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THE EFFECT OF GVS ON PATH TRAJECTORY AND BODY ROTATION IN THE ABSENCE OF VISUAL CUES DURING A SPATIAL NAVIGATION TASK

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Abstract

Background: The vestibular system has been shown to contribute to mechanisms of locomotion such as distance perception. Galvanic vestibular stimulation (GVS) is a tool used to perturb the vestibular system, and causes significant deviations in path trajectory during locomotion. Previous research has suggested that applying GVS during straight-line locomotion tasks is not sufficient to determine the effects of the vestibular system on locomotion. However, spatial navigation challenges one's ability to navigate throughout the environment using idiothetic cues to constantly update one's position. The purpose of the current study was to determine the effects of GVS on both path trajectory and body rotation during a task of spatial navigation in the absence of visual cues, and how accuracy of this task is affected by dance training. It was hypothesized that the delivery of GVS would significantly increase errors during the triangle completion task, and this increase would be more pronounced in the control participants compared to the dancers.

Methods: Participants (n=34, all female, 18-30 years) were divided into two groups: controls (n=18) had no experience with sport-specific training while dancers (n=16) had previously experienced dance training (M = 15.6 years, SD = ±4.1) and were still currently training in dance (M = 11.5 hours/week, SD = ±7.3). Monofilament testing (Touch-Test Six Piece Foot Kit) was used to determine the plantar surface cutaneous sensitivity threshold and a joint angle-matching task was used to quantify the proprioceptive awareness of each individual. Participants completed trials of the triangle completion task in VR (via Oculus Rift DK2), during which they would navigate along the first two legs of one of two triangles using visual input, and then accurately navigate back to their initial position with the use of vision. GVS was delivered at three times the participant's threshold in either the left or right direction prior to the final body rotation and until the participant reached their end position. The task was completed six times for each of the GVS conditions (with and without GVS) with the experimental GVS condition being further divided into right and left perturbation trials, for each of the two triangles, in both the right and left triangle directions, for a total of 48 trials (six trials x 2 GVS conditions x 2 triangles x 2 directions). Whole body kinematic data were collected at 60 Hz using an NDI Optotrak motion tracking system.

Results: No significant differences were observed between control subjects and dancers with respect to arrival error, angular error, path variability, cutaneous sensitivity or proprioceptive awareness. However, there was a significant effect of GVS on both arrival error and angular error. Conditions without GVS had significantly smaller angular error than both conditions with GVS. In addition, GVS conditions with the perturbation in the same direction as the final body rotation had significantly greater arrival error than both the condition without GVS and with the current in the opposite direction of the final body rotation. There was no significant difference between GVS conditions in path variability during the return to the initial position.

Conclusions: The significant effect of GVS on both arrival error and angular rotation demonstrates that vestibular perturbation reduced the accuracy of the triangle completion task. These findings suggest that the vestibular system plays a major role in both path trajectory and body rotation during tasks of spatial navigation in the absence of vision.

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List of Abbreviations

ANOVA	Analysis of Variance
AP	Anterior-Posterior
CNS	Central Nervous System
COM	Centre of Mass
COP	Centre of Pressure
CoV	Coefficient of Variation
EMG	Electromyography
GVS	Galvanic Vestibular Stimulation
GVSaway	Galvanic Vestibular Stimulation away from direction of turn
GVStoward	Galvanic Vestibular Stimulation towards direction of turn
NGVS	No Galvanic Vestibular Stimulation
HMD	Head-Mounted Display
IRED	Infrared Light-Emitting Diodes
M	Mean
ML	Medial-Lateral
NDI	Northern Digital
REB	Research Ethics Board
SD	Standard Deviation
VENLab	Virtual Environment Navigation Laboratory
VR	Virtual Reality

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1.0 Introduction

With every motor output that is produced, there is a variety of sensory information that has contributed to its characteristics. We are constantly taking information from the external environment and using it to produce a motor response. Postural control in humans is maintained by feedback from the somatosensory, visual and vestibular systems, and this information is then integrated by the locomotor and central nervous systems (Johansson & Magnusson, 1991). Previous research has supported that the contribution of each sensory system depends on the environment and the applied perturbations, and the process of adjusting these sensory contributions is referred to as sensory reweighting (Asslander & Peterka, 2014; Peterka R., 2002). During quiet stance, the central nervous system tends to give higher weight to the sensory system with the most accurate input. In a study by Peterka (2002), the author demonstrated that during conditions without visual input, subjects primarily used somatosensory or proprioceptive input in order to maintain postural control. However, during conditions with a moving support surface causing perturbation of the somatosensory system, subjects then became more reliant on graviceptive information, which is defined as a form of vestibular information providing individuals cues about their body orientation with respect to the vertical (Peterka, 2002). Clearly, relative weighting of sensory inputs changes depending on the environmental conditions and the accuracy of sensory inputs. Peterka followed up these findings by testing subjects using an apparatus to manipulate sway and proprioceptive information in participants. The protocol supported the previous research that sensory weighting is dependent on environment conditions, such that the corrective ankle torque required to maintain balance is generated in proportion to the combination of sensory cues weighted based on accuracy (Peterka & Loughlin, 2004). Aside from their contributions to quiet stance, visual, vestibular and proprioceptive information are also integrated in the central nervous system to accurately produce goal-directed movements during locomotion and for spatial updating in the environment (Horak & Macpherson, 1996; Frissen et al., 2011).

Across the lifespan, sensory manipulations have been used to determine that sensory reweighting is less effective in older adults (Deshpande & Patla, 2007). The opposite effect has been shown in high-level athletes, such that sport-specific training has been shown to improve the ability of an individual to accurately weight sensory inputs in order to produce the appropriate motor output (Bredin et al., 2005). However, current research is limited regarding individuals with extensive dance training and how they integrate the available sensory information during motor tasks. Thus, the general purpose of this research is to determine how vestibular perturbations affect tasks of spatial navigation, and how competitive dance training influences an individual's sensory weighting abilities compared to non-dancers.

1.1 Sensory Integration

According to previous research, there is a hierarchy in sensory input during motor tasks, and visual input is typically the dominant sensory system (Lee & Lishman, 1975; Woollacott et al., 1986). Lee and Lishman (1975) supported this finding when they conducted a well-known study titled the *Moving Room Experiment* that justly demonstrated the dominance of the visual system during postural control. Researchers placed subjects in a room with three walls and a ceiling that were detached from the ground. During the experiment, the walls oscillated synchronously in the anterior-posterior direction while the floor remained motionless, and researchers studied the sway in response to the perceived motion of the room. For all participants, their natural response was to sway in the direction of the movement of the walls, maintaining their balance as if the floor was actually moving in coordination with the rest of the room. Younger adults used an ankle strategy in order to maintain postural control during the perceived movement of the room. Older adults used a compensatory step, children fell on the ground, and even pigeons bobbed their heads back and forth in response to the movement of the walls. Thus, all participants were reacting as though the entire room, including the floor, was oscillating back and forth, when in reality their bodies were not experiencing any sort of physical movement. This experiment became a well-known study because it significantly contributed to the scientific body of knowledge; it used a visual perturbation to distinctly show that visual sensory input is the dominant sensory system during sensory integration for postural control (Lee & Lishman, 1975).

Subsequent studies have supported that vision is the dominant sensory system for balance and postural control in young adults. One experiment in particular used a similar protocol to Lee & Lishman (1975), but tested postural control during both a slight voluntary forward and backward lean in an attempt to increase the proprioceptive input during static stance to try and outweigh the perturbed visual information. Isableu and colleagues (2011) used a force plate to measure COP displacement during upright stance with a voluntary forward and backward lean and a revolving visual scene. The visual reference in front of each participant contained a stationary visual scene that served as the fixation point, with a peripheral scene that rotated medial-laterally up to 10 degrees.

Results showed that the motion of the outer visual frame affected the postural control of the unstable participants during both the forward and backward lean of the participants, such that they were using the visual frame to stabilize and orient themselves. According to the authors, the high dependence on visual information was emphasized by the effect of the movement of the outer visual scene, even with the availability of stationary central visual cues (Isableu et al., 2011). Evidently, there is ample evidence that in young adults, visual input is the dominant sensory system during tasks of balance and postural control.

The previously discussed study by Peterka demonstrated evidence that the postural system makes limited use of vestibular information when inputs from multiple sensory systems are redundant (Peterka, 2002). Vestibular information is thought to have lower weight than other sensory systems during postural control because the information has been shown to be less precise than visual or proprioceptive information during conditions without sensory manipulation (van der Kooij et al., 2001). Subsequent research has determined that normal vision overrides perturbed vestibular information for the optimization of performance during goal directed locomotion, suggesting down-regulation of vestibular gain (Deshpande & Patla, 2007). However, in the absence of vision, would the lack of visual cues cause an increase in the gain of the vestibular system? It is predicted that since the vestibular system provides information on the body's orientation with respect to the vertical, there may be an increased reliance or weighting of vestibular information during conditions in which visual and somatosensory information are not reliable (Peterka & Loughlin, 2004).

1.2 The Vestibular System

The vestibular system is responsible for providing the central nervous system with detailed information regarding the position and movement of the head in space. The vestibular system consists of two crucial components in the internal ear: semi-circular canals and otoliths. Semi-circular canals contain crista-receptors that provide information on the angular acceleration of the head, while otoliths provide information on linear acceleration of the head including gravity. Acceleration of the head causes movement of the endolymph fluid in the internal ear that deflects hair cells in the sensory organs. This deflection changes the cells membrane potential, and an electrical signal is sent via the vestibular nerve to the vestibular nuclei. From here, information is integrated and distributed to other brain structures for multiple purposes.

During tasks of dynamic stability, we also see an effect of GVS on motor response. This is because locomotion in itself is a mechanical perturbation, and requires the involvement of higher structures of the central nervous system to maintain stability. Sensory feedback is very important for not only sustaining balance, but also in maintaining a normal locomotor rhythm. Individuals use sensory information to modify locomotion based on the specific environment they are navigating through (Kandel et al., 2012). When navigating through the environment, visual, vestibular and proprioceptive information are used to determine the magnitude of distance travelled (Campos et al., 2012). Information from these sensory systems regarding the current state of the body within its environment is sent to the central nervous system, where it is integrated and produces the appropriate stepping behaviour for the individual in their current space. During locomotion in the absence of vision, vestibular information is used to estimate distance travelled, contributing to non-visual distance perception (Campos et al., 2012). In a study conducted by Frissen and colleagues (2011), vestibular and proprioceptive inputs were manipulated independently during a treadmill-walking task. When conflicting information was provided to the participants, spatial updating was determined using both systems, but a higher weight was attributed to the provided vestibular cues, demonstrating the contributions of the vestibular system to spatial navigation (Frissen et al., 2011). In addition to these vestibular effects on locomotion, the vestibular nuclei also distribute information from the otoliths and semicircular canals to many areas of the central nervous system, such as the oculomotor nuclei, the spinal cord, the cerebellum and the thalamocortical pathway (Fitzpatrick & Day, 2004). Thus, vestibular information is not only important with respect to the position and movement of the head; it is also involved in postural reflexes, gaze reflexes and central motor information (Kandel et al., 2012). The cerebellum is thought to integrate vestibular information of the position and movement of the head with proprioceptive input from the legs in order to regulate balance during locomotion. In addition, the system is responsible for the vestibulo-ocular reflex, which maintains eye position during movements of the head in order to project a stable image onto the retina. And finally, the vestibular system communicates with the somatosensory cortex, where the information is used for the perception and orientation of movement in the environment (Kandel et al., 2012). Clearly, the vestibular system is accountable for the position and movement of the head in space, but also contributes to a variety of aspects of locomotion and whole-body movements.

