Extending the Functional Cerebral Systems Theory of Emotion to the Vestibular Modality: A Systematic and Integrative Approach

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Throughout history, vestibular and emotional dysregulation have often manifested together in clinical settings, with little consideration that they may have a common basis. Regarding vestibular mechanisms, the role of brainstem and cerebellar structures has been emphasized in the neurological literature, whereas emotion processing in the cerebral hemispheres has been the focus in psychology. A conceptual model is proposed that links research in the 2 disparate fields by means of a functional cerebral systems framework. The claim is that frontal regions exert regulatory control over posterior systems for sensation and autonomic functions in a dense, interconnected network. Impairment at levels within the system is expected to influence vestibular and cognitive processes depending on the extent of frontal regulatory capacity. M. Kinsbourne's (1980) shared cerebral space model specifies the conditions under which dysfunction of the vestibular modality will influence higher cognitive levels. A position on laterality and associative relations within the right hemisphere is proposed to explain links among dizziness, nausea, and negative emotion.

Keywords: emotion, laterality, vestibular system, functional cerebral systems theory

The association of emotion and vestibular dysfunction is not without historical precedence. Aristotle was aware of vestibular phenomena and recorded dizziness experiences (Wade, 1994), but he did not include the vestibular system among the classical senses enumerated in *De Anima*. Vision, taste, hearing, and smell were identified with the eyes, tongue, ears, and the nose, respectively; the sense of touch, including sensations of friction, temperature, and pressure, was not as easily pinpointed to one specific organ (Wade, 2003). Likewise, the vestibular system was problematic to localize and was the last of the basic sensory modalities to be discovered. With the confirmation of vestibular end organs in the temporal bone by Prosper Ménière in 1861 (Baloh, 2001), neurological explorations focused on the cranial nerve pathways to the brainstem. The role of the cerebral hemispheres in the experience of dizziness and motion sickness was contested, overlooked, minimized, or largely ignored. The long-term effect of Aristotle's omission was to preclude the influence of emotion in vestibular system processes.

The literature has implicated emotional influences in sensory modalities including vision (Wittling & Roschmann, 1993), audition (Everhart, Demaree, & Harrison, 2008; Schmitt, Hartje, & Willmes, 1997), somasthesis (Borod, Vingiano, & Cytryn, 1988; Herridge, Harrison, & Demaree, 1997), olfaction (Vermetten & Bremner, 2003), and gustation (Yamamoto, 2006) as well as voluntary motor networks including premotor (Foster & Harrison, 2004; Mollet, Walters, Harrison, & Holland, 2005; Walters & Harrison, 2006; Williamson & Harrison, 2003) and gross motor (Demaree, Higgins, Williamson, & Harrison, 2002; Harrison & Pauley, 1990) functions. Recently, the emotional circuits involved in hostility have been implicated in the modulation of pain (Mollet & Harrison, 2007). It follows then that dizziness, motion sickness, and vection (an illusory sensation of directional self-motion) may also provoke substantial emotional reactions.

The cerebral role in emotion and vestibular processes are still a source of conjecture for two broad reasons. First, the limbic and prefrontal contributions to emotion are well established in the psychological literature; however, the field has not reached a definitive understanding of their role in vestibular processes. Second, hemispheric laterality has been reliably demonstrated in emotion for many years, whereas cerebral laterality in the vestibular modality has only come to light in the last 15 years. We propose a model to explain *how* this sense modality interfaces with negative affect. The primary aims of the article are as follows:

First, we provide a broad overview of vestibular neuroanatomical relations, with an emphasis on projections from the vestibular nuclei to the cerebral hemispheres. We highlight recent literature confirming pathways from the brainstem to the sensory cortical areas. We also emphasize a second, less acknowledged, cerebral innervation of the frontolimbic autonomic centers. Subsequently, neuroimaging evidence from vestibular induction paradigms is introduced to establish the notion of right-hemisphere dominance for vestibular sensory functions. We discuss how a prominent laterality theory may account for right-hemispheric dominance of

vestibular function in prenatal development, as well as a second line of evidence derived from the literature supporting vestibular treatment of neglect—a somatosensory disorder associated with right-hemisphere impairment.

Next, we introduce the functional systems subserving emotion. We restrict our discussion of emotion to pertinent anterior emotional circuits that overlap with those of the vestibular system so as to establish the principle of shared systems. In particular, we highlight the prefrontal region, including associated limbic structures. We present evidence for right-hemisphere modulation of negative emotion and the importance of considering arousal in emotion lateralization.

Finally, we describe a model in which the functional systems of emotion and the vestibular modality are integrated. Luria's appreciation of hierarchical systems of brain function is an early forerunner of the current model in that we conceptualize the interconnectedness of brainstem functions with higher order cognitive domains in the frontal lobes as an interdependent system (Luria, 1966). Kinsbourne's (1980) model extends this recognition to delineate the conditions under which competition for shared cerebral pathways can impair functional outcomes. The discussion includes examples from the anxiety and hostility literature to indicate the impairment that can arise from capacity limitations within the overlapping network. We end by arguing for the importance of integrating the psychological literature on emotion with the vestibular sensory literature given the foreseeable rise in vestibular dysfunctions among the burgeoning elderly population.

A comprehensive treatment of vestibular interactions with higher order cognitive functions other than emotion is beyond the scope of this review. Vestibular circuitry is implicated in spatial memory cognition, spatial perception, and divided attention. We provide some examples in these areas as they pertain to emotion, but readers who are interested in these other domains should see Hanes and McCollum (2006) and Smith, Zheng, Horii, and Darlington (2001) for reviews. We also do not make specific predictions about the implications of behavioral laterality in the vestibular system, such as a specific direction of falling, or imbalance in a particular extremity during locomotion. The reason for the latter caveat is that the role of emotion in vestibular processes has only recently been recognized, and evidence for the influence of lateralized emotion on vestibulospinal mechanisms underlying movement is sparse at this point. Rather, we focus primarily on establishing a principle of lateralized and associative shared systems of the vestibular modality and emotion and the potential detriment on overall behavioral function.

The Functional Vestibular System: Associative and Lateralized Relationships

Basic Neuroanatomy of the Vestibular System

The vestibular sensory organs.   The inner ear contains the bony and membraneous labyrinths of two sensory organs: the cochlea for audition and the vestibular end organs for equilibrium. Both reside within the temporal bone and share the vestibulocochlear nerve (cranial nerve VIII) pathway to the brainstem. The vestibular labyrinth is comprised of five membraneous organs filled with high content K^+ endolymphatic fluid. There are three semicircular canals and two otolith organs per ear. During head movement, the fluid displaces the tips of microscopic hair cell receptors embedded within the membrane, providing shearing forces that signal self-motion.

The semicircular canals are responsible for sensory detection of angular displacement (e.g., stationary rotation such as in an office chair, head rotation to indicate "no," and nodding to indicate "yes"). The three canals per ear are orthogonally arranged so as to correspond to three-dimensional space (Brandt & Strupp, 2005). Each ear jointly responds to head displacement in reciprocal activation patterns. For example, turning the head left displaces hairs at the base of the horizontal left ear canal in one direction, eliciting excitatory firing, while also deflecting the hair cells at the base of the horizontal right ear canal in the opposite direction, eliciting inhibitory firing. This concerted arrangement entails that both ears participate in detecting motion. Semicircular canals are typically activated during studies utilizing the caloric irrigation method, whereby water is injected into the ear canals.

Two otolith organs, the utricle and the saccule, contribute to sensory detection of linear displacement along an axis (e.g., movement to and fro, walking forward and backward). They are also responsible for detecting changes in gravity pressure, such as when one stands upright or tilts the head. Otolith stimulation is difficult to isolate but has been accomplished via vestibular evoked potentials, which utilize sound frequencies specific to these organs (Janzen et al., 2008; Schlindwein et al., 2008). Techniques that activate both otolith and semicircular canal organs include galvanic stimulation (electrical stimulation of the nerve), whole-body rotation, and head/body tilting.

