CHAPTER 1: ANATOMICAL AND PHYSIOLOGICAL ASPECTS OF POSTURAL CONTROL

The control of posture in healthy individuals involves the integration of multiple sensorimotor processes. The central nervous system receives input from several sensory systems, including the vestibular, visual and somatosensory systems. In order to maintain postural equilibrium, these inputs are integrated and various compensatory strategies are initiated to stabilize the centre of mass (CoM), maintain gaze, head and body posture as well as control static and dynamic balance. Both sensory orientation and the maintenance of equilibrium will be discussed in detail.

The Vestibular System

The main function of the vestibular system is to perceive movement and body (head) position relative to objects in space and to the body. Information from the vestibular system is integrated with input from other sensory systems, primarily the visual and somatosensory systems, to coordinate centrally mediated and reflexive motor responses that help maintain balance and equilibrium.

Peripheral Vestibular Anatomy

The peripheral vestibular system is located in the inner ear, which consists of the cochlea, the vestibule and the semicircular canals. The cochlea is involved in hearing with the latter two structures comprising the vestibular system. This system consists of two anatomical components; the semicircular canals and the otoliths. Each component is paired across the head with its counterpart (i.e. left and right semicircular canals) with each pair working in tandem to convey information regarding head position to the brain.

With respect to the detection of rotational movement, the three semicircular canals project posteriorly from the vestibule and correspond to each of the three dimensional anatomical planes; the sagittal, frontal and horizontal planes. Movement of fluid

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contained within these semicircular canals corresponds to rotational accelerations in the direction of the corresponding anatomical plane. The *crista ampullaris*, which is situated at the end of each canal, contains mechanoreceptors known as hair cells (Springhouse, 2002). Hair cells transduce mechanical movement, in this case the fluid within the canals, into electrical impulses. Mechanical stimulation in one direction results in depolarization of the hair cell and neurotransmitters are released from the base of the hair cell, resulting in increased neural discharge in the selected primary afferent neurons. Alternatively, if the hair cells are sheared in the opposite direction, hypopolarization of the hair cell ensues, resulting in decreased neurotransmitter release and decreased neuronal firing (Jones, Jones, Mills, & Gaines, 2009). When one side is activated by head motion, the opposite side is inhibited. This selective firing of primary afferent neurons allows information regarding the direction of movement to be relayed to the vestibular nuclei. Relative activation and inhibition will be discussed further under "Vestibulo-Ocular Reflex."

The otolithic organs, the utricule and the saccule, are membranous sacs suspended by a fluid contained in the vestibule of the inner ear. The hair cells of these organs detect linear and angular accelerations as well as gravitational changes (Springhouse, 2002). Essentially, these organs are responsible for providing information regarding the orientation of the head in space, both at rest and during movement.

Central Vestibular Anatomy

Vestibular nerves located at the base of hair cells in the otoliths and semicircular canals converge at the vestibular ganglion. From here, their axons travel in the vestibular portion of the VIIIth cranial nerve and enter the brain stem between the pons and the medulla. Most of these primary afferents synapse at second order neurons in one of the four vestibular nuclei (superior, lateral, medial and inferior), referred to as the vestibular nuclear complex (VNC). There is both a left and right VNC, which receives input from its respective peripheral organs. Some nerves, however, do travel directly to the cerebellum. Projections from the four vestibular nuclei extend to 1) the extraocular motor

nuclei, which control eye movements;2) the spinal cord, which controls head and body position; 3) the thalamus, which in turn extends to the cortex for conscious perception of movement; and 4) the cerebellum, which coordinates postural adjustments (Baloh $\&$ Kerber, 2010).

Vestibular Neurotransmission

The primary neurotransmitter of hair cell afferent synapses is glutamate, an excitatory neurotransmitter (Soto & Vega, 2010). Glutamate is also released where these primary afferent neurons synapse with secondary neurons of the vestibular nuclei.