1.3 Galvanic Vestibular Stimulation

A variety of studies have been conducted in order to study and better understand this particular sensory system, but one method in particular has generated a great amount of knowledge on the subject. Previous research has determined that when visual input is available, body responses to vestibular perturbations decrease (Bent et al., 2002; Britton et al., 1993; Welgampola & Colebatch, 2001). Thus, in order to properly examine how perturbing the vestibular system alters responses of the body, the majority of studies analyzing contributions of the vestibular system have removed or altered visual input. Galvanic vestibular stimulation (GVS) is a method used to perturb the vestibular system, during which a small current is sent across the mastoid processes, evoking sensations of movement (Fitzpatrick & Day, 2004). The current that passes between electrodes creates a perturbation of the vestibular system, causing subjects to elicit a postural response in the absence of vision. Galvanic vestibular stimulation has been used for close to two centuries, dating back to at least a dissertation by Johann Purkyne in 1819 stating that the galvanic current is capable of upsetting the balance and equilibrium of the body (Purkyne, 1819). This tool is frequently used throughout research to better understand the vestibular system due to its ability to isolate vestibular inputs from other sensory inputs without disturbing balance, and evoke strong balance responses in participants (Britton et al., 1993; Fitzpatrick et al., 1994). GVS is a safe methodology used for many years with low risk due to the use of currents of small amplitudes. The electrical current does not have any adverse effects on the participant, aside from a very low risk of nausea or dizziness. A particular study examining the safety of repeated sessions of GVS in stroke patients determined that GVS is tolerable at 1 mA when applied for 30 minutes consistently (Wilkinson et al., 2009). This proves that the instrument is safe for a young adult population, such as the sample in the current study.

Typically, a constant current of 1-2 mA in amplitude is applied, but the stimulation can also be designed as a proportion of the subject's threshold to the stimulus. Current amplitudes are small because even a stimulation of 1mA is enough to evoke a noticeable postural response in individuals. This small current is one of the main reasons that galvanic vestibular stimulation is considered a safe procedure. Based on a review by Fitzpatrick and Day, with only 1mA of GVS, a single afferent fiber would signal angular acceleration of 2 deg/s^2 in the semicircular canals and linear acceleration of 1.18 m/s^2 in the otoliths. Thus, only small and safe amplitudes of stimulation are necessary when using GVS to study the vestibular system. However, individuals have different thresholds when responding to galvanic vestibular stimulation, such that the delivery of the same amplitude of stimulation will not produce the exact same magnitude of response across all individuals. It is important to incorporate threshold concepts when investigating effects of GVS as opposed to using fixed stimulation levels (Bent et al., 2000). Specific amplitude thresholds are determined for each individual participant, and then GVS is administered in magnitudes of this original threshold in order to normalize the effect of stimulation and the body's response to GVS.

1.3.1 GVS and Head Position

As previously stated, GVS is a tool used to better understand the structure and function of the vestibular system. In a review by Fitzpatrick and Day (2004), the authors analyze a variety of studies on a large number of aspects of galvanic vestibular stimulation. Most importantly, they established a model regarding vestibular signals arising from GVS. They predicted that when the head is upright, the semicircular canal signal indicates lateral head rotation while the otoliths indicate lateral tilt or acceleration. While the head is pitched forward, they predicted the semicircular canal signal would indicate body spin on the vertical axis, but the otolith signal would still signify lateral body motion. In other words, the semicircular canals can distinguish between movements with the head upright and pitched forward, where as the functional significance of the otolith signal is predicted to remain the same in both head positions (Fitzpatrick & Day, 2004).

Cathers and colleagues (2005) took this model and applied it to their study analyzing head position during GVS stimulation. GVS was applied during two different conditions, both with a 90-degree rotation of the head accomplished with both head and trunk rotation. In the first condition, head-up, the head was elevated by 18 degrees. The second condition, head-down, depressed the head by 72 degrees. GVS was administered in both conditions, and researchers measured anterior-posterior sway and electromyographic activity of the tibialis anterior and the soleus. With respect to sway, the amplitude was greater during the head-up condition, whereas there was no significant change in sway during the head-down condition. In addition, the EMG results showed different latencies in muscle activation across the two conditions (Cathers et al., 2005). These results were interpreted to support the model by Fitzpatrick and Day predicting that maximal canal responses would be evoked in the head-up condition and would disappear in the head-down condition (Fitzpatrick & Day, 2004). This difference between the conditions is due to the fact that semicircular canals are unaffected by head position and were activated in both conditions. The three semi-circular canals are oriented such that they each respond maximally to a specific movement of the head, ensuring that they are activated during all head positions. Otoliths, on the other hand, are sensitive to the position of the head such that they are stimulated more during a forward pitch of the head, similar to the head-down condition. Since the otoliths were less activated during the head-up condition, there was more sway in the anterior-posterior direction. This study was successful in determining that head position affects an individual’s postural response to GVS stimulation. The EMG results also helped determine that otolith organs are responsible for eliciting short-latency muscle activation in response to GVS, whereas medium-latency muscle activation and large sway is driven by the semicircular canals (Cathers et al., 2005). Clearly, galvanic vestibular stimulation has been used to contribute to the knowledge of the structure and function of the vestibular system, showing that the semi-circular canals and otoliths do not function as one unit; they are separate sensory systems that operate through different pathways.

1.3.2 GVS Effects on Balance Control: Static and Dynamic

Since the semi-circular canals and otoliths have been shown to function independently through the use of galvanic vestibular stimulation, there has been a constant debate throughout academic literature as to which structure is stimulated during administration of GVS. Reynolds & Osler (2012) published a review analyzing a large number of studies using GVS in order to compare results and determine how the brain interprets the stimulation from the electrodes on the mastoid processes. The paper set out to disprove the theory of Cohen and colleagues that GVS stimulates both the otolith and semi-circular afferents, but only the otolith-related responses are induced; there is no sensation of rotation that would support stimulation of the semi-circular canals (Cohen et. al, 2012). The review then sources a variety of studies and their findings proving the exact opposite. A study by Fitzpatrick and colleagues in 2002 investigated the effect of GVS on subjects lying in a supine position. GVS was applied to individuals lying on a platform that only rotated around the vertical axis, removing any linear movement. The platform movements consisted of right, left or none, and the GVS stimulation occurred as anode left, right or none. During only movement conditions, subjects could accurately determine the direction of rotation. During only GVS conditions, subjects reported a rotation in the direction of the cathode when there was no physical rotation occurring. When the movement and GVS were applied congruently, subjects reported greater spin than when they were applied incongruently. Thus, the researchers concluded that GVS produces a signal of rotation affiliated with the semi-circular canals (Fitzpatrick et al., 2002). Reynolds and Osler used many additional sources in their review to support their theory that “GVS is primarily interpreted by the brain as head roll, consistent with activation of semicircular canal afferents” (Reynolds & Osler, 2012).

Regardless of which vestibular component is responsible for the reaction to GVS, it has also been of great interest to researchers how this perturbation affects the postural response of subjects. Previous research has shown that subjects tend to lean towards the anode during galvanic vestibular stimulation in the absence of vision, such that the head tilts on the trunk, the trunk tilts on the pelvis, and the pelvis tilts with respect to the ground (Fitzpatrick & Day, 2004). At the time of this original discovery, the mechanics behind this perception had yet to be fully understood. A study by Wardman and colleagues tested three different hypotheses as to why GVS causes subjects to lean without conscious awareness. The first hypothesis was that GVS might alter our perception of the vertical that we use to align the body. However, their study showed that participants still had a consistent perception of the vertical under GVS stimulation. The second suggestion was that subjects interpreted the GVS signal as a tilt in the support surface under their feet. But after comparing body angle responses of GVS to responses of an actual tilt in the support surface, it was determined the body angles were different. Finally, the last hypothesis was that the GVS signal produces the illusion of movement in subjects. Researchers compared perceptions of movement during freestanding and restricted conditions, but the perceptions did not coincide, disproving their last hypothesis. After determining that all three hypotheses were incorrect, they concluded that the lean observed in subjects towards the anode is due to the body's automatic response to maintain head position in space. A perceived change in head position is detected and the trunk and legs respond accordingly to counteract the destabilizing moment created (Wardman et al., 2003).

Specific studies have shown that using GVS to perturb the vestibular system causes path deviations in individuals in the absence of vision (Fitzpatrick, 1999; Bent, 2000; Jahn, 2000; Deshpande & Patla, 2007). In a study by Fitzpatrick, Wardman & Taylor in 1999, subjects were instructed to walk towards a previously seen target without vision while GVS was applied. This study aimed at analyzing the effects of GVS on path trajectory during locomotion without input from the visual system. A second condition was studied during which subjects were blindfolded and guided from one point to another while seated in a wheel chair. The objective of the second portion of the study was to determine the perception of path trajectory during GVS when there was no visual input. The results of the study showed that during locomotion, the path trajectory of the participants deviated towards the anode, in the direction of the current. In the wheelchair condition, participants perceived that they had travelled in the direction of the cathode, in the direction opposite of the current, as opposed to straight ahead. These results showed that not only does GVS during locomotion cause subjects to alter their path trajectory, but it also changes their perception of their path trajectory, because the GVS stimulation has altered their perception of position and acceleration of the head in space (Fitzpatrick et al., 1999). This supports the previous research on GVS during static balance that stimulating the vestibular system with an electrical current causes a perturbation of the vestibular system; stimulation during static stance causes a lean towards the anode, while stimulation during locomotion causes a path deviation towards the anode.

Once it was determined that GVS caused a deviation in path trajectory towards the direction of the current, many other aspects of the vestibular system's contributions to locomotion became of great interest. One particular study by Bent and colleagues used GVS at different magnitudes to study the relationship between the magnitude of the electrical current and the degree of path deviation during locomotion. Researchers determined the subject-specific anodal threshold levels for each participant, then applied stimulation at one, two and three times the threshold without vision. Results showed that the path trajectories of all participants deviated in the direction of the anode, similar to the findings of Fitzpatrick, Wardman and Taylor (1999). In addition, the degree of deviation from the intended path trajectory was shown to be proportional to the magnitude of stimulation; as the magnitude of the electrical current increased, the degree of path deviation also increased. This study has clearly shown that GVS is not only successful in perturbing the vestibular system during locomotion, but it has a proportional relationship with the resulting path deviation. It demonstrated that the vestibular system is able to identify the magnitude of stimulation and generate an appropriate response to this magnitude (Bent et al., 2000). GVS has shown that the system is capable of differentiating between different magnitudes of stimulation, and is capable of evoking the appropriate response.