The vestibular nuclei.   Vestibular afferents project ipsilaterally to the vestibular nuclei in the brainstem. The vestibular nuclei have descending motor projections that contribute to trunk posture (vestibulospinal reflexes) and to neck and sternocleidomastoid tone (vestibulocollic reflexes). A critical function of this brainstem structure is, in collaboration with the ocular motor nuclei, to regulate the vestibulo-ocular reflexes (VORs), which are critical in stabilizing the eyes relative to the head in space such that when the head is turned, the eyes can remain fixed on a target (Brandt & Strupp, 2005). The vestibular nuclei also project directly to the cerebellum for balance coordination.

Recently, the vestibular nuclei have been directly implicated in autonomic regulation and arousal. Although the autonomic aspects of the vestibular nuclei have not yet been fully defined, a consensus is that the vestibular system role is critical in maintenance of arterial blood pressure during posture and locomotion, cardiovascular control, vasodynamics of blood circulation during gravity challenges, and coordination of gastrointenstinal responses to stress (Balaban & Porter, 1998; Biaggioni, Costa, & Kaufmann, 1998). Balaban and Thayer (2001) have been instrumental in delineating the core autonomic vestibular pathways from the vestibular nuclei to the limbic structures for anxiety.

The Vestibular Cortical Areas: Associations Between the Sensory and Frontal Areas

Evidence for vestibular contributions to the cerebral hemispheres in humans extends as far back as observations by Penfield (1957), who stimulated areas proximate to the superior temporal cortex in epileptic patients and found endorsements of vection. It must be noted that there is no primary vestibular cortex in the

human; the vestibular cortex in the human is multimodal and receives inputs from visual, auditory, and somatosensory modalities (Brandt & Dieterich, 1999). In fact, over 50% of the neurons in the vestibular cortical areas respond to stimuli that are vestibular, visual, or tactile in nature (Guldin & Grüsser, 1998). The lack of a primary sensory region does not preclude vestibular cortical specialization, however, because gustation and olfaction also do not have a unique primary sensory cortex.

Over the last 20 years, Brandt and associates have spearheaded efforts to document the vestibular cortical projection areas in humans, using caloric irrigation, galvanic stimulation, vestibular evoked potentials, and optokinetic stimulation. The sensory areas are featured most prominently at the junction of the parietal, temporal, and posterior insular cortex (see Figure 1). Reliable activations across diverse experiments also include the superior middle temporal cortex, the motor and premotor cortex areas, prefrontal regions including the anterior cingulate gyrus, and the anterior insula extending to the inferior prefrontal cortex (Bense, Stephan, Yousry, Brandt, & Dieterich, 2001; Brandt, 1997, 1999; Brandt, Bartenstein, Janek, & Dieterich, 1998; Brandt & Dieterich, 1999; Dieterich et al., 2003; for a recent review, see also Dieterich & Brandt, 2008; Janzen et al., 2008; Schlindwein et al., 2008). Moreover, this laboratory has demonstrated dissociable activation patterns between the vestibular cortical areas and other cerebral sensory areas. For example, vestibular activation by caloric irri-

gation or galvanic stimulation bilaterally activates the vestibular cortex while concurrently suppressing the visual association cortex (Brandt et al., 2002; Wenzel et al., 1996). Likewise, when the stimulus is primarily visual in nature, the opposite pattern occurs, with relative suppression of the vestibular sensory areas (Brandt et al., 1998; Dieterich, Bucher, Seelos, & Brandt, 1998). In addition, this mutually inhibitory relation has also been demonstrated in comparisons of vestibular and somatosensory stimulation (Bense et al., 2001).

These sensory cortex areas also have direct interconnections with the frontal lobes; activations are reliably demonstrated for frontal motor and premotor areas in both animals and humans using retrograde tracer studies, caloric irrigation, vestibular nerve stimulation, and optokinetic paradigms (Akbarian, Grüsser, & Guldin, 1993, 1994; de Waele, Baudonnière, Lepecq, Tran Ba Huy, & Vidal, 2001; Dieterich et al., 1998; Fasold et al., 2002; Guldin, Mirring, & Grüsser, 1993; Lobel, Kleine, Le Bihan, Leroy-Willig, & Berthoz, 1998). Presumably, these components are responsible for mobilization and coordination of voluntary motor systems in conjunction with vestibular-based spatial inputs and for regulating eye movements via the frontal eye fields in the premotor cortex. It has been proposed that the frontal lobes exert regulatory control of motor network connections with the vestibular nuclei (Akbarian et al., 1994; Nishiike, Guldin, & Bäurle, 2000). Moreover, the prefrontal cortex has direct connections to
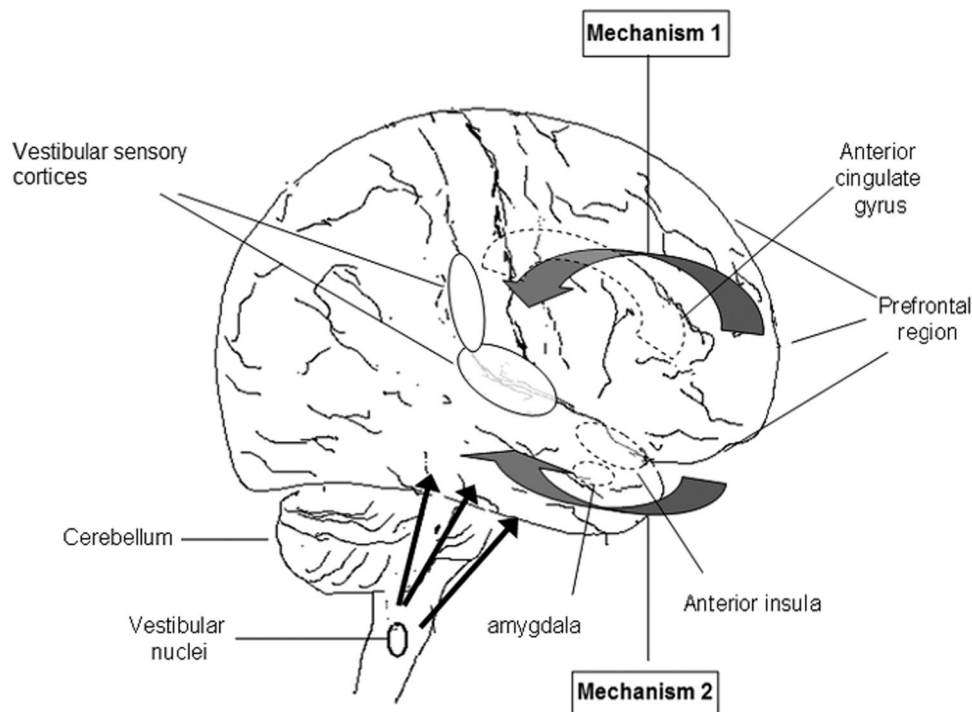

Figure 1. Schematic diagram of the functional cerebral systems mechanisms in the right hemisphere by which emotion is interrelated to the vestibular system. The arrows from the vestibular nuclei represent the inputs to the cerebral hemispheres. The shaded curved arrows represent the regulatory relationship of the frontal lobes over the posterior regions. Mechanism 1 (the sensorimotor-affective mechanism) represents the prefrontal regulation over the vestibular sensorimotor regions. Mechanism 2 (the autonomic-affective mechanism) represents an alternate mechanism by which the prefrontal regions may regulate the limbic and sensory regions associated with autonomic components of vestibular distress. Dotted structures represent subcortical location.

premotor regions (Damasio & Anderson, 2003), which have been implicated in various vestibular paradigms (de Waele et al., 2001; Dieterich et al., 2003).