The neurons of the vestibular nuclei extend glutamatergic, cholinergic and gamma-Aminobutyric acid (GABA)-ergic projections to various parts of the central nervous system (CNS) as discussed above. Acetylcholine (ACh) is likely the primary neurotransmitter in vestibulocerebellar pathways (Balaban & Porter, 1998; de Lacalle, Hersh, $\&$ Saper, 1993) and is also involved in thalamic neurotransmission (McCormick $\&$ Prince, 1986). Acetylcholinesterase (AChE), which is the enzyme responsible for the metabolism of ACh and is often used as a surrogate marker for cholinergic activity, is also found in cerebellum and the thalamus (de Lacalle et al., 1993).

Conversely to afferent vestibular neurotransmission, efferent neuronal synapses (i.e. neurons transmitting impulses from the central nervous system to the vestibular periphery) release ACh as the primary neurotransmitter (Soto & Vega, 2010). These efferent neurons originate in the brainstem and innervate hair cells and vestibular afferents to exert central control over vestibular responses based on the movement programming of the subject (Bridgeman, Hoffman, Wackym, Micevych, & Popper, 1996; Soto & Vega, 2010).

The Visual System

Simply put, the visual system is fundamental in providing information regarding the layout of the surrounding environment that is then used to develop appropriate motor responses (i.e. stepping onto a curb or avoiding an obstacle). It also serves as a reference point for other sensory and cortical functions that use visual cues to orient the body in space.

Like the peripheral vestibular system, the visual system also delivers its information to the vestibular nuclei, among other locations, for integration. More specifically, visual information is relayed from the retina to the accessory optic system (AOS) nuclei, which project to the vestibular nuclei. The main role of the AOS in maintaining posture is, with help from the vestibular system, to help distinguish between movements in the environment from movement of the body (Soto $\&$ Vega, 2010). In addition to their connections to the vestibular nuclei, the AOS nuclei have efferent connections to the cerebellum and midbrain. In turn, the vestibular nuclei receive afferent input from the visual cortex, which is responsible for processing visual information (Giolli, Blanks, $\&$ Lui, 2006).

Vestibulo-Ocular Reflex (VOR)

A reflex occurs relatively rapidly in response to sensory stimuli. The VOR is an example of a polysynaptic reflex (i.e. more than one synapse is involved). Alternatively, most peripheral muscle reflexes such as the "knee-jerk reflex" are monosynaptic (i.e. only one synapse is involved at the level of the spinal cord) (Barrett, 2010). This VOR serves to maintain a fixed image on the retina while the head is in motion. The VOR produces compensatory eye movements in the opposite direction of head movement. This is achieved when vestibular afferent neurons are activated on one side and subdued on the other, for example when the head turns to one side. To simplify, when the respective VNC is activated, signals travel through second order neurons to the IIIrd cranial (oculomotor) nerve on the same side. This nerve then crosses over to the opposite side, activating the opposite abducens nucleus (VIth cranial nerve). While these neurons are being activated on one side, they are being inhibited on the other. The neurons from the

abducens nucleus activate the lateral rectus muscle, which pulls the eye in the opposite direction of the movement (i.e. if the head turns right, the eye moves left). Motor neurons from the opposite oculomotor nucleus will contract the medial rectus muscle of the other eye to pull this eye in the same direction (opposite to the movement). The opposing muscles in each eye will relax as they have been inhibited by their respective motor nuclei (Jones et al., 2009). This reflex plays an important role in the complex sensorimotor integration that maintains balance. Nystagmus, which is the presence of compensatory eye movements in the absence of head movement, can in some instances cause blurred vision, postural imbalance, ataxia and gait disturbances (Jahn & Dieterich, 2011).

Ocular Neurotransmission

Most of the neurotransmitter pathways of the AOS utilize GABA, however other transmitters may be involved. However, as they are motor neurons, the medial rectus and abducens motoneurons, responsible for activating the muscles that turn the eyes horizontally as described above, utilize ACh (Leigh & Ramat, 1999).

ACh activity is also prevalent in the visual cortex and is purported to reduce "noise" signals during the processing of visual inputs (Gu, 2003). ACh may also be involved in neuroplasticity within the visual cortex (Maya-Vetencourt & Origlia, 2012).