Bent and colleagues built on this previous research by analyzing the information provided by the vestibular system contributing to the execution of a single forward voluntary step. In this study, the anode was placed either on the side of the stance limb or the swing limb and both ground reaction forces and body position were measured. Prior to the onset of a forward step, slight shifts were seen in both COP and COM at the onset of GVS stimulation. However, during the initiation of the forward step, no further deviations in either measurement were seen. This supports previous research that step initiation is unaffected by vestibular influences, and is an activity pre-programmed by the central nervous system (Lyon & Day, 1997). Once the body entered the dynamic phase of locomotion, particularly beginning at first heel contact, GVS-related COM displacements were seen for all subsequent events. However, COP displacements were only existent after second heel contact, prior to step termination. These results show that, without visual input, vestibular information is used differently across the phases of a forward voluntary step, such that it has less contribution during initiation of a step compared to the more dynamic phases of gait, including termination (Bent et al., 2002). Although the authors were unsure as to the mechanisms behind these differences in displacement, it is clear that the control of the vestibular system is dependent on the phase of locomotion.

Soon after, Bent & colleagues continued their research by investigating the interaction of the vestibular and visual system during the transition from quiet standing to a single forward voluntary step. Their research demonstrated that the importance of visual and vestibular sensory input during human gait is also dependent on the phase of locomotion. These sensory systems are weighted and integrated differently across the phases of a single forward voluntary step (Bent et. al., 2002). A subsequent experiment was then conducted that separated the single forward voluntary step into three phases: anticipatory postural adjustment, toe-off of the first swing limb and heel contact of the first swing limb. It was determined that the magnitude of the response of lower body foot placement was different depending on the phase of the step cycle that the GVS was delivered. These results support that even foot placement is dependent on the point during gait at which the stimulation occurs (Bent et al., 2004). Overall, Bent and colleagues have successfully used GVS to show that the sensory input of both the vestibular and visual systems are dependent on the phase of the gait cycle. Sensory weighting is altered based on the step phase that the subject is performing, as well as which phase the perturbation is delivered.

1.3.3 GVS as a Tool to Assess Sensory Integration

Many studies involving galvanic vestibular stimulation, are conducted without visual input, because there have been many instances where it has been stated that GVS is only effective in altering path trajectory during locomotion if visual information is not present. Visual input from the environment is said to outweigh any vestibular perturbation that alters the perception of the position and acceleration of the head in space. Based on the prediction that the visual and vestibular systems may work together to maintain stability during the onset of human gait (Bent et al., 2002), a study was conducted by Kennedy and colleagues that focused on the contributions of both the visual and vestibular system during gait. The objective of the study was to perturb both the visual and vestibular system separately and together to study the effects that these conditions would have on the path trajectory of subjects during locomotion. Vision was perturbed using prisms that altered the visual scenery by 20° to the right or left, and the vestibular system was perturbed in both directions using galvanic vestibular stimulation. When the prisms or GVS were presented alone, the subjects deviated accordingly; subjects veered towards the direction of the prism during the visual conditions and towards the anode during the GVS conditions. However, when both the prisms and GVS were presented together, subject's path trajectory deviated toward the direction of the prism, regardless of which direction the GVS current was travelling. This is evidence that the sensory system is capable of reweighting information based on the most reliable input that is available. In this case, the body determined that the visual input was more relevant than the vestibular input, which caused an increase in visual gain that produced a response correlated with the prism direction rather than the anode position. In addition, when the visual-vestibular conditions were congruent in direction, the deviation in path trajectory was even greater than the condition with the visual perturbation only (Kennedy et al., 2003). Clearly, the visual and vestibular systems are working together and are both important in the control of locomotor trajectory, but vision is the dominant sensory system providing input during human gait.

A similar study was conducted a few years later in 2005, when Carlsen and colleagues repeated the same conditions as Kennedy and colleagues, only using visual targets to guide locomotion. Participants were exposed to varied combinations of prisms and galvanic vestibular stimulation in order to study the contributions of both the visual and vestibular systems during forward locomotion towards a visual target. Similar to Kennedy et al., the results showed that when the prism and anode placement were congruent, the deviation in path trajectory of the subjects was approximately equal to the summation of deviations of the visual and vestibular conditions presented alone. Thus, it is clear that there is an additive effect on human gait when both perturbations are combined. However, when the prism and anode placement were not congruent in their direction, the deviation was significantly smaller, almost zero. These results conflicted with those found by Kennedy et al., who found that the deviation shifted towards the effect of the prisms and the GVS had no effect on the resulting locomotion (Kennedy et al., 2003). Carlsen and colleagues discovered that during their trials, the visual and vestibular perturbations seemed to cancel each other out during locomotion, resulting in a path trajectory with very little deviation regardless of the perturbations occurring in both the visual and vestibular systems. Researchers stated that this cancellation of perturbation shows that the nervous system integrates the inputs from the vestibular and visual system equally, rather than the visual system having a higher gain. They argued that during target-directed locomotion, the information from the systems is continuously integrated at the same weight, because both are important in the perception of trajectory (Carlsen et al., 2005). Apparently, the simple addition of a visual target during locomotion reduced the participant's reliance on vision and equalized the weighting of sensory systems during the integration of inputs in the CNS.

Aside from the studies discussed above, the majority of studies using galvanic vestibular stimulation have observed the effects of GVS during locomotion without vision, since visual input has been shown to override vestibular input during locomotion (Kennedy et. al., 2003). Many of the locomotor studies remove vision by studying gait simply with the eyes closed or using a blindfold. But, in a study conducted by Deshpande & Patla in 2007, the researchers were more interested in the visual-vestibular interaction during GVS than the actual path trajectory. The objective of the study was to use GVS to determine how age-related visual deterioration influenced the visual-vestibular interaction during locomotion. Nine young adults and nine healthy older adults were studied under both normal and blurred conditions while walking towards a target with or without GVS. During normal vision conditions, younger adults were more successful in walking towards the target than older adults, whose locomotor pathways were more affected by GVS. These results indicate that younger adults are able to successfully reduce their vestibular gain and rely more heavily on visual input to determine their body orientation in space and path trajectory during locomotion. Younger adults can control their sensory systems more efficiently than older adults, and are able to increase the gain of their visual input to outweigh the perturbation of the vestibular system. During the blurred vision condition, the study did not find any further increase in path deviation for both young and older adults. Since the subject’s vision was only blurred and visual input was not completely removed, it is possible that the amount of vision provided was still sufficient enough to allow subjects to maintain path trajectory and outweigh the perturbation of the vestibular system. However, it would have been expected that reduced vision should have elicited a re-weighting of the sensory systems, increasing the gain of the vestibular system and eliciting a greater path deviation (Deshpande & Patla, 2007). One explanation is that locomotion in a straight line, on a flat surface, without obstacles is not challenging enough to induce sensory reweighting towards the vestibular system. A more challenging task may elicit a greater reliance on the input from the vestibular system causing the GVS to create a greater path deviation during locomotion in both young and older adults.

With this thought in mind, McFadyen and colleagues (2007) generated a study that analyzed the influences of both the visual and vestibular systems during obstacle avoidance. Subjects were instructed to complete trials of level walking or obstacle avoidance, during a variety of conditions with vision present or occluded and with or without galvanic vestibular stimulation. During the trials of obstacle avoidance without vision, gait speed decreased and clearance of the leading foot increased compared to the results of the level walking trials. This is expected since the reduction in visual input has been shown to produce the exact same results during obstacle avoidance in previous studies (Mohagheghi et al., 2004). When GVS was applied during level walking, deviations in body orientation and foot trajectory were observed, similar to the results of the previous research (Bent et al., 2004). However, during obstacle avoidance, these deviations were no different than those present during level walking. This suggests that vestibular information is not an important sensory input during the completion of obstacle avoidance. These results clearly show that there is a heavy reliance on vision during obstacle avoidance, but no contribution of the vestibular system. The authors contrasted their findings with those of Carlsen and colleagues in 2005, which found that the visual and vestibular systems contributed equally to producing locomotion when a visual target was available. However, the present study did not use a visual target, and the authors stated that although stepping over an obstacle is goal-oriented, it is transient in nature (McFadyen et al., 2007). Thus, although locomotion requires vestibular input to produce movement, obstacle avoidance is only reliant on the visual system for sensory input.

1.4 Spatial Navigation

However, obstacle avoidance is not the only task that is more difficult than straight-line walking without vision. A specific task that has increased difficulty compared to basic locomotion is the triangle completion task, created to analyze an individual's spatial navigation proficiency. Spatial navigation is the ability to constantly update one's position in space while moving through the environment (Smith et al., 2013). This process is composed of cues from the visual, vestibular and somatosensory system that provide feedback of the body's movement within space. The latter two contribute to a process termed path integration, which is defined as using movement information or idiothetic cues from the vestibular and proprioceptive systems as feedback to update our position in the environment (Mittelstaedt, 2001; Smith et al., 2013). According to Loomis and colleagues (1993), an individual's spatial navigation can be classified according to three types of information. Position-based navigation relies on visual cues or landmarks to give the individual information on their position and orientation in the environment. Velocity-based navigation relies on optical flow, acoustic flow, and proprioception to gain information on characteristics of the individual's self-motion such as speed and direction of travel. And finally, acceleration-based navigation relies on vestibular information about linear acceleration and rotational velocity and acceleration. Humans use all three components of navigation—position, velocity, and acceleration— during spatial navigation within an environment (Loomis et al., 1993). This highlights how all three sensory systems are integrated in order for an individual to successfully navigate throughout space. As with any form of integration, removing visual information from an individual will cause the weight of the vestibular and proprioceptive information to be increased, and force the participant to rely solely on path integration to gain information on self-motion within the environment.

1.5 Triangle Completion Task

The triangle completion task is an analysis of spatial navigation during which participants navigate along two sides of a triangle, then must navigate their way back to the origin without guidance or vision (Smith et al., 2010). The individual will either be guided by the researcher in the absence of vision (Loomis et al., 1993; Smith et al., 2013) or actively navigate with vision along the first two legs of a triangular pathway. Participants typically navigate in a straight line from the starting point, then are rotated 90 degrees to the right or left before navigating along the second leg of the triangle (Smith et al., 2013). The researcher can manipulate the characteristics of the triangle, such as angles and side lengths, in order to analyze different responses. Participants are then instructed via physical cues or verbal instructions to navigate their way to the origin at which they started the task, without the use of visual cues or guidance from the researcher. Individuals are expected to use idiothetic cues such as vestibular and proprioceptive input (path integration) to return to their starting position. By calculating the error between the participant’s estimated end-point and the actual origin or start position, the individual’s interpretation of both the distance and angular relationship can be analyzed to determine the participant’s path integration abilities (Smith, 2013). When conducting studies that utilize the triangle completion task, it is important to ensure that participants do not receive any feedback on their performance of the task. These studies tend to be more interested in analyzing the performance of the participant across different conditions, as opposed to the learning effects of providing feedback during tasks of spatial navigation in the absence of vision. However, the lack of feedback may also act as a hindrance on performance, as individuals may perceive this as feedback in itself. Participants may see this as a lack of correction; they believe they are performing the task properly every time and that is why they are not receiving feedback. This would cause participants to continue to perform in the same manner for all succeeding trials. Alternatively, participants may interpret this lack of feedback as failure, and perceive the subsequent trials as an opportunity to correct their performance. This would cause participants to alter their behaviour across all of the following trials. However, even though this lack of feedback could manipulate a participant’s behaviour, providing performance feedback would create a learning effect across trials that would influence the effect of the conditions on the performance of the task. Thus, in the majority of studies utilizing the triangle completion task to analyze an individual’s ability to navigate throughout space in the absence of vision, feedback on performance is not provided to the participants.