Evidence for Laterality in the Vestibulo-Cortical Network

Technological advances in imaging have provided support for right-hemisphere superiority in the vestibular modality. Specifically, several studies using a variety of methodologies have noted greater right- than left-hemisphere activation in the vestibular cortical projection areas (Bottini et al., 1994, 2001; Dieterich et al., 1998, 2003; Fasold et al., 2002; Friberg, Olsen, Roland, Paulson, & Lassen, 1985; Janzen et al., 2008; Kahane, Hoffmann, Minotti, & Berthoz, 2003; Lobel et al., 1998; Schlindwein et al., 2008). Moreover, diffusion tensor tractography has noted asymmetrically denser right-hemisphere than left-hemisphere white matter tracts connecting the posterior temporal lobe with the intraparietal lobe, which would anatomically support greater capacity for multimodal integration in these areas (Barrick, Lawes, Mackay, & Clark, 2007).

Kahane et al. (2003) directly stimulated the vestibular cortical areas while patients underwent epileptic foci localization. They found that patients endorsed counterclockwise (leftward) sensations of vection 4 times as much as clockwise vection, and that this pattern was found most often with right-hemisphere stimulation. This is consistent with studies of caloric irrigation (Dieterich et al., 2003) and otolith stimulation (Schlindwein et al., 2008) in which a sensation of leftward tilt is endorsed commensurate with right-hemisphere activations. Furthermore, right-hemisphere integrity is associated with leftward gaze direction (Borod et al., 1988; Meador et al., 1988).

Dieterich, Brandt, and associates have challenged right-hemisphere superiority for vestibular processes, preferring instead the term *non-dominant* hemisphere (Dieterich et al., 2003; Janzen et al., 2008; Schlindwein et al., 2008). Presumably, they are referring to the hemisphere that is not specialized for speech, language, and fine motor control, although they do not clarify this in their studies. They proposed that vestibular stimulation has differential hemispheric activation patterns for right- and left-handed individuals, dependent on which ear is stimulated. In a follow-up to a previous functional magnetic resonance imaging (fMRI) study in which greater right- than left-hemisphere activation for optokinetic stimulation was found in a right-handed population (Dieterich et al., 1998), Dieterich et al. (2003) included an equal proportion of right- and left-handed participants in a caloric irrigation study. They found that cerebral blood flow was more prevalent in the hemisphere ipsilateral to the preferred hand and stimulated ear in the vestibular cortex area, insula region, and portions of the frontal gyrus. That is to say, caloric irrigation of the right ear primarily activated the right hemisphere in right-handers, and irrigation of the left ear activated the left hemisphere in left-handers. They concluded that hemispheric dominance of vestibular processes depended on the handedness of the individual and the ear of stimulation.

Dietrich et al.'s (2003) conclusions concerning hemispheric dominance of vestibular function warrant some caution. First, there is a dearth of research on left-handers in both the vestibular and emotion literature, rendering conclusions about vestibular contributions to behavioral laterality premature at this point. More importantly, however, their conclusions fail to appreciate the complexity of hemispheric dominance and handedness by incorrectly assuming that left- and right-handers possess mirror-opposite cerebral composition, when evidence suggests otherwise (Foundas, Hong, Leonard, & Heilman, 1998).

Behaviorally, left-handers tend to be more versatile in their hemibody preference (Bryden, Hécaen, & DeAgostini, 1983), and this inconsistency in functional asymmetry extends to the cognitive domain. For example, the association between language dominance and handedness has been strongly supported in the literature (e.g., Knecht et al., 2000; Pujol, Deus, Losilla, & Capdevila, 1999), and yet approximately 50%–70% of left-handers have language functions represented in the left hemisphere (Rey, Dellatolas, Bancaud, & Talairach, 1988; Strauss & Wada, 1983). Thus, the assumption of right-hemisphere specialization for vestibular functions in left-handers may still apply given that a significant proportion of this population has the same hemispheric organization as right-handers or tends to be more bilaterally distributed. In fact, in more recent investigations using vestibular evoked potential studies, left-handers had more bilateral activations in the insula, parietal, and temporal areas (Janzen et al., 2008) when compared with the more consistent finding of right-hemisphere dominance in right-handers (Schlindwein et al., 2008), although a direct comparison was not performed.

The Vestibular System and Laterality: An Early Connection?

Dieterich and associates should be commended for addressing hemispheric specialization because the vestibular modality has often been overlooked in discussions of laterality. In a recent review of cerebral modulation of upper limb use and hand preference, Goble and Brown (2008) argued that limb dominance and performance is largely dependent on the type of sensory processing for motor feedback. They suggested that the preferred arm is specialized for visual feedback, whereas the nonpreferred arm is relatively more specialized for proprioceptive feedback.

The omission of the vestibular system in Goble and Brown's (2008) review is striking given a prominent theory purporting the early formation of right-hemisphere specialization underlying subsequent postural and motor asymmetries. Previc (1991) has asserted that the origins of cerebral asymmetry emanate from disparities in the intrauterine environment, specifically from factors related to the prenatal positioning of the fetus in the mother's womb. By the third trimester, about 85% of fetuses are positioned in the cephalic position in utero (vertically with head down), with the back of the torso situated to the left of the mothers midline (Sørensen, Hasch, & Lange, 1979). The position of the infant at birth highly correlates with the intrauterine position of the fetus in the third trimester for approximately 98% of births (Hughey, 1985).

Although estimates vary, the fetus' head position is typically biased with the right ear facing outward and the corresponding left ear facing inward (Fong, Savelsbergh, van Geijn, & de Vries, 2005; Matsuo, Shimoya, Ushioda, & Kimura, 2007). Previc theorized that this position results in unequal stimulation of the otolith organs during locomotion of the mother (Previc, 1991). Given that the left ear is not fixed against the pelvic bone within the womb, the otolith organs in this ear would receive the greater bulk of vestibular stimulation. With the left otolith's indirect pathways to

multiple sensory areas in the right hemisphere, this would provide the initial organizing schema for maturation of the right-hemisphere vestibular cortex.

Because vestibular organs develop prenatally in humans (Freeman, Geal-Dor, Sohmer, 1999; Porowski, Radziemski, Piotrowski, Skórzewska, & Woźniak, 2003), it is difficult to directly test whether unequal otolith shearing occurs. Consequently, evidence is inferred from behavioral neonate studies showing rightward head turning preference and moro response (Coryell, 1985; Fong et al., 2005; Rönnqvist & Hopkins, 1998; Rönnqvist, Hopkins, van Emmerik, & de Groot, 1998; Vles, van Zutphen, Hasaart, Dassen, & Lodder, 1991), consistent with left otolith specialization.

Neglect, the Right Hemisphere, and Vestibular Contributions

Another line of evidence in support of right-hemisphere dominance of vestibular function derives from the hemineglect literature. *Hemineglect* refers to a disorder in which the patient seemingly ignores the side of space contralateral to the impaired hemisphere. Neglect occurs in sensory modalites, including vision (Heilman, Watson, & Valenstein, 2003), somatosensory (Smania & Aglioti, 1995), and audition (De Renzi, Gentilini, & Barbieri, 1989). A preponderance of hemineglect patients are characterized by temporal and parietal lesions in the right hemisphere (Critchley, 1966; Gainotti, Messerli, & Tissot, 1972; Heilman et al., 2003; Leibovitch et al., 1998; Meador et al., 1988; Mort et al., 2003), especially in areas corresponding to vestibular functioning (Karnath, Himmelbach, & Küker, 2003). This overlap has led some researchers to surmise that spatial neglect reflects a failure of vestibular processing of spatial representation at the cortical level (Brandt, 1999; Karnath & Dieterich, 2006; Philbeck, Behrmann, & Loomis, 2001).

In line with this hypothesis, rehabilitative vestibular therapies that incorporate compensation for right-hemisphere neglect syndromes (left neglect of extrapersonal space) have met with preliminary, but not indisputable, success. Vestibular therapies have demonstrated temporary remission of hemineglect symptoms (mostly in patients with right-hemisphere impairments) in whole-body clockwise rotation (Philbeck et al., 2001) and left auditory canal caloric stimulation (Bottini et al., 2005; Geminiani & Bottini, 1992). Moreover, in a derivative of a classic study by Bisiach and Luzzatti (1978) in which representational hemineglect was validated by having hemineglect participants describe well-known landmarks in a Milan plaza from memory, Rode and Perenin (1994) found that irrigation of the left auditory canal (stimulation of the right hemisphere) improved memory recall of landmarks on the left side of a map of France.