The Somatosensory System

The main function of the somatosensory system may be drawn from its name, that is to say, somatic sensation. This complex arrangement of neurologic connections is omnipresent throughout the body with receptors on the skin, bones, muscles, joints, and internal organs. These receptors are responsible for detecting pressure, pain, hot and cold as well as chemical and osmotic stimuli. For the purposes of postural control, the most relevant receptor types are mechanoreceptors and proprioceptors, responsible for

detecting pressure and body positions (relative to other body parts and the environment), respectively.

For example, plantar mechanoreceptors (located in the skin) provide information regarding contact pressures on the sole of the foot, making them capable of detecting changes in body orientation relative to the ground (MacLellan & Patla, 2006). These receptors are divided into two subtypes, rapidly or slowly adapting. Rapidly adapting mechanoreceptors detect the rate and degree of change in the pressure exerted on the foot and slowly adapting mechanoreceptors provide constant information on how pressure is spatially and consecutively applied (Kavounoudias, Roll, & Roll, 1998).

Alternatively, proprioceptors are located in the joints, muscles and tendons. They provide sensory information regarding joint angle, muscle length, and muscle tension, which is used to detect the position of the limb in space. Muscles spindles are proprioceptors located parallel to muscle fibers and activate a primary sensory afferent neuron when the muscle is stretched. Alternatively, the Golgi tendon organ is located in tendons, in series with muscle fibers, and activates primary sensory afferent neurons when the attached muscle contracts (Purves et al., 2001).

When neurons carrying proprioceptive information reach the level of the spinal cord, most form synapses with interneurons that relay the information to higher levels of the CNS. Interestingly, the brainstem and cortex are able to exert descending control over these neurons that also allows them to filter the ascending information. Most proprioceptive information travels through the dorsal lateral tracts or the spinocerebellar tracts of the spinal cord. The dorsal lateral tracts, thought to carry most of the information that is consciously perceived, travel from the dorsal root ganglia to thalamic nuclei and then on to the somatosensory cortex. The somatosensory cortex is located in the parietal lobe, where central processing occurs. Conversely, the spinocerebellar tracts travel to the cerebellum, where the signals are integrated with descending information and input from other afferent tracts. It is hypothesized that the spinocerebellar tracts are involved in transmitting unconscious proprioceptive information, such as limb position or muscle

length, which is used for local reflexes as well as automatic and voluntary movement (Riemann & Lephart, 2002; Warren, Yezierski, & Capra, 1997).

Somatosensory information is translated into motor commands and responses via complicated interconnections with the primary motor cortex, which is beyond the scope of this discussion. The motor portion of the sensorimotor system consists of a central axis and "associate" areas. The central axis is comprised of the spinal cord, brainstem, and cerebral cortex. The associate areas include the cerebellum and basal ganglia, which coordinate the motor commands (Matthews, 1997).

Briefly, the spinal cord is responsible for the transmission of information to and from the central nervous system as well as local reflexes and the cerebral cortex (sensorimotor cortex and supplementary motor area) is involved in sensory integration, initiating various motor commands and performing executive functions related to maintaining gait, posture and balance. The cerebellum is responsible for timing and fine-tuning motor output and the basal ganglia, which will be discussed further in subsequent sections, are responsible for learning, planning, initiating, executing, and terminating motor programs. The mesencephalon (midbrain) is an important brainstem structure containing the substantia nigra and is closely linked to motor pathways of the basal ganglia. The substantia nigra will also be discussed in subsequent sections (Sousa, Silva, & Tavares, 2012).

Somatosensory Neurotransmission

With respect to the somatosensory cortex, there is animal evidence that ACh is released in large quantities following mechanical sensory stimulation(Kurosawa, Sato, & Sato, 1992). There is also evidence that following sensory stimulation (visual, tactile, olfactory, auditory), large amounts of ACh are released in the hippocampus and frontal cortex, linking cholinergic mechanisms with attention and arousal following sensory stimuli (Inglis & Fibiger, 1995).