As previously stated, the triangle completion task uses both distance and angular error to determine the spatial navigational abilities of an individual. Distance error is typically defined as the difference between the position at which the participant started, and the end position they predicted to be their origin. Angular error is the difference between the heading that was required to reach the correct origin, and the actual direction of the participant’s path trajectory. These components were further analyzed in a study by Worsley and colleagues (2001), which used the triangle completion task to examine the performance of individuals that had experienced either right or left-hemisphere temporal lobectomies. Distance and angular errors were measured to determine if the mechanisms were processed by the same systems. The study found no difference between groups in terms of distance error, however the right-hemisphere patients had a great impairment in their angular error. These results determine that distance and direction are processed by different mechanisms during spatial navigation. In addition, the results suggest that the right temporal lobe plays a role in idiothetic spatial memory (Worsley et al., 2001). Thus, this research supported that both distance and angular error are components of path integration that are processed separately (Berthoz et al., 1999; Smith et al., 2010; Worsley et al., 2001), and both should be analyzed when conducting studies with spatial navigation tasks.

Another study, by Loomis and colleagues (1993), used the triangle completion task to examine spatial navigation of adventitiously blind, congenitally blind and blindfolded sighted individuals. Results showed that all participants were sensitive to the manipulations of angle and distance characteristics of the triangle pathway, such that there was an overestimation of short distances and an underestimation of large distances. In addition, Loomis and colleagues stated that the results showed that triangle completion is a very difficult task. Subjects over all three groups showed significant error in both distance and angular estimations, demonstrating that individuals had inadequate proprioceptive and vestibular cues to navigate successfully through the environment (Loomis et al., 1993). Thus, it would be a more challenging task than normal locomotion with respect to a population of young adults. Although untrained young adults have difficulty successfully performing the triangle completion task, would there be similar results for individuals that are sport-specifically trained to navigate throughout their environment?

1.6 Virtual Reality

Most of studies that use the triangle completion task to investigate accuracy of spatial navigation typically blindfold individuals and lead them across the first two legs of the triangle. However, if the visual environment could be more efficiently manipulated, participants could use vision to navigate the first component of the task on their own, and then visual cues could be effectively removed for the final leg of the triangle. A technological component such as virtual reality could be used in order to allow participants to navigate through the environment on their own rather than with the guidance of the researcher. In a study by Harris and Wolbers (2012), researchers examined the navigational abilities of younger and older adults in a virtual navigation task. The triangle completion task was combined with a virtual environment that the individuals were instructed to perform within. The virtual reality consisted of a widescreen monitor displaying one of the two environments, and participants navigated throughout the scenery using a joystick. The first scene was a “dot floor” environment; a dark grey floor with 5,000 white dots. These dots appeared in randomized locations for only 2 seconds at a time, ensuring the participant was given optic flow information, but no fixed reference points. The second environment included mountain scenery that did provide visual reference points for the participants. The triangle completion task was performed in both environments, during which participants were automatically moved along the first two legs of the pathway, then instructed to use the joystick to turn and face their starting position, then move towards it. Results for both age groups showed similar results to previous studies; an overshooting of small distance and an undershooting of large distances (Harris & Wolbers, 2012). Since the study of triangle completion using virtual reality found similar results to the physical completion of the triangle task, is it fair to assume that virtual reality can successfully be used to examine spatial navigation characteristics in individuals?

The study by Harris and Wolbers (2012) presents an interesting combination of virtual reality for tasks of spatial navigation. However, this approach is limited because the display does not allow the participants to physically interact with the virtual space. A study by Grant & Magee (1998) guided participants along a route in both a real environment that individuals physically navigated through, and a virtual environment that allowed them to effectively explore the space while walking in place. Results showed more accurate performance when the participants were physically navigating throughout the environment, and the researchers attributed these findings to the abundance of idiothetic information they were receiving from actively moving through the space (Grant & Magee, 1998). Previous research has determined that active navigation throughout an environment better contributes to spatial learning (Chrastil & Warren, 2012). Clearly, participants would benefit from actively navigating through a space because it would increase the amount of somatosensory and vestibular information contributing to spatial navigation.

In 2002, a paper by Tarr & Warren highlighted the use of virtual reality in behavioural neuroscience, from desktop virtual reality to head-mounted systems. The authors introduced the VENLab system, stating that it was the "largest walkable immersive virtual reality system in existence for scientific research" (Tarr & Warren, 2002). The system combines a head tracker with high-end graphics and a head-mounted display to create an immersive and realistic virtual environment. The success of this technology is based on the wide field-of-view, the speed at which the display is consistently updated, and the effect of the participant's own movements creating changes in the virtual environment. VENLab has been used to analyze aspects and characteristics of locomotor behaviour, and provides the means to effortlessly manipulate visual information for self-motion (Tarr & Warren, 2002). Although this technology has created an avenue for immersive virtual environments to study aspects of behavioural neuroscience, the system is still fairly expensive and not affordable to the general public. According to Parkin (2014), a new virtual reality technology has recently emerged aimed at being used as a visually immersive interface for entertainment and communication. Palmer Luckey designed the oculus rift using cheap smartphone components to create a rich virtual environment that follows the movement of your head in real time to create a realistic and believable atmosphere. The device creates a 3-D image by turning a scene into two warped side-by-side views, with a resolution higher than 1,920 by 1,080 pixels per eye. Previous technology for virtual reality in the mid-1990's received many complaints of nausea from users. However, the latest version of oculus rift claims to have almost completely eliminated any effects of nausea in users. Although virtual reality technology has been explored before, this is the first high-quality device that has been priced accordingly for the consumer market; it's affordable to the general public (Parkin, 2014). This technology may have been created for use during video games to create a more realistic and immersive environment, but could it also be used in scientific experimental studies in order to allow participants to navigate through a simulated environment?

1.7 Effects of Sport-Specific Training on Spatial Navigation

Research has supported that athletes have superior ability with regards to spatial navigation compared to the untrained population (Bredin et al., 2005; Ozel et al. 2002; Smith et al., 2010). A study conducted by Bredin and colleagues (2005), examined how athletes navigate through the environment without visual cues compared to untrained individuals. The purpose of the study was to determine if athletes were better able to calibrate idiothetic cues of self-motion to improve their accuracy of path integration. The participants were blindfolded and instructed to walk towards a previously seen goal at slow, normal and fast speeds. Participants were instructed to terminate gait at their estimated location of the goal, and their error in distance to the actual goal was measured. Results demonstrated that both groups were most accurate at the normal or preferred velocity. At slow speeds, both groups overestimated the distance of the goal. During the conditions of fast velocity, athletes were more accurate in determining the position of the goal, and thus demonstrated more accurate path integration. The authors suggested that this improvement in accuracy was due to the fact that athletic training typically involves movement at high speeds, and the participants in the athlete group have more experience with processing multi-sensory information at fast velocities (Bredin et al., 2005). However, this particular study is limited in many ways. First, the research does not include how the varied speeds were controlled; did the researchers ensure participants were walking at 50, 100 and 150% of their normal walking velocity? In addition, the methods of data collection used in this study did not use precise instruments, and could largely have been affected by human error. This was also a very simple, straight-line, forward-walking task, and is not definitive representation of all spatial navigational tasks. And finally, the sample athlete group consisted only of athletes involved in rugby, handball, or volleyball. Therefore, the findings of this research cannot be generalized to all athletes. However, despite the limitations of this study, it does support the possibility that the sport-specific training that athletes endure may improve the computation of idiothetic cues of self-motion (Bredin et al., 2005).

Clearly, athletes have demonstrated that sport-specific training may improve the accuracy of an individual's path integration. Interestingly, it has been argued that an individual's spatial abilities are scale-invariant, such that behaviour of an individual at one spatial scale may not interchange when exposed to a different spatial scale (Montello, 1993). With this suggestion in mind, Smith and colleagues (2010) conducted a study with the purpose of determining if the spatial scale of athletic training affected an athlete's accuracy of path integration. The authors entertained the possibility that sport-specific training may only improve path integration when it is a similar scale to that of the athletic training. The study examined two groups of trained athletes: rugby players and martial artists. Rugby players are trained at a large spatial scale, while martial artists are trained at a small spatial scale. All participants performed the triangle completion task on an outdoor sports field, or large spatial scale. There was no difference between groups on their distance error, but rugby players were significantly more accurate at determining the correct angular component during the triangle completion task, thus reducing their overall landing error. The author attributed this difference to the spatial demands of rugby, stating that the athletes may have greater experience in computing idiothetic cues during locomotion. In addition, the researchers suggested that rugby players experience more situations requiring that they make inferences about spatial location without visual input regarding the multiple components of play (Smith et al., 2010). Not only does this research support that distance and angular components are processed by separate mechanisms, but it also supports that the spatial scale of training affects the spatial navigation ability of an individual.

Research has clearly supported that the spatial-scale of training determines an individual’s accuracy of path integration, such that athletes trained in large spatial scales perform tasks of path integration more accurately in large environments and vice versa (Smith et al., 2010). Dancers, however, are specifically trained on both a small and large spatial scale. These specific athletes are trained to use idiothetic cues in their personal space with respect to the proprioception of their limbs such as martial artists, but also must continually make inferences of their location within the environment without the use of visual cues such as rugby players. They must be aware of the performance of their bodies in space, but also of the other individual and the environment surrounding them on a larger scale. Thus, dancers are trained on both small and large spatial scales, and would be expected to demonstrate improved accuracy in spatial navigation.

As much as this hypothesis seems plausible, there is a very limited amount of research studying the accuracy of spatial navigation or path integration in professional dancers. Dance training has been shown in previous research to have beneficial effects on postural stability (Kattenstroth et al., 2013; Lin et al., 2014; Panchuk & Vickers, 2011; Simmons, 2005; Thullier & Moufti, 2004), sensorimotor performance (Golomer et al., 1999; Golomer & Dupui, 2000; Kattenstroth et al., 2013; Simmons, 2005), cognition (Kattenstroth et al., 2013; Kimura & Hozumi, 2012), long-term memory recall (Blasing et al., 2009; Blasing, 2010; Stevens et al., 2010), and subjective well-being (Kattenstroth et al., 2013). However, even with the existing research supporting that dance training improves many aspects of motor and cognitive behaviour, very few studies have studied any aspects of spatial navigation in the professional dancer population. It has been suggested in previous research that spatial awareness, body representation and perception of time are the main cognitive abilities acquired through dance training (Jola, 2010). Motor skills such as dance movements involve the integration of rhythm, spatial pattern, synchronization to external stimuli and coordination of the entire body (Brown et al., 2006). So with this complex integration of multiple movement and spatial components, do dancers develop a more advanced technique for processing information?