Multiple inputs converging in the vestibular cortical areas and pronounced dominance of these inputs in the right hemisphere argue for overlapping neural networks in neglect. This asymmetry in vestibular functioning is consistent with the right hemisphere's predominance in models of global attention (Goldberg, Podell, & Lovell, 1994; Heilman et al., 2003; Mesulam, 2000). Although the left hemisphere is specialized for surveying the contralateral side of space, Heilman and Van Den Abell (1980) provided evidence that the right hemisphere is predominant for allocating attentional resources to both sides of extrapersonal space. This suggests that vestibular contributions at the cerebral level may be an adaptive sensory precursor to stages of attentional allocation favoring specialization of the right hemisphere.

The Functional Emotional System: Associative and Lateralized Relations

The Overlap of Associative Vestibular Circuits With Frontal Emotion Centers

The frontal lobes play an active, but largely undefined, role in vestibular processes. The pathway from the vestibular sensory cortex to the motor association areas and the prefrontal regions provides a crucial interface for the visuospatial, cognitive component of the vestibular cortical network and emotion. The anterior portion of the cingulate gyrus is integral to the division of frontal attentional resources during conflicts among sensory inputs (Bush, Luu, & Posner, 2000; Mesulam, 1999). This filtering role is not exclusive to emotion but can be generalized to cognitive processes associated with conflict during cognitive inhibition tasks, such as the Stroop task (Kerns et al., 2004; Macdonald, Cohen, Stenger, & Carter, 2000), the traditional Go/NoGo task (Garavan, Ross, Murphy, Roche, & Stein, 2002), and the assessment of risk during a decision task (Ernst et al., 2002). Thayer and Lane (2000) suggested that this area filters somaesthetic, attentional, and affective information necessary for executive functioning, especially for self-monitoring of affective state. This interface of the attentional/affective components is evident in studies noting cingulate gyrus activation during exposure to negative words in an affective Go/NoGo task (Chiu, Holmes, & Pizzagalli, 2008) and an emotional Stroop Task (Canli, Amin, Haas, Omura, & Constable, 2004; Whalen et al., 1998). Hence, the anterior cingulate gyrus may provide a bridge between the vestibular sensorimotor areas and the affect divisions of the prefrontal regions that entail motivational states (Bush et al., 2000).

The vestibular system might also exert an influence on emotion via the arousal autonomic pathway that is integral to emotion (Heilman & Gilmore, 1998). In the brainstem, autonomic regulation in emotion is likely accomplished through multiple networks that converge on the parabrachial nucleus in the brainstem. This nucleus serves as the focal point for autonomic processes associated with vestibular functioning (Balaban, 2004). Vestibular nuclei project multiple ascending outputs to the parabrachial nucleus (Balaban, McGee, Zhou, Scudder, 2002; Porter & Balaban, 1997). Hence, the parabrachial nucleus is the initial brainstem mechanism by which the vestibular nuclei likely derive their influence on emotional circuits (Balaban & Thayer, 2001).

The amygdaloid bodies are worth noting because they receive from and project to the parabrachial nucleus (Petrovich & Swanson, 1997) and are involved extensively in autonomic aspects of negative emotion, including hostility (e.g., Demaree & Harrison, 1997) and anxiety (e.g., Everhart & Harrison, 2002). The amygdala fulfills a critical role in the interpretation and production of angry and/or fearful affective responses (LaBar, Gatenby, Gore, LeDoux, & Phelps, 1998; Larson et al., 2006) and in conditioned fear and anger responses (Morris et al., 1996; Morris, Ohman, & Dolman, 1998). Neurons in this structure fire in response to conditioned auditory threat stimuli prior to neurons in the auditory cortex (Quirk, Armony, & LeDoux, 1997), consistent with its role as an early modulator of negative experience. Moreover, Hariri,

Mattay, Tessitore, Fera, and Weinberger (2003) found that activity in the amygdala was attenuated when the right prefrontal cortex was engaged in cognitive appraisal of a threatening visual stimulus, signifying the regulatory relation of the prefrontal cortex to this subcortical structure.

Generally, the prefrontal regions regulate posterior sensory systems at the cerebral level by suppressing sensory stimuli that can overwhelm cognitive capacity limitations or by reducing the impact of irrelevant or distractible sensory inputs. Specifically, the prefrontal region modulates arousal components of sensory thresholds (Angrilli, Bianchin, Radaelli, Bertagnoni, Pertile, 2008; Kallman & Isaac, 1976) and of habituation to auditory and somatosensory stimulation (Butters, 1964; Rule, Shimaura, & Knight, 2002). Damage to the prefrontal region has resulted in attenuated evoked potential responses to somatosensory stimulation (Yamaguchi & Knight, 1990, 1991) and visual brightness (Blenner & Yingling, 1994). In addition, the prefrontal region regulates negative affective appraisal and unpleasant visceral sensations associated with vestibular stimulation (Balaban & Thayer, 2001; Miller, Rowley, Roberts, & Kucharczyk, 1996; Nagai, Kishi, & Kato, 2007). The prefrontal regions exert their influence over the sensory regions ipsilaterally, such that the right hemisphere regulatory capacity is strongest for the right sensory region (Knight, Staines, Swick & Chao, 1999). Given the ipsilateral direction of prefrontal operation, research suggests that the prefrontal region plays an important role, perhaps indirectly, in attenuating the sensory components of the vestibular cortical regions through its indirect connections with the premotor areas and the temporal lobes (Damasio & Anderson, 2003).

The right prefrontal region has a regulatory role, including behavioral inhibition to undesired affective motor responses (Chiu et al., 2008; Garavan et al., 2002), performance of spatial fluency tasks (Foster, Williamson, & Harrison, 2004; Williamson & Harrison, 2003), restraining arousal during affective memory recollection (Foster & Harrison, 2002), and observance of social propriety rules (Demaree, Harrison, & Everhart, 1996; Tranel, Bechara, & Denburg, 2002). Moreover, the ventral portion of the prefrontal region—the right orbitofrontal cortex—is implicated in inhibitory control over the anterior insula and amygdaloid bodies for autonomic modulation of arousal during negative emotional states and associative emotional learning. Evidence for the inhibitory role of the orbitofrontal cortex has been demonstrated anatomically through electrophysiological recording in rhesus monkeys (Ghashghaei & Barbas, 2002) and cats (Royer, Martina, & Paré, 1999), and, functionally, in humans, during negative emotional states such as anger, anxiety, and sadness (Davidson, 1998; Everhart & Harrison, 2002; Levesque et al., 2003; Sander et al., 2005).

Another route of prefrontal regulation has been overlooked in the vestibular cortex literature. The vestibular nuclei project to areas in the brainstem associated with nausea (Miller & Grélot, 1996) and these areas have direct connections to the parabrachial nucleus en route to the amygdala, cingulate gyrus, insula, and orbitofrontal cortex (see Balaban & Thayer, 2001, for a precise description of the relevant neural circuitry). By way of these vestibular autonomic associations then, the prefrontal limbic circuits are involved in one of the chief negative concomitants of motion stimulation: nausea. Nausea is not exclusive to vestibular distress but can also be elicited by a number of varied stimuli

unrelated to motion sickness (Miller, 1999). Nonetheless, a preponderance of research suggests that vestibular stimulation via whole-body passive rotation (Golding, 1992; Golding & Stott, 1997) or optokinetic drum rotation (Himi et al., 2004; Hu, Grant, Stern, & Koch, 1991; Hu et al., 1999) produces autonomic changes associated with vestibular-induced nausea.

If the vestibular system influences autonomic networks associated with visceral sensations that are also cerebrally mediated, then this would account for at least one important mechanism by which emotion and the vestibular system are interlinked. This mechanism would be through the autonomic pathways directly from the vestibular nuclei.