The Stretch Reflex

The stretch reflex, or the myotatic reflex, is a reflex involving a sensory neuron and a motor neuron and is essential in the involuntary control of posture (Shemmell, Krutky, $\&$ Perreault, 2010). The most commonly known example of the stretch reflex is the "kneejerk" reflex, but stretch reflexes also occur in postural muscles of the spine as well as in destabilizing and stabilizing muscles involved in responses to postural perturbations. If a muscle is stretched, the muscle spindle (described previously) is stretched and neuronal output is increased, thereby increasing alpha motor neuron activity. This causes the muscle fibers to contract and oppose the stretch. The opposing muscle also relaxes to accommodate this contraction (Yessis, 2000).

Stretch reflex responses have divided according to their onset latencies on electromyogram (EMG) into short- and medium- and long-latency components. Both short and long latency responses are considered involuntary as they occur before even the most rapid voluntary reaction to a stimulus, however they can be modulated under certain situations (Shemmell et al., 2010). The relative roles and timing of these responses are debated however, it is thought that the short-latency reflex is involved in regulating muscle stiffness, or rather compensating for transient decreases in muscle stiffness following joint perturbation, thereby reducing muscle yielding following the perturbation (Cronin, Carty, & Barrett, 2011). These short-latency responses occur in the stretched muscle. Medium-latency responses are deemed to be destabilizing and also occur in the stretched muscle (i.e. in the triceps surae following a toes-up platform rotation) and longlatency responses are considered stabilizing and occur in the antagonist muscle (i.e. the tibialis anterior following a toes-up platform rotation). As demonstrated in an EMG study of 33 PD patients undergoing 4-degree toes-up platform rotations, the latencies of EMG responses in these muscles are usually normal in PD patients, with the exception of an increased short-latency response (Scholz et al., 1987) in the triceps surae muscle. However, the amplitude and duration of certain of these responses are affected in PD, which will be discussed in subsequent sections.

The following excerpt from an article published by Bloem and colleagues (Bloem et al., 1996) aptly describes the role of these responses in the control of upright stance following toes up platform rotations:

"[Medium latency] stretch responses induced by toe-up rotations are functionally destabilizing since their plantar flexion force aggravates the posterior body sway induced by the toe-up rotational perturbation. In contrast, the dorsiflexion force of [long-latency] responses is functionally stabilizing."

Cholinergic Projections

ACh is a critical neurotransmitter in the central nervous system where it plays a role in arousal, attention, executive functioning and neural plasticity (Yarnall, Rochester, $\&$ Burn, 2011). The striatum is supplied with ACh via cholinergic interneurons that make up 1-2% of intrinsic striatal neurons (Zhou, Wilson, & Dani, 2002). The nucleus basalis of Meynert (nbM) is responsible for providing most of the cholinergic input to the cerebral cortex and appears to be important for several aspects of cognition, including attention (Sarter, Gehring, & Kozak, 2006). However, the PPN is responsible for providing most of the cholinergic input to the subcortical systems including the thalamus as well as the brain stem and cerebellum(Perry, Walker, Grace, & Perry, 1999). The PPN also possesses connections with the basal ganglia, notably the substantia nigra, subthalamic nucleus, globus pallidus, and extends directly to the spinal cord and the cerebral cortex (Jenkinson et al., 2009)The role of both the basal ganglia and the PPN in the pathophysiology of PD will be discussed in following sections.

Role of Cognitive Processing

Sensory Integration

Postural control relies on the integration of information from several systems and the selection of an appropriate motor program to deal with both expected and unexpected

perturbations. Neural integration of information from multiple sensory, motor and cognitive systems occurs in the VNC (Jones et al., 2009). The vestibular nuclei receive input from the three sensory systems (vestibular, visual and proprioceptive) and transmit this information to the spinal cord for postural stabilization. Interestingly, some hypothesize that abnormal activation or dysfunction in the vestibule-spinal pathways are a cause of postural imbalance and ataxia. Information is also relayed from the vestibular nuclei to the vestibular thalamus and cortex (for spatial orientation, perception of movement and sensorimotor transformation), as well as the brainstem and cerebellum (for the vestibulo-ocular reflex) (Dieterich, 2004).