One study in particular by Cortese and Rossi-Arnaud (2010) investigated professional dancers and how motor and spatial tasks interfered with their recall of movement and spatial location. The purpose of the study was to use multiple experiments to determine if dancers were better able to recall movement and location combinations from their working memory even when presented with a task of interference. Previous research in the area has shown that a variety of motor tasks cause interference in the function of spatial working memory (Logie & Marchetti, 1991; Quinn & Ralston, 1986). Thus, it was expected that both tasks of motor and spatial interference would reduce the ability of participant's to recall movements and spatial locations from the working memory. In each experiment, a group of professional ballet dancers were instructed to learn a set of ballet movements orally in a specific sequence. The control group would always perform an articulatory suppression task as the movement sequence was presented verbally to them, where as the experimental performed either motor or spatial tasks along with the verbal task as the movement sequence was presented verbally. All participants were then instructed to recall the sequence of movements by physically repeating each movement separately, but in the correct order. When the interference was a spatial task, there was no decrease in performance in the serial recall of dance movements, most likely because movement and spatial location are processed through separate systems. A second similar experiment was conducted during which the ballet movements were combined with spatial locations presented visually to the participant. As expected, a motor interference task interrupted the recall of the ballet movements, due to the fact that the task and movements were using the same system. However, the presentation of a spatial interference task did not decrease performance in the recall of spatial location. This result was not concurrent with previous research in untrained populations, and caused the authors to hypothesize that dancers encode spatial information differently than non-dancers. Following this, a third experiment was conducted during which dancers were required to only recall a spatial location without the association of ballet movement, during a task of spatial interference. Results of this experiment showed a decrease in performance in dancers when recalling spatial location. Thus, the authors interpreted their research to insinuate that dancers have a distinctly separate system for encoding combined movement and spatial information (Cortese & Rossi-Arnaud, 2010). This research clearly demonstrates that dancers process spatial information differently than the untrained population, such that their specific training has created a subsystem specifically for processing spatial locations combined with movement.

Since dancers have developed different means for processing spatial information, would this transfer to improved performance in tasks of spatial navigation or path integration? Dancers have been shown to organize dance movements into spatial patterns that encompass a trajectory map of the body within the environment (Brown et al., 2006; Longstaff, 2000). Blasing and Schack (2012) further analyzed this organization of movement within the surrounding environment by studying the representations of dance movement in long-term memory, specifically with regards to spatial parameters. Three groups of dancers—expert, amateur and novice—were to match the components of two well-known ballet movements to their associated spatial parameters. Results showed that expert dancers were more adequate at identifying the spatial parameter associated with each phase of the ballet movement, demonstrating that dance training shapes the cognitive representation of spatial information of movement concepts in expert dancers. This research supports the findings of Cortese & Rossi-Arnaud (2010) that expert dancers have special embodied representations of movement including information on spatial parameters in an egocentric frame of reference (Blasing & Schack, 2012). Thus, it is expected that dancers would excel in a task of spatial navigation such as the triangle completion task.

1.8 Effects of Ballet Training on Sensory Dominance

Returning now to sensory integration during motor control, a study conducted by Perry and colleagues determined that aspects of locomotion such as gait termination are under feedback control (Perry et al., 2001). Thus, sensory systems contribute to locomotion and provide constant feedback of the body in the environment to adapt locomotor characteristics accordingly. Studies of untrained young adults have shown that vision is the dominant sensory system during dynamic balance and postural control (Lee & Lishman, 1975). However, researchers have examined the effect of athletic training on dynamic motor control and have found that sport-specific training may improve multi-sensory integration in the absence of vision in athletes (Bredin et al., 2005). More specifically, dance training in particular has demonstrated a reduction in reliance on vision for balance control in individuals. In a study by Mouchnino and colleagues (1992) dancers and naive subjects were instructed to perform unilateral leg movements in response to a light in order to analyze different aspects of the posturokinetic sequence in both populations. The purpose was to determine how their sport-specific training affected the coordination strategies used by dancers during leg movement. As expected, the researchers determined that dancers shifted their center of gravity to the supporting foot in a shorter amount of time and minimized this displacement towards the supporting side. But more importantly, it was determined that while maintaining equilibrium during leg movement, dancers were less vision-dependent. The authors stated that this was because dancers may have developed a new sensorimotor program without visual feedback (Mouchnino et al., 1992). Regardless of the reasoning, this study clearly showed that dancers are less dependent on vision than naive subjects in tasks of postural control and balance. Even so, plenty of research has supported that sensory feedback is a major component in maintaining balance, particularly during tasks of dynamic nature. Thus, if dancers are not using vision as the dominant sensory system, what sensory input is the central nervous system increasing reliance on in order for the population to maintain balance?

Research has shown that dancers tend to shift their sensorimotor reliance from vision to somatosensory input, particularly proprioception, during dynamic balance tasks (Golomer et al., 1999; Golomer & Dupui, 2000; Simmons, 2005). During a performance, dancers use visual information for a variety of purposes that do not necessarily apply to untrained individuals. Dancers must navigate across the stage and around other dancers in their environment while performing complex movements. They are also expected to use their eyes for artistic expression in order to improve the performance quality of their movement. Not to mention there are typically blinding stage lights that prevent dancers from using many visual cues on stage while performing. Thus, researchers have explored the idea that dancers may not rely on visual input for postural control as much as an untrained individual. A study conducted by Golomer and colleagues (1999) studied both dynamic balance and the degree of dependence on vision for postural control in professional male ballet dancers. Dynamic balance of participants was analyzed by measuring the amplitude of sway in both the anterior-posterior and medial-lateral directions on a seesaw platform. Visual dependence was examined using the rod and frame test, in which participants must align a rod with their subjective interpretation of the vertical regardless of the orientation of the frame. Results showed that the professional dancers had significantly less sway in the anterior-posterior direction and were less reliant on vision for balance control. The researchers suggested that this is because training creates a more accurate position sense of lower limbs. This strengthening in the accuracy proprioceptive inputs has caused professional dancers to switch their dominant sensory system for motor control from vision to proprioception. In addition, dancers that were less visually dependent were the individuals that had less sway and were more stable. This shift in reliance to the somatosensory system in dancers is what allows their visual input to be used for other aspects of their performance rather than balance or postural control. Clearly, professional dance training has been shown to alter which sensory input has the largest contribution to the resulting motor outputs, such that dancers are more reliant on proprioceptive cues rather than vision for motor control (Golomer et al., 1999).

Subsequent studies have supported the findings of Golomer and colleagues that the somatosensory system is the dominant form of input for dancers with respect to motor control. Golomer and Dupui (2000) used a similar paradigm as Golomer and colleagues (1999), such that a seesaw platform was used to isolate sway in both the anterior-posterior and medial-lateral directions, under conditions with eyes opened and eyes closed. This particular methodology was used to examine the contribution of visual information to the regulation of postural control in professional dancers of variable age. The results showed that participants aged 14 and 23 showed improved balance control in the eyes closed conditions compared to the individuals aged 11 and 18. Researchers suggested that the results supported previous research that dance training reduces the reliance on vision for the maintenance of postural control, since dancers of older ages and increased training demonstrated a reduction in sway. However, dancers tend to have a delayed onset of puberty such that males tend to undergo growth acceleration between the ages of 14 and 18. The authors suggested that the 18 year old participants had experienced pubertal changes in their bodies that may have disturbed their proprioceptive references and internal body representations, increasing their reliance on vision and reducing their postural stability (Golomer & Dupui, 2000). Thus, regardless of the increase in sway in the 18 year-old participants, the results of this study still support that dance training reduces an individual's dependence on vision for postural control and causes dancers to rely more heavily on information from the somatosensory system.

Additionally, Simmons (2005) conducted a study of dynamic balance in professional ballet dancers during manipulation of both the visual and somatosensory systems. Six balance tests were used under conditions in which vision and/or somatosensory information were either completely removed or made unreliable. Results showed that dancers were significantly less stable than control subjects during the manipulation of somatosensory information alone and when combined with the unreliable visual input. Specifically, dancers were forced to use a hip strategy in order to maintain balance during the sensory perturbations (Simmons, 2005). This study contributes to the literature supporting that dancers are significantly more reliant on somatosensory input during dynamic assessment. Thus, there is an abundance of research supporting that dance training reduces an individual's reliance on vision for postural control, such that dancers rely more on the input from their somatosensory system. This would allow dancers to potentially increase the gain of their somatosensory system when applying galvanic vestibular stimulation during locomotion and result in smaller errors attributed to the vestibular perturbation.

The somatosensory system is a broad term consisting of a variety of sensory inputs that contribute to producing the desired motor output. Two components of the somatosensory system include cutaneous mechanoreceptors and proprioceptors (muscle spindles and Golgi tendon organs). Cutaneous mechanoreceptors are responsible for detecting tactile sensations such as pain, pressure, touch and temperature. On the other hand, proprioceptors provide information regarding the body's position in space; this includes factors such as muscle length, muscle tension and joint angle. So this creates the question, that if dancers shift their reliance to somatosensory input during locomotion, are they relying more on cutaneous mechanoreceptor or proprioceptive input? In the study by Simmons (2005) that was previously discussed, the researchers manipulated both visual and somatosensory input during a dynamic balance task comparing dancers and control subjects. The perturbation specifically manipulated the proprioceptive information by rotating the participant's support surface in reference to their A-P sway. In addition, they used the Semmes-Weinstein monofilaments to demonstrate that the cutaneous sensitivity of the control subjects and dancers were not significantly different from each other. Thus, they were controlling for cutaneous sensitivity while manipulating proprioceptive input during a dynamic balance task. Their results showed that dancers were significantly less stable than control subjects during this somatosensory perturbation (Simmons, 2005). Since the perturbation was a direct manipulation of their proprioceptive input, these findings support that dancers rely more heavily on their somatosensory input, but specifically the sensory information from their proprioceptors.