Vestibular-induced nausea has been demonstrated to negatively influence prefrontal areas via magnetic source imaging and electrophysiological techniques (Chelen, Kabrisky, & Rogers, 1993; Miller et al., 1996). In turn, reduction of frontal lobe capacity in the context of emotional strife has been associated with concomitant deleterious influence on autonomic regulation (e.g., Demaree & Harrison, 1997; Foster & Harrison, 2004; Snyder, Harrison, & Shenal, 1998). This would imply that, in addition to the sensory and motor gating role of the prefrontal regions, the nausea correlates of vestibular motion sickness can also tax capacity as a prefrontal "stressor" disrupting autonomic mechanisms.

Evidence for Laterality in Emotion: The Right-Hemisphere Predominance for Negative Emotions

In models of the hemispheric specialization of emotion, it has become increasingly apparent that the perception and experience of negative emotion—broadly including anger, fear, and disgust—are lateralized (for recent comprehensive reviews of emotion theories, see also Cox & Harrison, 2008; Demaree, Everhart, Youngstrom, & Harrison, 2005; Mollet & Harrison, 2007). Most prominently, the right-hemisphere model asserts that expressive and receptive features of emotion are predominantly relegated to the right hemisphere (Heilman & Gilmore, 1998; Heilman, Scholes, & Watson, 1975). Other models have purported a left-hemisphere specialization for positive emotions (Davidson, 1998; Davidson & Fox, 1982; Tucker, 1981).

In support of right-hemisphere specialization are experiments demonstrating right-hemisphere dominance (a) in the visual modality for perception of negative emotional faces (Adolphs, Damasio, Tranel, & Damasio, 1996; Herridge, Harrison, Mollet, & Shenal, 2004; Mandel, Tandon, & Asthana, 1991; Wittling & Roschmann, 1993) and eye gaze during emotional provocation (Borod et al., 1988; Tucker, Roth, Arneson, & Buckingham, 1977); (b) in the auditory modality with respect to emotional prosodic speech (Borod, Andelman, Obler, Tweedy, & Welkowitz, 1992; Borod et al., 1998, 2000; Emerson, Harrison, & Everhart, 1999; Schmitt et al., 1997); and (c) through the somatosensory modality for negative emotional facial gestures (Herridge et al., 1997). It should be reiterated that these sensory modalities correspond to those that contribute to the vestibular network.

Heilman and Gilmore (1998) have postulated that emotional experiences are predicated on three dimensions: valence, motivation (approach/withdrawal), and arousal. The importance of considering all dimensions in the study of emotion is underscored in a recent study by Wager, Phan, Liberzon, and Taylor (2003), who conducted a meta-analysis of more than 65 neuroimaging studies

of emotion and brain asymmetry. They considered the dimensions of valence and motivation, but they did not include studies that controlled for arousal. As a result, the meta-analysis did not support the right-hemisphere model. Yet, when the level of arousal is controlled, evidence for right-hemispheric dominance of negative emotion is supported (Canli, Desmond, Zhao, Glover, & Gabrieli, 1998). The pertinence of arousal in the design of emotion paradigms is not a new concern (see Pizzagalli, Shackman, & Davidson, 2003, for cautions). Arousal is important because the vestibular system mechanisms in cortical sites are dependent upon arousal as well (Furman, O'Leary, & Wolfe, 1981).

Functional Cerebral Systems Theory Integration

The Functional Cerebral Space Model

Up to this point, we have presented research indicating associative and lateralized parallels in the structures implicated in the vestibular modality and emotion. Luria's (1966) conceptualization of functional cerebral systems entails an organization of cerebral systems in which multiple units of the brain are connected through a hierarchy of analyzer modules for cortical tone and arousal (brainstem), sensation and perception (sensory regions), and executive (regulatory) and inhibitory functions (frontal regions). Luria's primary contribution was in unifying brainstem nuclei and frontal systems in understanding that impairment can arise at different levels of these systems yet yield similar functional outcomes. The shortcoming of the functional cerebral systems approach is that it insufficiently delineates the conditions under which emotion and vestibular processing interact.

Kinsbourne (1980) extended the functional systems approach to address this deficiency by proposing a more specific model of cerebral activation under challenging conditions. According to his functional cerebral space model, facilitation or impairment of concurrent performance in multiple tasks depends on the degree of task relatedness and the degree to which the multiple networks involved in the task are "close" in physical space. If the tasks are highly related and the networks are in close proximity within the brain, then performance will be expedited via sharing of networks. If, however, the tasks are dissimilar and involve common cerebral networks, then poor performance will occur. In essence, task complexity increases demands on functional resources—such as attention allocation, autonomic control, and behavioral comportment—resulting in decreased cerebral capacity.

In dual-processing tasks, the processing of one task may lead to interference on a second consecutive or concurrent task (see Pashler, 1994, for a review of various dual-task models). Proficient completion of dual tasks is dependent on the extent to which neural networks overlap. For example, Chan and Newell (2008) found that performance on different primary tasks (object recognition vs. spatial localization) was influenced by how similar the primary task was to the distractor task, and not by which sensory modality the task utilized. Performance entailed separate cerebral pathways for an object recognition task and a spatial perception task. When a distractor task that was slightly different also activated these same pathways, the resultant conflict yielded interference on the primary task. Whether the distractor tasks involved either visual or haptic stimuli was irrelevant because the modalities themselves have different primary sensory areas. Hence, no conflict stemmed from dissimilarity in the sensory modalities.

Kinsbourne's (1980) model originally delineated the circumstances under which the hemispheres divided specialization for dissimilar tasks. Although dual-task performance can be enhanced when the tasks draw on resources within the same hemisphere (e.g., Hiscock & Kinsbourne, 1977; Yazgan, Wexler, Kinsbourne, Peterson, & Leckman, 1995), this is not always the case (Boles & Law, 1998). Applying the model to the hemispheric specialization of emotion, Root, Wong, and Kinsbourne (2006) used a dual-task approach to facial affect recognition and choice reaction time for each hand. They surmised that if emotional faces were presented concurrently to both cerebral hemispheres, responses would be faster with the left hand if the face displayed negative emotion, whereas response times would be faster with the right hand for positive emotions. The results of their facial affect recognition task showed that, as expected, performance was most efficient when the hemisphere that processed emotion and the response hand were congruent; the right hand was faster for positive emotions, whereas the left hand was faster for negative emotions.

The shared space principle is also applicable to frontal–posterior associations. The frontal lobe space is "shared" by a number of abstract cognitive processes all competing to utilize cerebral resources, cortically and subcortically, to regulate behavior. This principle has received a resurgence of support in similarly themed models extending the notion of capacity limitations in cerebral resources during cognitive tasks, such as the resource depletion model (Persson, Welsh, Jonides, & Reuter-Lorenz, 2007) and the cortical field hypothesis (Roland & Zilles, 1998). These models share the perspective that the heterogeneity of frontal lobe functions increases the likelihood of cognitive conflicts.

With respect to laterality, the shared space model provides a counterpoint to Previc's (1991) theory of prenatal lateralization, which emphasizes the role of vestibular end organs, but it does not explain either the hemispheric specialization that accompanies development or the contributions of the frontal lobes to regulation of the posterior vestibular sensory modality. The model also complements previous laterality models culled from the neglect literature (see Karnath & Dieterich, 2006). Hemineglect shares vestibular and somatosensory networks; thus, the attention dysfunction inherent in neglect is mediated or even abolished when vestibular stimulation is applied to neglect patients because of the enhanced compensation of the multimodal centers.