Sensory Reweighting

Under normal conditions, healthy adults rely mostly on somatosensory (70%) information, but vision (10%) and vestibular (20%) information are also important (Peterka, 2002). Because sensory information is not always available (i.e. in a dark room) or reliable (i.e. compliant support surface), the dependence on each system must be reweighted in order to accommodate. For example, when standing on an unstable support surface, reliance on visual and vestibular input increases while plantar and ankle proprioceptive information is minimized (Peterka, 2002) as it is unreliable or conflicting. The ability to re-weight sensory information is important to adapt to changing environments (i.e. changes in lighting) or sensory deficits (i.e. neuropathy). Persons with deficits in any or several of the sensory systems involved in postural control are at an increased risk of falling as their ability to re-weight dependence to that system is limited. It also appears that sensory re-weighting is limited in individuals with CNS or cognitive dysfunction (i.e. Alzheimer's disease (AD)) as the ability and rapidity of sensory reweighting is reduced, even if peripheral input is adequate and reliable (F. B. Horak, 2006).

Attention

Balance control requires a certain level of attention on behalf of the subject and the attention required increases with the difficulty of the task at hand. For example, it has been shown that standing requires more attention than sitting and walking more attention than standing (Lajoie, Teasdale, Bard, & Fleury, 1993). In their experiment, Lajoie and colleagues demonstrated that reaction times were significantly increased when subjects were in the single-support phase compared to the double-support phase of straightforward gait. Because the base of support is smaller during the single-support phase, this represents a more difficult postural task. In this instance, balance was maintained at the expense of the subject's reaction time. Because attentional performance deteriorated under a more difficult postural condition, this study represents a good example of the involvement of attention in the maintenance of balance.

Dual Tasking

The experiment cited above by Lajoie and colleagues employed the use of a dual-task to demonstrate the involvement of attention in balance control. The theory behind dual tasking is that postural stability is not simply an automatic spinal reflex, but as previously mentioned, a task that also requires cognitive control. By dividing attention between a cognitive and postural task, one should observe a deterioration of one, the other or both tasks, depending on the difficulty of the task and the priorities, capacities or focus of the individual (Siu, Chou, Mayr, van Donkelaar, & Woollacott, 2008).

The concept of dual tasking in an experimental setting is important to consider as performing two tasks simultaneously is common in daily life (i.e. walking and talking on a cell phone). Including dual-tasks in study design allows extrapolation of experimental data to more real-life settings.

Functional magnetic resonance imaging (fMRI) evidence has shown that the cerebellum plays an important role in processing dual motor and cognitive tasks. In a study combining a motor task (finger tapping) with a counting task (counting the number of times a certain letter was displayed on a screen), various cerebellar regions were activated

on fMRI (Wu, Liu, Hallett, Zheng, & Chan, 2013). These cerebellar regions had extensive connections with motor and cognitive regions of the brain including the sensorimotor cortex, the supplementary motor area, the premotor cortex, the parietal cortex and the thalamus. Training resulted in less activation in several areas, however it increased connectivity between the cerebellum and some of the motor and cognitive areas, providing evidence that a learning effect or habituation may occur. Others have shown, again with fMRI, that dual cognitive tasks rely mostly upon the prefrontal cortex (Szameitat, Schubert, Müller, & Von Cramon, 2002), however it is unknown if the cerebellum is also heavily involved in the performance of dual motor tasks (i.e. reaching while walking).

Strategies to Maintain Postural Equilibrium

Various voluntary and involuntary as well as anticipatory and compensatory strategies are involved in postural control and will be discussed in the following sections. Evidence exists supporting a cortical role in postural responses (Jacobs & Horak, 2007). However, it is clear that not all postural responses are cognitive in nature as humans can walk and remain upright without conscious effort. Therefore, postural control is simultaneously a complex cortical and subcortical function.