Based on this previous research, it can be inferred that dancers may rely more heavily on their proprioceptive input, rather than just their somatosensory system as a whole. Since the cutaneous sensitivity was controlled for, and the proprioceptive perturbations were isolated, it seems that dancers may be relying more specifically on proprioceptive input from their joint receptors in order to produce the appropriate motor output. Another study looked to directly quantify the proprioceptive abilities of the lower limb in a group of professional dancers compared to a matched control sample. Kiefer and colleagues (2013) used a joint angle-matching task to determine the accuracy of the participants when reproducing a desired joint angle at the hip, knee and ankle. Individuals closed their eyes and stood on one leg, stabilizing themselves with a walker, while the experimenter manipulated the joint to a particular angle. The limb was then returned to a resting position, and participants were asked actively reproduce the joint angle without assistance. A manual goniometer was used to measure the joint angle and determine the absolute difference between the actual and estimated joint angles. Results of this study showed that dancers had significantly less error and were more accurate in reproducing the desired joint angles than control subjects at all three joints, with the greatest significance shown at the ankle joint. Clearly, the findings of this particular study support that dancers may have improved proprioceptive awareness of their lower limb joints in space. Their increased reliance on proprioception therefore puts them at an advantage compared to control subjects, particularly in tasks of perturbed visual input. Since dancers are relying more heavily on proprioceptive input during motor tasks, removing or altering visual input does not have as great of an effect on their motor output. Thus, it seems that dancers have a greater accuracy with respect to proprioceptive awareness, and it is predicted that they would rely specifically on this input when attempting to navigate through the environment during visual and vestibular perturbations.

1.9 Purpose and Objectives

Currently, there is limited research perturbing the vestibular system in dancers during a task of spatial navigation. However, based on previous literature, it was expected that dancers would rely more heavily on their somatosensory input during vestibular perturbation without visual cues, and would be more successful when navigating throughout their environment compared to non-dancers. The purpose of this study was to examine the effect of perturbing the vestibular system with GVS on path trajectory and body rotation during a triangle completion task in virtual reality, and to analyze how this task is affected by dance training. By using virtual reality and GVS to perturb the individuals, participants had to navigate throughout the environment with inaccurate vestibular information and without visual cues. Baseline tests of cutaneous sensitivity and proprioceptive awareness were also conducted and compared between groups in order to justify the expected main effect of dance training during the triangle completion task.

The hypothesis of the study was that there would be a main effect of GVS on both path trajectory and body rotation in both the dancer and control samples, such that there would be significantly greater errors in navigation when GVS was administered. Since the vestibular system has been shown to largely contribute to navigational tasks in the absence of vision (Campos et al., 2012; Frissen et al., 2011), it would be expected that GVS would reduce the accuracy of individuals attempting to navigate throughout the environment. In addition, it was expected that there would be no significant difference in errors between the two triangular pathways used in the protocol. It was also hypothesized that there would be a significant main effect of training, such that dancers were predicted to show fewer errors and better accuracy in navigating throughout the virtual environment. This hypothesis was based on the previously discussed research, highlighting their superior representations of spatial parameters (Blasing & Schack, 2012; Brown et al., 2006), as well as their increased reliance on somatosensory information (Golomer et al., 1999; Golomer & Dupui, 2000; Simmons, 2005). Dancers were expected to have a greater reliance on the input from their somatosensory system to override the inaccurate vestibular and unavailable visual information during these trials. Finally, it was hypothesized that dancers would not significantly differ from the control subjects with respect to cutaneous sensitivity, but were expected to demonstrate greater accuracy in tasks of proprioceptive awareness, based on previous literature (Kiefer et al., 2013).

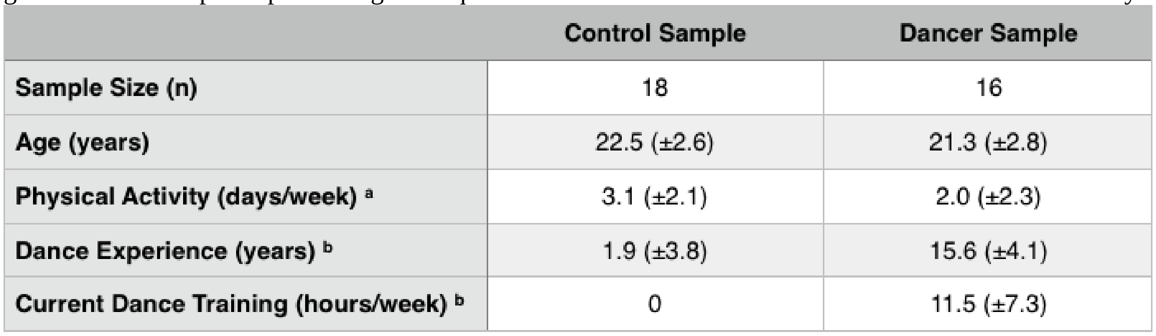
The objective of this study was to use the findings to create a better understanding of the role of the vestibular system in the absence of visual cues during tasks of spatial navigation. In addition, the study also aimed to understand the effects of dance training on both the reweighting of sensory input, and the accuracy of spatial navigation in the absence of visual cues. This research will contribute to the gap in current literature on sensory weighting during spatial navigation, specifically in dancers, by exploring how individuals adapt to the manipulation of both the visual and vestibular systems while attempting to navigate throughout a virtual environment.

2.0 Methodology

2.1 Participants

Participants were recruited from Wilfrid Laurier University and local dance studios in Waterloo, Ontario. All participants were female between the ages of 18-30 years that were able to walk 10 meters unassisted and understand English instructions. This was in order to remove any effects of gender on performance. Females were selected for the study based on the increased availability of female dancers in the correct age range compared to male dancers. Sample sizes of each group were selected based on convenience and availability particularly with respect to the sample of dancers; there were a limited number of competitive dancers in the particular age range and location that were available for recruitment within the time frame of the data collection. In addition, the required sample size based on a power analysis could not be calculated because there were a limited number of pre-existing studies examining the effect of GVS on dancers, and pilot work was not conducted prior to data collection. The control group consisted of eighteen individuals (n=18) that had not participated in sport-specific or athletic training at the varsity level or higher. The experimental group included sixteen dancers (n=16) that had a minimum of eight years of training experience and all participants in this group were, at the time of the study, still training on a weekly basis. Training duration across the dancers ranged from 8-22 years of experience in a variety of styles including ballet, pointe, jazz, tap, hip hop, contemporary, acrobatics, and traditional Indian dance. Dancers were selected as the experimental group in the current study based on previous research that has supported that dancers rely more heavily on somatosensory information during dynamic balance tasks (Golomer et al., 1999; Golomer & Dupui, 2000; Simmons, 2005) and encode spatial information differently than untrained individuals (Blasing & Schack, 2012; Cortese and Rossi-Arnaud, 2010). Participants were excluded from the experimental group of dancers if they were not training in at least one of the dance styles listed above on a minimum weekly basis. Individuals were excluded from the overall study if they had any sensory disorder, vestibular deficits, vertigo, peripheral neuropathy, visual impairments that cannot be counteracted with the use of corrective lenses, functional limitation of the limbs, medical conditions, or any other neurological disease. Individuals that fit the inclusion criteria were recruited via email and social media outlets. A recruitment email was also distributed specifically to the Wilfrid Laurier Competitive Dance Team and dance teachers in the Waterloo area. Research ethics approval was received from the Wilfrid Laurier Research Ethics Board (REB) and each participant gave written informed consent before completing the study. Each participant completed a background questionnaire regarding the inclusion and exclusion criteria of the study, with emphasis on previous athletic training and experience. This information was used to ensure that each participant fit the inclusion criteria of the sample group they were included in (Table 2-1). The entire study took approximately 2 hours to complete and participants received monetary compensation of $10/hour for completing the study.

Table 2-1. Participant Demographics: Characteristics of controls subjects (n = 18) and dancers (n = 16) gathered from the participant background questionnaire based on the inclusion criteria of the current study.



	Control Sample	Dancer Sample
Sample Size (n)	18	16
Age (years)	22.5 (±2.6)	21.3 (±2.8)
Physical Activity (days/week) [a]	3.1 (±2.1)	2.0 (±2.3)
Dance Experience (years) [b]	1.9 (±3.8)	15.6 (±4.1)
Current Dance Training (hours/week) [b]	0	11.5 (±7.3)

[a] Physical activity is defined as exercise that is not sport-specific and does not include dance training.
[b] Styles of dance included in the categories dance experience and current dance training: ballet, pointe, jazz, tap, hip-hop, contemporary, acrobatics, Highland and traditional Indian dance.

2.2 Baseline Testing

2.2.1 Mechanoreceptor Sensitivity (Monofilaments)

Baseline sensory testing was conducted to analyze any differences between control subjects and dancers in mechanoreceptor sensitivity and proprioception. Plantar surface cutaneous sensation was measured using monofilaments to determine the touch sensitivity in both the control participants and the dancers. The test locations and application were standardized across all participants. Individuals were tested at four locations on both the right and left feet: the great toe, first metatarsal, fifth metatarsal, and heel (Figure 2-1). Prior to data collection, the experimenter visually located each foot site. All individuals were seated on a table with their knees extended at 180° and their feet resting on a stool in front of them, with the plantar surface of the foot facing the experimenter. The monofilaments (Touch-Test Six Piece Foot Kit) used in this study were 2.83, 3.61, 4.31, 4.56, 5.07 and 6.65 in evaluator size, which is equivalent to 0.07, 0.4, 2, 4, 10 and 300g of force when the filament is applied perpendicular to the plantar surface of the foot and bent to half it's length (Perry, 2006). Participants were instructed to close their eyes, and verbally respond with a yes or no if they could feel the pressure of the monofilament in the specified location. The experimenter counted down to prepare the participant, and then subsequently applied the monofilament to the plantar surface of the foot for two seconds with enough pressure to initiate a bend in the filament. Three trials of each monofilament were conducted at each location on both feet, and were applied descending in size. The largest monofilament (6.65 evaluator size) was first used on all four locations of the right foot. Locations that were sensitive enough to detect the force of the monofilament were then further tested with the next monofilament of descending size (5.07, 4.56, 4.31, 3.61, 2.83) until the threshold of each specific location was determined. The entire process was then repeated on the left foot. The threshold of each participant was defined as the force that a participant could detect 2/3 of the time (Perry, 2006). If the participant could detect the force of the monofilament for at least two of the three trials (2/3), the experimenter continued with the next monofilament of descending size and force. Once the participant could no longer detect the pressure of the filament, the experimenter returned to the monofilament of increasing size to ensure that it was the correct threshold of the participant. Catch trials, where there was no physical contact of the monofilament with the plantar surface of the foot, were inserted throughout the trials at all sites to ensure the accuracy of detection of the participants.

Figure 2-1. Monofilament Test – Monofilaments of varying evaluator size were used to determine the cutaneous sensitivity of the plantar surface of the foot at four locations on both the right and left feet: great toe, first metatarsal, fifth metatarsal and heel.