Current vestibular models fail to sufficiently incorporate the prefrontal contributions of emotion in the sensory experiences of dizziness or disorientation. A model proposed to explain studies of anxiety resulting from vestibular complaints comes close, however. According to Jacob, Furman, and Perel (1996), patients with vestibular disorders rely primarily on visual (Dieterich, Bauermann, Best, Stoeter, & Schlindwein, 2008) and secondarily on proprioceptive (Bles, de Jong, & de Wit, 1984) cues to negotiate the environment. When this information is inadequate, deceptive, or confusing, the patient integrates erroneous sensory information. Patients learn to become wary of false sensory integration, which develops into a constellation of fears about falling or the propensity to fall. The authors refer to this disorder as *space and motion discomfort* and have proposed its inclusion in the *Diagnostic and Statistical Manual of Mental Disorders* (4th ed., text rev.; *DSM–IV–TR*; American Psychiatric Association [APA], 2000) as a separate entity. Support for their proposal comes from an experimental vestibular paradigm combining whole-body rotation and mental

arithmetic (Yardley, Masson, Verschuur, Haacke, & Luxon, 1992). High state anxious individuals exhibited a significantly increased slow phase nystagmus component of the VOR (Yardley et al., 1992), indicative of risk for dizziness. Essentially, patients with emotional dysregulation combined with a failure to regulate the kinesthetic and visual inputs in vection display showed diminished performance on a cognitive task relative to controls (further studies are discussed in the section on anxiety and vestibular integration).

The space and motion discomfort model does not incorporate a role for the frontal regulatory mechanisms that have been postulated by vestibular researchers in the animal literature (Akbarian et al., 1994; Nishiike et al., 2000). Although the model does not include prefrontal mechanisms, it appears consistent with Kinsbourne's (1980) cognitive load model, which includes a role for frontal capacity integration of multiple sensory inputs. The model by Jacob and associates is not the first one to forego frontal integration. As discussed previously, Brandt and associates (Brandt, 1999; Brandt et al., 2002) have also postulated a sensory conflict model in which they specify the circumstances under which certain sensory areas inhibit other sensory areas, such as the inhibition of visual association areas by the vestibular cortical areas during caloric stimulation. In effect, these models preclude the involvement of emotion in shaping mechanisms that can enhance or impair vestibular functioning.

Hanes and McCollum (2006) have raised another concern, namely, that the interpretation of studies using dual-task paradigms may be complicated by unevenly taxing demands. For example, a vestibular task—such as maintaining postural balance on a tilting platform—may inherently draw more cognitive resources than a concurrent mental arithmetic task, not because of cerebral competition but simply because safety is prioritized. Although this may be a legitimate caveat, this concern does not detract from evidence suggesting that a vestibular patient will likely exhibit greater difficulty in dual-processing situations than patients with other types of disorders. Vestibular demands impact cognitive processing in normal and brain-damaged individuals, and indices of cognitive demands, even when vestibular handicaps are minimized by keeping the participants stationary or seated, may still impact normal and impaired people differently.

A pertinent limitation of the shared space model is that it was designed from studies using readily observable behaviors in dual-task paradigms, such as the concurrent performance of a motor task and a speech task, or a finger tapping and a speech task. Consequently, there is no recognition that autonomic regulation of emotion also exerts demands on prefrontal resources that are used for other cognitive activities. In our own laboratory, we have extended the functional cerebral systems notion of dual-processing demands to include autonomic regulation. We have examined the impact of cognitive tasks on cerebral activation and cardiovascular functioning in both hostile populations and anxiety-prone populations. For example, Williamson and Harrison (2003) used concurrent fluency tasks that are sensitive to activation in either the left or right frontal lobe (also see Foster & Harrison, 2004) to examine directional and disordinate influences on parasympathetic and sympathetic activation in high-hostile men. High-hostile men demonstrated increased systolic blood pressure in response to a design fluency task that challenged the capacity of the right frontal system (Foster & Harrison, 2004), whereas a verbal fluency task that challenged left frontal capacity (Benton & de Hamsher, 1976)

resulted in decreased systolic pressure. Moreover, high-hostile men showed heightened perseverative errors in the design fluency task—a common clinical finding with diminished right frontal capability. Finally, Everhart and Harrison (2002) found that fluency tasks negatively influenced heart rate and verbal generativity in participants who were anxious and depressed.

If we accept that the processing of internal psychophysiological states diminishes frontal lobe capacity to regulate cognitive processes and that cognitive and autonomic functions compete for frontal lobe resources, then it seems plausible that vestibular functions might also utilize crucial cerebral resources. These demands would have a deleterious impact on the ability to regulate emotion when stressed by a concurrent vestibular challenge. If so, then it may (at least partially) account for the disproportionate experience of pathologic vestibular sensations in anxiety-prone individuals under dual challenges. In the next section, we present evidence to delineate the specific anxiety-subtype and the rationale that is consistent with the functional cerebral systems model underlying vestibular/affective interactions.

Anxiety, the Right Hemisphere, and Balance Disorders

In considering the relation between anxiety and vestibular dysfunction, anxiety subtype is crucial. There is a fundamental distinction between diagnoses of panic disorder (PD) and generalized anxiety disorder that differs on the basis of an immediate, concentrated arousal versus an elevated, prolonged arousal response to stress. The *Diagnostic and Statistical Manual of Mental Disorders* (3rd ed.; *DSM–III*; APA, 1980) separated the diagnostic categories of PD and general anxiety disorders (GADs) along the basis of cognitive and autonomic characteristics, and the *DSM–IV–TR* (APA, 2000) further clarified the distinction, with PD emphasizing the intense somatic and autonomic lability of anxiety, and GAD indicating the anxiety dimension of cognitive worry, with less pronounced autonomic arousal compared with panic (Friedman et al., 1993).

Panic has been associated with reduced right frontal activity under stress (Wiedemann et al., 1999), whereas ongoing verbally mediated worrying is associated with left-hemisphere regulation (Hoehn-Saric, Lee, McLeod, & Wong, 2005; Hofmann et al., 2005). Heller, Nitschke, Etienne, and Miller (1997) interpreted right frontal reductions and right temporoparietal activation during an emotionally charged narrative as supporting an associative model of anxiety subtype differentiation in which the frontal sites responded to the cognitive aspects of the situation, whereas autonomic responses were associated with activation of right posterior sites. This arousal component appears to be a key determinant of the degree of right-hemisphere involvement. Patients with GAD can escalate arousal to detrimental levels. When arousal is introduced to GAD individuals, they show higher rates of right-hemispheric bias than PD individuals. A meta-analysis of electroencephalography (EEG) anxiety studies showed activity in the right frontal (Nitschke, Heller, Palmieri, & Miller, 1999; Papousek & Schulter, 2001), right cingulate (Gottschalk et al., 1992), and the metabolism of the juncture of the right parietal and temporal areas (Wu et al., 1991). Prasko et al. (2004) recorded glucose metabolism with fluorodeoxy-glucose positron emission tomography in patients with PD and found that treatment with either cognitive–behavioral therapy or selective serotonin reuptake inhibitor pre-

scription over 3 months reduced right prefrontal and temporal lobe uptake, as well as increased left medial prefrontal uptake and middle temporal regions, consistent with a right-hemisphere bias hypothesis. Essentially then, studies alleging left-hemisphere involvement in negative affect or negative approach-related motivation may benefit from considering arousal, as the autonomic features may play a key role in the degree hemispheric asymmetry.

Until recently, the psychological concomitants of vestibular disorders, namely anxiety and panic, have largely been relegated to a secondary role. This has not always been the case. In the very first instance in which Freud (1895/1962) defined his concept of *Angstneurose*, he made specific reference to sensations of illusory movement and gastrointestinal disturbances among his nine cardinal criteria for anxiety neurosis. The *DSM–IV–TR* (APA, 2000) stipulates dizziness, lightheadedness, and subsequent gait instability among the varied list of indicators for a diagnosis of a panic attack. Yet whether the relation between anxiety and vestibular dysfunction is associative, causal, interrelated, or simply false positive findings is still a matter of debate (Jacob et al., 1996). Vestibular disorders, such as vestibular neuritis, can lead to increased anxiety complaints (Eagger, Luxon, Davies, Coelho, & Ron, 1992; Pollak, Klein, Rafael, Kossych, & Rabey, 2003; Yardley et al., 1992). Likewise, anxiety can create vestibular dysfunctional symptoms when the aural apparati are intact (Sklare, Stein, Pikus, & Uhde, 1990; Staab, 2006).