Biomechanical Considerations

In order to maintain balance under static and dynamic conditions, the CoM, which represents the centre of gravity of the whole body, must remain within the limits of stability. The limits of stability are three-dimensional (in the shape of a cone) and represent the distance the CoM can travel before a loss of balance occurs. The CNS creates an internal representation of this cone of stability to determine appropriate movements to maintain upright equilibrium. The magnitude of these limits is determined by the size and integrity of the base of support, in this case the feet. Any physiological or external constraint (i.e. pain, foot size, support surface) will affect these limits and the subsequent risk of falling. When the CoM travels outside of the limits of stability,

balance is lost and a reaction must occur (i.e. taking a step or grabbing an object) to prevent a fall (F. B. Horak, 2006).

Movement Strategies

A number of movement strategies are in place to maintain the CoM within the limits of stability. These movement strategies are implemented to maintain and reestablish postural equilibrium, depending on the nature of the disturbance. These strategies can be divided into three categories: ankle, hip and stepping or reaching strategies (F. B. Horak, 2006).

In the ankle strategy, the body moves around the ankle as an inverted pendulum. This type of movement is usually adequate to account for small degrees of postural disturbance or sway, particularly when standing on a firm surface. Alternatively, the hip strategy involves an exertion of torque (or bend) at the hips and is employed when the CoM must be relocated quickly or to a larger degree. The hip strategy is commonly used when the support surface is variable or ankle torque is ineffective. When the disturbance is large and the CoM travels outside the limits of stability, a step or a reach must occur to prevent a fall. Selecting a movement largely depends on the individual's expectations and experience and in general, those at a lower risk of falling employ the ankle strategy, with those at higher risks of falling (i.e. the elderly) employing hip and stepping strategies more frequently (F. B. Horak, 2006). These strategies may be anticipatory, voluntary or compensatory. Automatic postural reactions (APRs) represent responses to sensory (visual, vestibular and somatosensory) input, which signal postural disturbances in relation to movement. Anticipatory postural adjustments (APAs) occur prior to the initiation of voluntary movements and serve to counteract the disturbance that movement will impose on balance (Kim et al., 2013).

Anticipatory Postural Adjustments (APAs)

The main function of APAs is to compensate for the destabilizing forces associated with moving a limb. The subsequent disturbance, be it internal or external, is predicted by the CNS and select muscles are activated to maintain the CoM within the limits of stability. It is hypothesized that APAs may originate from the supplementary motor area (Massion, 1992).

Therefore, these APAs occur prior to, or in anticipation of, voluntary movements, such as before taking a step. In the instance of stepping, the centre of pressure (CoP), which is the projection on the ground plane of the vertical ground reaction force distribution under the base of support (Iqbal, 2011), is shifted via selective joint repositioning and muscle contraction (in this case the tibialis anterior) backward and towards the swing leg before the movement is initiated. This helps neutralize the induced interaction torque caused by lifting the leg to take a step (Hyodo et al., 2012; Iqbal, 2011). However, APAs are also scalable to the magnitude (velocity and size) of the perturbation, usually based on preconceptions regarding the difficulty or the resources required to complete a task. This brings attention to the observation that APAs, and all postural adjustments for that matter, are learned, individualized and dependent on the task.

Interestingly, APAs are smaller when an individual is unstable, which results in further destabilization following movement of a limb owing to inadequate preparation (Aruin, Forrest, & Latash, 1998). APAs are also smaller or absent when visual or proprioceptive information is unreliable (i.e. vision is impaired and the subject is required to catch a falling object), confirming the anticipatory nature of these adjustments and supporting a feed-forward theory of postural control (Mohapatra, Krishnan, & Aruin, 2012a, 2012b).