2.2.2 Proprioception (Joint Angle-Matching)

Proprioception was measured using a static joint angle-matching task to determine how well participants were able to detect their limb position in space in the absence of visual cues. The tools and procedure used were similar to those described in the aforementioned study by Kiefer and colleagues (2013), that analyzed the reproduction of a target joint position at the hip, knee and ankle in dancers and control participants (Kiefer et al., 2013). Individuals were seated at the edge of a table with the lower leg extending towards the floor unsupported, creating a natural 90° flexion at both knees. This position was chosen to remove any somatosensory input from the plantar surface of the feet and isolated the individual’s proprioceptive awareness. A goniometer (Vernier Software and Technology) was used to measure the target angle at the specified joint. The goniometer connected to the computer, and the program Logger Pro 3 was used to collect the data and export it to Excel. Goniometer placement at the joint was determined by specific anatomical landmarks and standardized across all participants. At the knee, the fulcrum was placed at the lateral epicondyle of the femur, the stationary arm was attached to the midline of the thigh, and the moving arm along the leg, in line with the fibula. At the ankle, the fulcrum was positioned at the lateral malleolus, the stationary arm was attached to the midline of the leg, along the fibula, and the moving arm was aligned with the lateral surface of the foot along the fifth metatarsal (Figure 2-2) (Kiefer et al., 2013). The knee was manipulated to 30°, 45°, and 60° extension, where 0° was defined as the neutral 90° flexed position that was naturally produced in the seated position. The ankle was manipulated to 0°, 15°, and 30° plantarflexion, where 0° was classified as 90° flexion at the ankle joint. The experimenter manipulated each joint to one of the defined angles to produce the target position, and then returned the joint to its original starting position. The participant was then instructed to actively reproduce the target angle with the same limb, without assistance from the experimenter. The target position was held for three seconds, averaged, and reported as the individual's estimated target joint angle. This process was performed three times for each of the three angles of both the ankle and knee joints, and the entire process was conducted on both legs. Thus, the task consisted of a total of 36 trials (three trials x three angles x two joints x two legs).

Figure 2-2. Joint Angle-Matching Task: Top) 0° at the knee joint (defined as the neutral 90° flexed position naturally produced in this seated position) prior to target angles of 30°, 45°, and 60° extension. Bottom) 0° at the ankle joint (defined as 90° flexion at the ankle joint) prior to target angles of 0°, 15°, and 30° plantarflexion.

2.2.3 GVS Threshold

Galvanic vestibular stimulation was used to perturb individuals during the experimental conditions of the study. However, individuals have been shown to have different thresholds when responding to GVS, such that the same amplitude of stimulation will not necessarily produce the same magnitude of response across two different individuals. Therefore, as opposed to using fixed stimulation levels, it is important to incorporate threshold concepts when studying the effects of GVS (Bent et al., 2000). In the current study, specific GVS thresholds were determined separately for both right and left sides of each participant by altering the direction of the current, and therefore altering the placement of the anode. Participants stood in a natural stance, with their feet approximately hip-width apart, and with their eyes closed. Binaural, bipolar GVS was delivered to participants through two electrodes placed on the left and right mastoid processes. An A395 Linear Stimulus Isolator (World Precision Instruments) was used to deliver a square-wave impulse of stimulation to the participants for 3s at each increment. Testing began at 0.1mA, and was increased in 0.1mA increments until the individual’s personal threshold was established. The threshold of each participant was defined as the point at which individuals exhibited visible sway that was related to the onset of stimulation. Once the threshold was found, the experimenter decreased the stimulation, and then re-tested the threshold value for validation. The level of stimulation used during the experimental trials in the current study was three times the participant’s individual threshold. When the right and left threshold values were asymmetrical, the higher of the two values was used.

2.3 Experimental Design

The current study measured the body kinematics of the individual as they navigated through the environment to calculate path trajectory and body rotation. Oculus Rift DK2 was used to simulate a basic virtual environment (built using Vizard 5 from World Viz, California) with a ground plane for the participants to navigate throughout. The headset (Head Mounted Display, HMD) was worn on the participant’s head and completely occluded any vision from the real-world lab space, immersing the individual in the virtual environment. Individuals were exposed to a room with grey tiles on the floor, walls and ceilings, and navigated between both red and green poles as locomotor targets during the task (Figure 2-3).

The use of the Oculus Rift allowed the participants to actively navigate along the first two legs of the triangle, without assistance from the experimenter. This methodology is beneficial, since previous research has supported that active navigation throughout an environment better contributes to spatial learning because of the idiothetic information the individual receives (Chrastil & Warren, 2012; Grant & Magee, 1998). In addition, the Oculus Rift allowed for the precise removal of visual cues (instead of removing visual information via closing one’s eyes) once the individual reached the second target, which was cued by the movement of the head-mounted display through the second target pole in the virtual environment. Thus, the vision of participant’s was not completely occluded; visual cues were simply and efficiently removed from the individual’s surrounding environment.

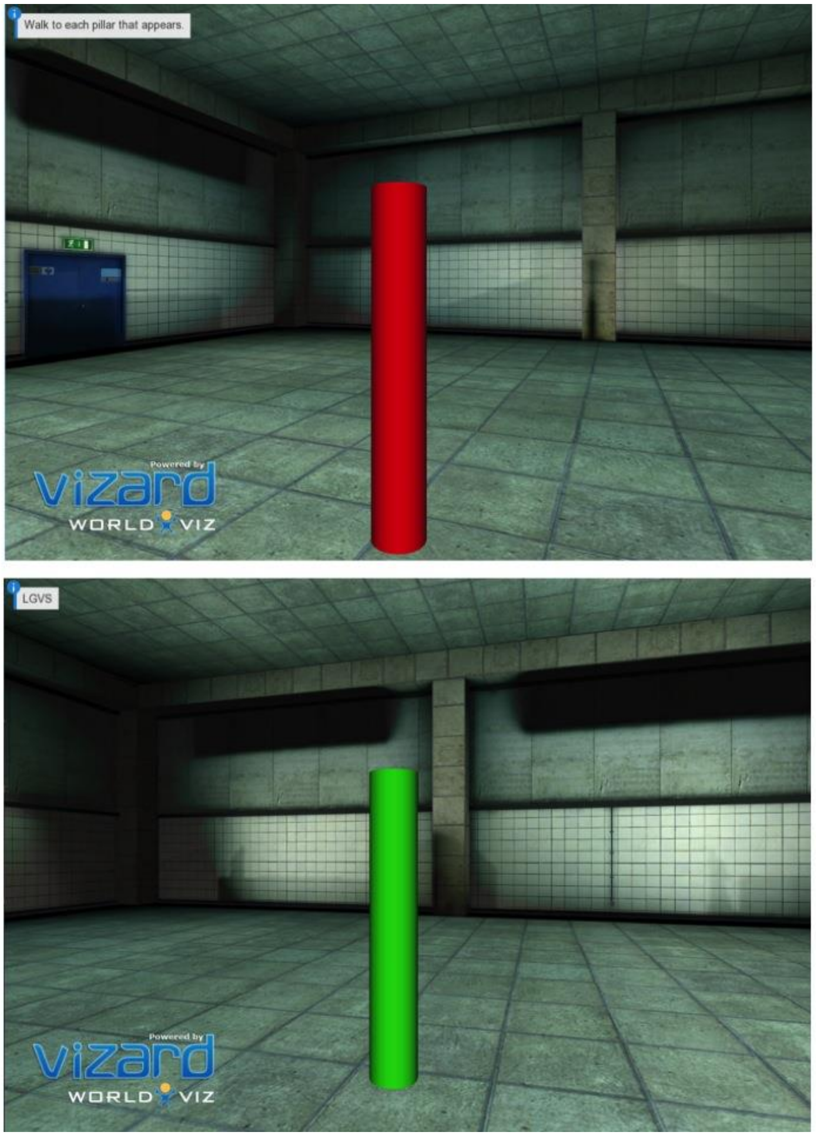


Figure 2-3. Virtual World: The red poles (top) identified the origin or initial position and the green poles (bottom) identified the target positions for each of the trials. Participants were instructed to step inside the pole with both feet and turn to face the next target.

Whole body kinematic data were collected at 60Hz throughout the entire trial using an NDI OptoTrak motion tracking system. For the purpose of this study, rigid bodies were used to track body segment motion. Each rigid body contained three Infrared Light Emitting Diodes (IREDs) arranged in a triangle. Participants were outfitted with 4 forward-facing rigid bodies that were placed on the head (front of HMD), trunk

(Xyphoid), and each leg (distal end between malleoli). Four digitized points were used to calculate COM, and marked specific anatomical landmarks including: left and right glenohumeral joints and left and right anterior-superior-iliac-spines. A single rear-facing rigid body was placed on the trunk (between the scapulae), along with 4 additional digitized points that were used if the anterior trunk rigid body was not visible: left and right glenohumeral joints and left and right posterior-superior-iliac-spines. Five Optotrak cameras were dispersed around the outer border of the lab space in order to have 360-degree coverage of the IREDs throughout the entire procedure. A camera was placed in each of the four corners of the room, and an additional camera was positioned at the end of the designated space where the body rotations occurred, in order to improve the quality of data collection and ensure kinematics were collected during the entire trial (Figure 2-4). The digitized points were used to calculate a weighted whole body center of mass (COM), previously used by Winter (2008), in order to properly analyze body position and path trajectory of each participant.

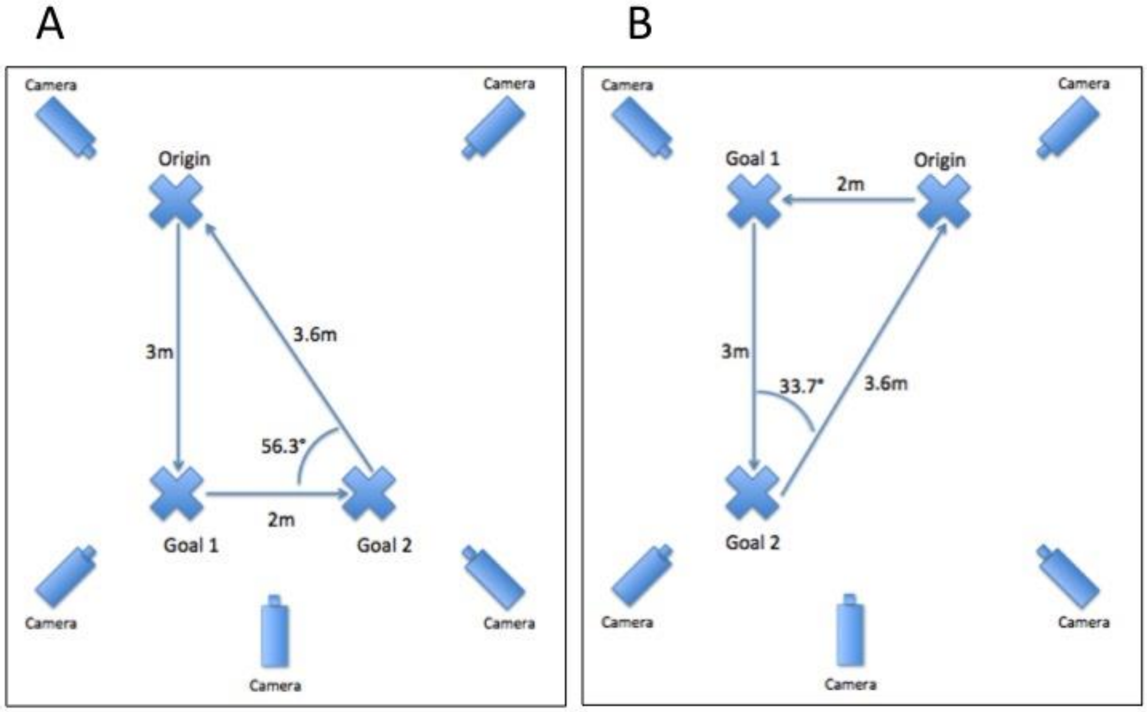


Figure 2-4. Experimental Design: Four cameras were placed in each corner of the lab space and one was positioned at the end adjacent to the final body rotation. Participants navigated to Goal 1, Goal 2, then returned to their initial position (Origin). Example pathways are shown above such that A) Triangle 1, Right Start Position, B) Triangle 2, Left Start Position.