In an early study linking vestibular symptoms in PD patients, Jacob, Lilienfeld, Furman, Durant, and Turner (1989) found that 70% of their sample endorsed complaints of frequent lightheadedness. At first, Jacob et al. speculated that this could be due to the lack of CO_2 resulting from hyperventilation. However, 30% of their sample also endorsed complaints of vectional disturbances, and 24% reported that these even occurred between panic attacks. The vestibular system contributes to the antigravity reflexes implicated in postural stability independently from other sense modalities (Aiello, Rosati, Serra, Tugnoli, & Manca, 1983). Yet, labyrinthine-intact PD patients have shown observable abnormal responses during postural stability tasks when under dual challenges (Perna et al., 2001; Redfern, Furman, & Jacob, 2006). Moreover, in patients with vestibular dysfunction, research indicates that the onset of anxiety symptoms, especially for fears of imbalance, is immediate, often occurring after the first instance of clinical dizziness (Godemann, Linden, Neu, Heipp, & Dörr, 2004; Pollak et al., 2003). In effect, anxiety features serve to severely hinder progress toward recovery of balance independence and self-assuredness.

The added dimension of *agoraphobia*, which is a fear of being trapped in situations or places where escape is unlikely, elicits a worse prognosis than PD alone. Sklare et al. (1990) found that 71% of his sample of patients with a diagnosis of PD with agoraphobia (PD w/A) and no history of pathological vestibular diseases had abnormal VOR functioning. These patients were also more likely than GAD, depressive, and healthy normal individuals to have an abnormal response on at least one vestibular battery test (comprised of rotation, VOR testing, posturography, and caloric irrigation; Jacob, Furman, Durrant, & Turner, 1997). Furthermore the PD w/A patients in this study also endorsed vestibular symptoms between panic attacks. PD w/A patients also had high levels of postural instability during a standing stance challenge on a tilting platform, more so than those without agoraphobia (Jacob et al., 1997).

The literature on anxiety and vestibular dysfunction lacks a coherent theoretical account of associative and asymmetrical hemispheric dominance. If the fearful aspect of anxiety is best illustrated by the degree of panic, then it follows that the dissimilarity of vestibular demands and emotional regulatory demands would entail a conflict within shared systems. Yet, anxiety tends to utilize bilateral resources to the extent that verbal processing is recruited as in the case of the worry aspect in GAD. Given the complicated profile of anxiety, our laboratory sought to investigate whether the functional cerebral systems theory could be applied to another population with noted frontal dysregulation and negative affect. Specifically, we examined whether the deleterious effects of dizziness could differentially impact a hostile sample versus a nonhostile sample. These findings are discussed in the next section.

Hostility and the Vestibular Modality: Evidence for Functional Cerebral Systems

Unlike the case of anxiety, Freud (1895/1962) did not provide a rationale for the emotional experience of anger with nausea and/or dizziness. Moreover, there is little *a priori* reason to suggest that the two phenomena frequently co-occur. Hostility may affect the vestibular modality, however, if there is a disturbance in the functional cerebral systems network. Specifically, in line with Kinsbourne's (1980) cerebral space hypothesis, anomalous vestibular sensations may arise if the overlapping substrates involved in a particular phase of anger clash with those involved in vestibular processing. Though the precise structures involved in both have not clearly been identified (but see Balaban & Thayer, 2001), dual-processing conflicts may originate when cortical areas associated with anger reactivity, autonomic lability, and vestibular sensation overlap. With regards to hostility, this laboratory has found ample evidence to support frontal regulation of the anterior temporal region (proximal to the amygdala and anterior insula) for autonomic reactivity (Demaree et al., 1996; Foster & Harrison, 2002, 2004; Williamson & Harrison, 2003).

Luria (1973) first noted cases of spatial delusions in the temporoparietal cortical areas, whereby patients believed that they were simultaneously present in two separate towns. Later, Everhart, Demaree, Harrison, and Williamson (2001) described the case of a man who sustained a closed head injury secondary to a motor vehicle accident. The patient reported feeling as if he was "forced in a box" and hurtled through extrapersonal space. The patient reported extreme hostility and homicidal cognitions associated with loss of spatial control during these delusions. EEG was recorded during an anger induction phase, and the patient was encouraged to imagine a spatial episode. Results indicated marked right-hemisphere beta activation at temporoparietal electrode sites during the session.

The case described above illustrates the possibility that vestibular interactions with anger or hostility may converge on a theme of control. Although evidence to support this hypothesis is sparse at this time, the assertion has been supported in a case study by Nighoghossian, Trouillas, Vighetto, and Philippon (1992). They described a patient with a right internal capsule infarct whose spatial delusion consisted of sensations of traveling through

European cities on various days. He insisted on leaving the house, despite the protests of his family.

Recently, research in our laboratory, using rotary vestibular stimulation, has found a relation between vestibular function, hostility, and arousal that was predicted on theoretical grounds on the basis of the functional cerebral systems approach. Twenty whole-body rotations about the vertical neuroaxis elicited differences in autonomic arousal as a function of hostility level in a healthy population (Carmona, Holland, Stratton, & Harrison, 2008). In contrast, a mild orthostatic tilt test, composed of simply elevating the body to the upright position, did not (Sloan et al., 2001). The conflicting findings suggest that strongly lateralized and/or unpleasant emotional vestibular paradigms, such as those inducing dizziness, may be a crucial factor in understanding the relation between vestibular and emotional networks.

In support of this assertion, our laboratory has pursued a case study using quantitative EEG recorded scalp activity in a woman with an anoxic encephalopathy who complained of extreme anger episodes and concomitant frequent panic attacks (Carmona, Holland, Foster, Harrison, & Harrison, 2008). EEG was recorded while the woman was instructed to mentally rehearse imagery of a recently stressful attack. The stress imagery yielded prominent bilateral delta activity at the frontal lobes and a surge in right-hemisphere beta, with clinical correlates of sympathetic activation (profuse sweating), leftward vection, left facial synergy, and fear. A single-subject experiment was undertaken to follow up the case study's findings with respect to frontal/temporal interactions. To maximally tax frontal capacity in the vestibular modality, we subjected a female volunteer to whole-body passive rotation to the point of dizziness and nausea while quantitative EEG was recorded pre- and post-rotation. As the model predicted, there was heightened delta band activity across the frontal electrode sites and pronounced beta over the right temporal and parietal sites. Delta band activity has been associated with adverse states, such as mental lethargy (Fernández et al., 1995), as well as with various pathological disorders, such as major depressive disorder (Nyström, Matousek, Hällström, 1987), schizophrenia (Fehr et al., 2003), and Alzheimer's disease (Valladares-neto et al., 1995). Beta band activity is typically associated with increases in arousal to emotionally charged stimuli (Foster & Harrison, 2002; Ray & Cole, 1985; Schellberg, Besthorn, Pfleger, & Gasser, 1993). Interestingly, in our single-subject experiment, the delta at the frontal sites was slightly higher at the right frontal sites, consistent with our right-hemisphere hypothesis, though this did not reach the level of statistical significance.

A Proposed Integration Model for Competing Vestibular and Emotion Systems

The findings from the hostility experiments and case studies have led to our proposal for the relations among cerebral systems. We propose that the integration of the vestibular system and negative emotion converges on two mechanisms (see Figure 1). The first mechanism, which we call the *sensorimotor-affective mechanism*, is an extension of the aforementioned vestibular sensory areas. This mechanism appears to involve dorsal areas and involves the dense interconnection of the vestibular sensory areas with the anterior cingulate gyrus and prefrontal cortex. It entails a functional overlap between the vestibular cortical areas and the frontal limbic area. The prefrontal regions indirectly, by way of motor association cortices and anterior cingulate gyrus, exert regulatory influence over the vestibular sensory areas for attenuation of sensory stimulation. As stated previously, the role of this pathway was intimated anatomically by prior vestibular researchers (Akbarian et al., 1994; Nishiike et al., 2000).