Voluntary Movements

Centrally-mediated voluntary movements may be performed to maintain equilibrium in response to identified disturbances (i.e. stepping around an object), however, balance must also be maintained during all types of voluntary movements, whether the effort to remain upright is conscious or not. Therefore, voluntary movements inherently render

balance control more difficult. The simultaneous conduction of a voluntary movement and stabilization of balance is determined by the sum of the internal (i.e. voluntary movement of an arm) and external forces (i.e. gravity) acting on the body (Bouisset $\&$ Do, 2008). To successfully neutralize destabilizing forces and perform voluntary movements, postural adjustments occur before (APAs), during (synchronous postural adjustments) and after the movement (consecutive or compensatory postural adjustments; CPAS) (Bouisset & Do, 2008). Clearly, the relative difficulty of voluntary movements can differ greatly depending on the task (i.e. waving an arm versus getting out of a chair). However, tasks involving multiple body segments (i.e. walking) and an unstable, rather than stable, base of support are generally more challenging in terms of postural control (F. B. Horak, 2006).

Automatic Postural Reactions (APRs)

Compensatory, or reactive, strategies help stabilize the body following inappropriate or absent anticipation of movement or following external perturbations. These responses are triggered automatically, unlike APAs, which precede voluntary internal perturbations (Jacobs & Horak, 2007). If a perturbation were self-initiated (i.e. moving an arm) an APA would precede the movement, helping to maintain stability. If the perturbation was recognized in advance (i.e. an object obstructing the path), a voluntary movement could also be employed to avoid destabilization. However, it is when APAs are insufficient or perturbations are not predicted that reactive strategies must be used. These reactive postural responses occur secondary to sensory information from the visual, vestibular and somatosensory systems regarding movement. In these instances, a mechanical and then neuromuscular response occurs following the perturbation. For example, when a subject receives an unexpected perturbation during straightforward gait, the tendons and ligaments surrounding the ankle, knee and hip are stretched in sequence, which is rapidly followed by a neuromuscular adjustment in the muscles that control and stabilize the joint. The muscles surrounding the hip are likely the most important owing to the unexpected nature of the perturbation and the magnitude of compensation that is required (Ferber, Osternig, Woollacott, Wasielewski, & Lee, 2002).

However, in some cases compensatory adjustments are not sufficient to prevent destabilization. For example, APAs may be minimal during compensatory stepping and therefore the CoM tends to travel toward the swing leg side during, rather than before, the step causing a lateral instability and a subsequent risk of falling (Hyodo et al., 2012).

There is evidence that postural adjustments are under cortical control (Jacobs & Horak, 2007); therefore one can imagine that any decline in cortical function would be detrimental to postural control. Indeed, it has been shown that when performing a simultaneous cognitive math task, the response latency and amplitude of tibialis anterior and gastrocnemius muscle activity following standing platform perturbation is reduced (Rankin, Woollacott, Shumway-Cook, & Brown, 2000). This is known as the dual-task paradigm, discussed previously.

However, divergent to these processes which typically occur in a predictable environment, there appears to be a "first-pass" effect in terms of APRs in that subjects will rapidly develop adaptation or habituation following a first-time or unexpected balance perturbation. Therefore, the hierarchal organization of subsequent responses (as described above) is naturally different than the first. Both repetition and, to a lesser extent, instruction appear to induce a learning effect with respect to CoP responses to balance perturbations (Maki & Whitelaw, 1993). In fact, the learning response observed with computerized dynamic posturograhy appears to be so marked that some have suggested its utility as physical therapy for patients with PD (Rossi-Izquierdo et al., 2009). With respect to data analysis, however, it appears that analyzing first trials or pooled data from multiple trials makes no difference (J. Visser et al., 2010).

