study (Dieterich et al., 2003).

Cortical localization studies can be beautifully informative, as revealed by historical patient lesion-case reports demonstrating the role of, Broca's area for speech, or, area V5 for visual-motion perception (Zeki, 1991). However, predominantly focusing upon localization can be accompanied by an associated neglect of identifying the underlying neuro-physiological mechanisms that underpin cortically mediated vestibular functions. This latter point is important, as such knowledge regarding the neural control mechanism allows us to understand; (i) how vestibular functions operate under normal circumstances and why they become impaired following either peripheral or central dysfunction, and further (ii) how compensatory neurological mechanisms can be best aided for

rehabilitation. Another argument against over reliance upon cortical localization, especially in vestibular neuroscience, is that functionality and behavior inherently associated with the vestibular system, such as spatial orientation and verticality perception, are strictly not exclusive vestibular functions, in that they additionally rely upon integrating either visual and or somatosensory cues via a process termed sensory integration. Functionally speaking, it is sensory integration rather than a single sensory channel, that informs us about the relative 'position' and 'motion' of our body referenced to the external world (Brandt and Dieterich, 1999). Moreover, it is the case that human perception typically requires interaction between different sensory modalities, as evidenced by data that show enhanced neural responsiveness when simultaneous sensory signals from different modalities are congruent (i.e. additive) (Macaluso and Driver, 2005). More relevant to the current proposition, it is the case that electrophysiological studies have identified multi-sensory neurons for visual, vestibular and somatosensory stimuli in the macaque ventral intraparietal area (VIP) (human homologous the posterior parietal cortex). Furthermore, studies in human subjects have demonstrated that the convergence of visual and vestibular signals mediates self-motion perception and that convergence of vestibular and somatosensory signals can modulate temperature and pain sensations (Andersen and Gnatdt, 1989; Brandt et al., 1998; Gu et al., 2007; Morgan et al., 2008; Stein and Stanford, 2008; Cullen, 2012).

Accordingly, given that sensory integration is a prerequisite for vestibular cortical functions, it is consistent then and also my personal view, that (i) cortical areas associated with vestibular processing are distributed among several multisensory areas which are focused predominantly in the fronto-parietal and temporal cortices (Suzuki et al., 2001; Fasold et al., 2002; Dieterich et al., 2003; Ventre-Dominey, 2014), converging in the tempo-parietal junction (Blanke et al., 2005; Ventre-Dominey, 2014; Kaski et al., 2016), (ii) that vestibular cortical areas considerably overlap with cortical areas devoted to spatial attention (Suzuki et al., 2001; Corbetta and Shulman, 2002; Fasold et al., 2002; Dieterich et al., 2003) and additionally that (iii) although vestibular and spatial attention areas are bilaterally represented, there is considerable hemispheric asymmetry and handedness-related hemispheric dominance (Dieterich et al., 2003; Arshad et al., 2013b, 2015a; Nigmatullina et al., 2016).

Current support for the above viewpoint (i.e. points i–iii, preceding paragraph) is provided by, (i) the existence of widespread and overlapping neuro-anatomical correlates between spatial attention and vestibular processing (Suzuki et al., 2001; Corbetta and Shulman, 2002; Dieterich et al., 2003), (ii) behavioral data in both healthy individuals and patients that demonstrates strong bi-directional influences between vestibular and spatial attention mechanisms (Rubens, 1985; Miller et al., 2000; van Elk and Blanke, 2012; Arshad et al., 2013a,b; Arshad, 2014; Arshad et al., 2016b), (iii) the previous suggestions that head and eye movements are the motor

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