The second mechanism is an autonomic one that links vestibular and emotion circuitry. This mechanism, which we call the *autonomic-affective mechanism*, derives from the linkage of the vestibular nuclei directly with the limbic structures such as the amygdala within the temporal lobes and the insula region (see Figure 1). As the frontal lobes have been demonstrated to exert inhibitory control over the vestibular nuclei and vestibular innervated cerebellum for motor coordination (Akbarian et al., 1994; Diamond, 2000; Middleton & Strick, 2001; Nishiike et al., 2000), we propose that the same principle may be applied to the autonomic regulation of vestibular distress. This route may also be implicated in the sensory attenuation of arousing sensory stimulation.

We propose that intense negative experiences induce stress, whether from concerns of dizziness, disorientation, motion sickness, or even anger over lack of control for some individuals. Under vestibular stressors, frontal resources are burdened, resulting in diminished capacity to allocate resources for attenuating activations in the posterior regions. In effect, if cognitive capacity limitations in the prefrontal region are exceeded, then difficulties arise in maintaining sensorimotor coordination in balance and in regulating arousal. The experience of salient negative emotion within the right-hemisphere results in a challenge that further depletes the resources of the prefrontal regions for regulation over key limbic areas in vestibular processes.

The more posterior the impact of dysfunction in the right hemisphere, the more likely disorientation and possibly dizziness will occur in the absence of negative affective correlates. For example, posterior temporal lobe and posterior insula impairments appear to be associated more with dizziness and disorientation than with unpleasant concomitants, such as anxiety or nausea (Bogousslavsky, Caruzzo, Meuli, & Maeda, 1997; Brandt, Bötzel, Yousry, Dieterich, & Schulze, 1995; Cereda, Ghika, Maeda, & Bogousslavsky, 2002; Papathanasiou et al., 2006). The temporal lobes appear to be a crucial transitional and interface zone linking the spatial processing properties of the vestibular cortex (which formally extends into the superior temporal lobe) and the autonomic properties of the prefrontal and limbic emotional centers. Anatomical support for this assertion can be found in research linking right asymmetry for temporal and parietal interconnectivity (Barrick et al., 2007). Also, more directly, support can be found in the description by Spena, Gatignol, Capelle, and Duffau (2006) of 3 patients undergoing exploratory cortical stimulation of the longitudinal fasciculus prior to a surgery for intractable seizures. The longitudinal fasciculus connects the frontal lobe to the posterior regions. Two of the patients with temporal and parietal stimulation felt sensations of objects in the environment rotating, whereas the patient with the left-hemisphere stimulation did not. Furthermore, as there was no direct stimulation to the frontal emotional circuits, there was no reason to expect emotional distress.

The model predicts a dissociable effect of impairment localized to the vestibular sensory areas alone versus impairments that impact the frontal lobe in addition to the vestibular sensory areas.

Impairments located approximate to the vestibular sensory areas can manifest in vection disturbances or neglect, but anxiety or anger-control features may not be readily endorsed by the patient. However, increased sensory stimulation and demands on the limbic and autonomic zones may result in diminished inhibitory capacity of the frontal lobes during vestibular challenges leading to a worse prognosis for the patient's ability to cope. When the prefrontal region is stressed because of overwhelming vestibular activation, the patient may be more inclined to endorse anxiety or frustration, which in turn would further limit resources for adaptive vestibular regulation. In effect, this might explain why PD w/A patients have a worse prognosis than patients who have GAD. The GAD patients tend to have an activation that is more bilaterally distributed, with increased recruitment of left-hemisphere resources in moderating stress.

Summary of Main Points

In this article, we have noted historical links between the vestibular system and emotional functions. Here, we summarize our main points in merging disparate perspectives to inform a neuropsychological understanding.

First, research has established that shared networks are asymmetrically distributed within the hemispheres. The preponderance of evidence from optokinetic, caloric irrigation, and direct stimulation studies in the vestibular literature suggests that the right hemisphere is specialized for vestibular awareness, including perception of horizontal displacement and illusory motion. Furthermore, the onset of this lateralization may be as early as during prenatal development. The hemineglect literature provides behavioral support for right-hemisphere superiority in multisensory vestibular areas. Likewise, the emotion literature suggests that the right hemisphere is dominant for expression, reception, and experience of negative emotions. These models all converge on the right hemisphere as being the dominant hemisphere for cerebral processing of vestibular disturbances with affective components.

Second, there is evidence that the vestibular brainstem apparatus contributes substantially to distributed multisensory areas within the cerebral hemispheres. The vestibular nuclei are the first point of input from the vestibulocochlear cranial nerve and project to the cerebral hemispheres. The vestibular cortical areas have links to the motor and premotor cortex areas for balance and voluntary movement coordination. The cortical areas also have links both directly and indirectly with limbic areas within the prefrontal regions. The prefrontal regions are implicated in a number of concurrent regulatory roles, including attention to internal affective state, affective modulation of motor components, attenuation of sensory overload, determining attention to appropriate sensory input, autonomic inhibition during stressful vestibular challenges, and affective appraisal of dizziness and disorientation. Two mechanisms linking these prefrontal regions are key to understanding the integration. The first is an associative network from the vestibular nuclei to the sensory areas and from there to the frontal lobes for affective modulation of sensorimotor functions. The second concerns the less recognized autonomic features of the vestibular processes. The prefrontal regions serve to inhibit the limbic structures and temporal lobes during emotional vestibular adversity.

Justification for the Integration of Neuropsychological Perspectives and Future Directions

With the steady rise in the number of elderly adults in the U.S. population over the next 20 years, effective diagnosis and treatment of vestibular disorders will become an increasingly critical aspect of public health. Dizziness is one of the most common complaints from adults as reported in hospital intakes and in primary care settings, and it accounts for 1%–2% of all visits (McGee, 1995; Sloane, 1989). The elderly are especially vulnerable to vestibular decompensation (e.g., Yardley, 1998). In fact, dizziness has been reported at least once as a primary health complaint in as many as 30%–40% of the elderly 65 years of age and above (Colledge, Bar-Hamilton, Lewis, Sellar, & Wilson, 1996; Colledge, Wilson, Macintyre, & MacLennan, 1994; Jönsson, Sixt, Landdahl, Rosenhall, 2004). Furthermore, in a survey of 442 people from a primary care medical facility who experienced dizziness, a sizeable percentage (43.7%) reported that these symptoms interfered with their daily activities (Nazareth, Landau, Yardley, & Luxon, 2006).

Szirmai et al. (2005) performed a neuro-otological evaluation of patients with vestibular disorders and concurrent PDs. They commented that patients with vestibular symptoms in remission frequently harbor anticipatory worries that their disorders might return and that these worries restricted their range of independent activities. Their concerns may be justified. Bisdorff et al. (1999) found that the vestibular startle response, which is integral in reacting to an impending fall, was delayed in the elderly. The delay was more than what could be attributed to age-related neuromuscular decline, and it suggests a decline in the performance of arousal circuits. Essentially, the vestibular prevalence research indicates that there is a great need for multidisciplinary participation (including psychology practitioners) in treatment of these disorders, which will no doubt increase in the future.

An interesting possibility for further research would be to investigate the perception of illusory movement in emotionally charged imagery, whether intentional or hallucinatory. In a survey of 150 patients drawn from a primary care facility, Walters and Harrison (2006) found that those who endorsed visual formaesthesias (illusionary figures) in the right visual field (RVF) deemed them to be pleasant, whereas those who endorsed figures in the left visual field (LVF) judged them as fearful. Mollet and Harrison (2007) described a patient with a right thalamic stroke and a history of PD who reported pleasant jovial characters in the RVF. When asked to describe the images in the LVF, she reported intimidating, nefarious characters that she called "eye-drillers." Future researchers might examine the direction of movement of affective images. Patients reporting fearful images in the RVF may endorse movement to the LVF, commensurate with theories associating the right hemisphere and negative affect.

Finally, consideration should be given to the negative implications of reporting dizziness in a clinical setting, especially for the elderly. As vection can be interpreted as a vestibular "hallucination," reporting of illusory sensations may be seen by the elderly patient as endorsing psychiatric abnormality leading to possible fears of social stigma, fears of a diagnosis of dementia, or pragmatically, fears of loss of independence.

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