It is also likely that these "first-pass" reactions are not universal or generic and that significant inter-personal variability exists. This is particularly important to consider when analyzing the studies found in Chapters 4 and 5 as multiple trials were conducted in sequence and, in Chapter 5, across several patients. Corbeil et al. (Corbeil, Bloem, van Meel, & Maki, 2013) were able to demonstrate said occurrences by focusing solely on

first-trial arm reactions evoked by small perturbations (that would ideally not require the use of arms for stabilization) to balance using a motor-driven platform. Their hypothesis was that responses would not be stereotypical across subjects and would alternatively be modulated according to the direction of the balance perturbation and the presence or absence of environmental factors (e.g. handrail). In their study of 12 healthy adults, they found that most subjects initiated active movement of both arms in response to the provocation. This response influenced by the perturbation direction (rightward or forward platform movement), which suggests a functional strategy rather than a reflexive or stereotyped response. The handrail also modulated responses in the speed of arm reaction. There was large inter-subject variation with respect to amplitude, velocity and timing of these movements. The results were statistically significant despite a small sample and together are inconsistent with a generic or stereotypical reaction.

The Centre of Pressure (CoP)

A commonly employed measure of postural sway is the centre of pressure. Referred to commonly as the CoP, it may be defined as the application point of the force vector that is equal to the sum of the forces acting between the foot and support surface. The CoP is an indirect measure of body sway and is proportional to ankle torque, which is a combination of descending motor commands and muscle activity around the ankle used to keep the whole body centre of gravity (or the CoM) within the base of support (Baratto, Morasso, Re, & Spada, 2002; J. E. Visser, Carpenter, van der Kooij, & Bloem, 2008). The CoP is usually described in terms of its displacement (amplitude and frequency) in the medial-lateral and anterior-posterior directions which is thought to be independently controlled by the CNS and represents the overall neuromuscular response required to maintain control of the CoM within the limits of stability (Pasman, Murnaghan, Bloem, & Carpenter, 2011; Winter, Prince, Frank, Powell, & Zabjek, 1996).

By measuring the change in mean CoP velocity, which is defined as the total distance travelled by the CoP (i.e. the total sway path) divided by the duration of the sampling period (cm/s), one can estimate the amount of activity or effort required to control

balance; the greater the velocity of the CoP, the more compensatory adjustments required to maintain stability (Maki, Holliday, & Fernie, 1990). As a dependent variable in quantitative research, the mean velocity of the CoP is a validated measure of postural stability and fall-risk (Maki et al., 1990). Studies have shown that the velocity of CoP displacements is indeed higher in PD than controls (Rocchi, Chiari, & Horak, 2002).

Posturographic Analysis

Posturography can be a useful clinical tool for detecting and characterizing balance problems. Data collection is typically achieved through the use of force plates to quantify the CoP. The most widely accepted measure involves computerized dynamic posturography, which employs the use of moveable (sway-referenced to the subject's postural sway) force plates to measure displacement of the CoP under various sensory conditions. The sensory organization test (SOT) typically uses up to six conditions to isolate the effects of vision, proprioception and vestibular input during upright balance by selectively limiting or altering sensory input. The most commonly used SOT protocol measures standing balance on a 1) static support with eyes open; 2) static support with eyes closed; 3) sway-referenced support with eyes open and 4) sway-referenced support with eyes closed. This allows the clinician to elucidate the etiology of balance problems using various outcome variables.

In addition, the mean velocity of the CoP as described above, the time structure of the CoP may reveal pathological postural specificities. Thus, structural posturographic parameters may be calculated by means of a sway density plot method (Baratto et al., 2002). The sway density plot is computed by totaling the number of consecutive samples during which the postural oscillations remain inside a 2.5 mm radius. The mean value (duration) of all peaks, the mean of all distances between one peak and the successive peak (spatial distance) and the mean time distance between peaks (time distance) are then derived from the sway density curve. The peaks of the sway density curve relate to periods of relative CoP stability (postural stabilization), whereas troughs indicate periods where the CoP is rapidly shifting in order to maintain balance (postural adjustment

control) (Baratto et al., 2002; Corbeil, Blouin, & Teasdale, 2004). The peak duration reflects the amount of time spent in a stable position (with respect to ankle torque and associated motor commands). The spatial distance corresponds to the amount of effort (postural commands) required to resume a stable position, whereas the time distance represents the amount of time required to resume a stable position or rather the rate of production of postural commands (Baratto et al., 2002). Together these variables can aid in the diagnosis of balance problems, however they must always be interpreted in the context of an individual patient.

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