2.4 Procedure

Each trial was based on the triangle completion task, during which participants would complete the first two legs of a triangle by walking towards two separate goals in the virtual environment, and then navigate back to their starting position with a blank visual screen. The triangle completion task was selected in the current study based on the previous research that stated that a more difficult task than straight-line, forward walking on a flat surface was necessary to induce sensory reweighting towards the vestibular system (Deshpande & Patla, 2007). In addition, previous studies have supported that the vestibular system largely contributes to tasks of spatial navigation in the absence of vision (Campos et al., 2012; Frissen et al., 2011). Thus, the task was selected for the current study in order to develop a better understanding of the contributions of the vestibular system to spatial navigation in the absence of vision, and how the body responds to vestibular perturbations during this task. Verbal instructions and directions were delivered to the participant during each trial. Prior to completing the trials of the study, individuals were given a practice trial that involved navigating to four poles placed in the four corners of the border of the virtual environment. Individuals were instructed to step inside the pole, turn to the right, and step inside the next target pole until all four targets were reached. This allowed participants to experience locomotion throughout the virtual environment, and develop an understanding of the cues in the virtual world. They were able to learn that stepping directly inside the target pole caused it to disappear, and was necessary in order for the next target to appear. This also helped to develop trust between the participant and the experimenter; allowing participants to navigate the outer border of the data collection space in the virtual environment demonstrated that participants were not in danger of colliding with any obstacles in the real world.

Following the practice trials, the experimenter began the study trials during which data was collected and the conditions were applied. Participants were instructed to step inside the (red) starting pole and turn to face the first target (green) (Figure 2-3). They were then instructed to navigate along the first leg of the triangle in the direction of the first target (green) pole, and once inside the target they were instructed to walk along the second leg of the triangle in the direction of the second (green) target pole (Figure 2-3). Once they reached the second (green) target, the visual input from the virtual world was removed, and participants were instructed to turn and walk back to their starting position in the absence of visual cues. Once the individuals had returned to their estimated starting position, they were instructed to stand with both feet shoulder width apart to produce a well-defined final position.

Two separate triangles with different dimensions were used as the designated pathways in this study. Triangle One was 3m x 2m, with a final angle of rotation of 56.31° (Figure 2-4A), and Triangle Two was 2m x 3m with a final angle of rotation of 33.69° (Figure 2-4B). The triangular pathways consisted of an equal amount of clockwise and counter-clockwise triangles, allowing for both right and left turns at the final angle of rotation. During the experimental conditions, binaural, bipolar galvanic vestibular stimulation (GVS) was delivered when the participant reached the second target pole (approximately 100ms before the final body rotation) and continued until the participant reached their estimated starting position. A research assistant was responsible for delivering the GVS once the individual reached the second target and visual cues from the environment were removed. Unfortunately this allowed for human error, such that there could have been inconsistencies in the delivery of GVS, including a delay between when the individual reached the second target and when the GVS was actually delivered by the research assistant. GVS was administered in both right and left directions (anode right and anode left) for an equal amount of trials and the amplitude of stimulation was 3 times each participant’s personal threshold (Bent et al., 2002). Control conditions did not include GVS stimulation during the final turn and return. Participants performed an equal amount of trials with and without GVS. The task was completed six times for each of the GVS conditions (with and without GVS) with the experimental GVS condition being further divided into three cathodal and three anodal trials, for each of the two triangles, in both the right and left directions. Thus, the study consisted of a total of 48 trials (six trials x 2 GVS conditions x 2 triangles x 2 directions).

2.5 Data Analysis

Three dependent variables were analyzed during this study: 1) arrival error was used to determine the distance error from the original starting position; 2) angular error was measured to determine the error in body rotation; and 3) average instantaneous angle was determined to examine variability in path trajectory. Arrival error was determined by comparing the distance from the participant's estimated point of origin to the actual starting position using a radial distance (i.e., hypotenuse of AP and ML distances). Angular error was calculated by comparing the ideal angle of body rotation necessary for the participant to reach the origin, to the actual angle of body rotation that each participant produced before the final leg of the triangle. This absolute value was calculated for each trial and then averaged across conditions. These first two dependent variables were measured based on previous studies that use both distance and angular error in order to determine an individual's spatial navigational abilities in the absence of visual cues (Berthoz et al., 1999; Loomis et al., 1993; Smith et al., 2010; Worsley et al., 2001). In the current study, a third measure was added to the analysis. Variability in path trajectory was calculated during the final leg of the triangle by calculating the instantaneous trajectory angle at ten equally spaced points along the final trajectory during each condition. Standard deviation values were calculated, and then divided by the mean angle of the trajectory in order to represent variability as a value of coefficient of variation, normalizing the variability across each trial. This variable was added in order to develop a better understanding of each participant’s path trajectory between the final body rotation and gait termination at the predicted origin. This analysis was used as a means of analyzing if individuals adjusted their path trajectory on the final leg of the triangle, possibly indicating adjustments in their sensory weighting during the task. Variability in trajectory could represent the central nervous system altering the weight or gain of each sensory input during the trial. All three of these dependent variables were used to determine the accuracy of spatial navigation of participants without visual cues, in the presence and absence of vestibular perturbation.

The factors in this study produced a total of twelve separate conditions: three levels of GVS (no GVS, GVS anode right, and GVS anode left), two triangles, and two final turning directions. Missing kinematic data were fixed using a cubic spline interpolation. Whole body kinematic data were used to calculate a weighted center of mass (COM) based on previous literature (Winter, 2008). These values were calculated for the x, y and z planes using the following equation:

$$\mathit{COM} = 0.46 * ((\textit{Left Glenohumeral Joint} + \textit{Right Glenohumeral Joint} + \textit{Xyphoid}) / 3) + 0.22 * ((\textit{Left ASIS} + \textit{Right ASIS}) / 2) + 0.16 * (0.625 * \textit{Left ASIS} + 0.375 * \textit{Left Ankle}) + 0.16 * (0.625 * \textit{Right ASIS} + 0.375 * \textit{Right Ankle})$$

The initial starting position of the participant for each trial before movement began was calculated by averaging the COM values of the first 30 frames of the trial prior to any observed changes in the AP and ML axis. The final position was classified as the point in which the participant came to rest (i.e., velocity in plane of progression was < 10cm/s).

2.6 Statistical Analysis

The cutaneous sensitivity values from the monofilament test were averaged across right and left feet. The values were submitted to a 2 (group: controls vs. dancers) x 4 (great toe, first metatarsal, fifth metatarsal and heel) mixed model repeated measures ANOVA comparing location between groups.

In the joint angle-matching task, the absolute difference scores were calculated for each of the 36 trials for each participant by comparing the angle of the target position to the participant's estimated target position. These error scores were then averaged across trials of the same condition, target position (angle) and leg. The remaining scores were submitted to a 2 (group: controls vs. dancers) x 2 (location: ankle vs. knee) mixed model repeated measures ANOVA. This process quantified each participant's joint positioning accuracy in order to determine proprioceptive awareness in the ankle and knee and compare between control subjects and dancers.

Arrival errors, angular errors, and instantaneous angles were analyzed as three separate dependent variables to quantify each participant's spatial navigation abilities during sensory perturbation. Each variable was averaged across the three trials in each of the twelve conditions for all participants. All three variables were first submitted to a 2 (group: controls vs. dancers) x 2 (triangle: 1 vs. 2) x 2 (start position: left vs. right) mixed model repeated measures ANOVA comparing triangles and direction between groups, only for the control conditions (i.e., without GVS). This analysis was used to determine if there was a significant effect of starting position (left or right) in the absence of GVS. The ANOVA showed that there was no main effect of side on arrival error (F(1,32) = .175cm, p = .678), angular error (F(1,32) = 2.504°, p = .123), or path variability (F(1,32)

= .642, p = .429). Thus, since there was no significant difference between left and right start positions in any of the three dependent variables, the data were collapsed across direction of triangle to produce the three GVS conditions: no GVS (NGVS), GVS away from the direction of the turn (GVSaway), and GVS towards the direction of the turn (GVStoward). The GVSaway conditions consisted of all trials when the anode was on the opposite side of the direction of the turn (participants turned away from the anode), while the GVStoward conditions included the trials when the anode was on the same side as the direction of the turn (participants turned towards the anode). The resulting data were submitted to a 2 (group: controls vs. dancers) x 3 (No GVS, GVS away, GVS towards) x 2 (triangle: 1 vs. 2) mixed model repeated measures ANOVA comparing GVS conditions and triangles between groups, to determine if there was a significant main effect of GVS or triangle. This analysis was also used to determine if there was a significant difference between groups (control subjects and dancers), to identify if there was a main effect of dance training. Lastly, the coefficient of variability (CoV) was also calculated for each of the dependent variables in the twelve conditions. The CoV values were submitted to another 2 (group: controls vs. dancers) x 3 (No GVS, GVS away, GVS towards) x 2 (triangle: 1 vs. 2) mixed model repeated measures ANOVA comparing GVS conditions and triangles between groups. This analysis was to determine if there were any differences in variability between control subjects and dancers, and if GVS condition or triangle had a significant effect on variability across participants.

3.0 Results

3.1 Baseline Testing

Baseline tests of cutaneous sensitivity and proprioceptive awareness were used in an attempt to differentiate between the sensory qualities of control participants and dancers. Monofilament testing was used to determine the cutaneous sensitivity of the mechanoreceptors on the plantar surface of the foot. Reported mean values are in evaluator size, not grams of force. A 2 x 4 mixed model repeated measures ANOVA showed that control participants (M = 4.002, SD = .501) and dancers (M = 4.007, SD = .531) did not show a significant difference between monofilament testing scores when averaged across location ($F(1,32) = .002$, $p = .969$) (Table 3-1). However, there was a significant main effect of location ($F(3,96) = 12.092$, $p < .001$, $\eta^2 = .274$). The heel (M = 4.301, SD = .099) had significantly reduced sensitivity ($p < .001$) compared to the great toe (M = 3.824, SD = .571), first metatarsal (M = 3.895, SD = .566), and fifth metatarsal (M = 3.999, SD = .496), and the great toe is significantly more sensitive than the fifth metatarsal ($p = .025$). There was no significant interaction between location and group ($F(3,96) = .717$, $p = .544$).

A joint angle-matching task was used to determine the proprioceptive awareness of the participants by determining their error in reaching a target joint position without vision. A 2 x 2 mixed model repeated measures ANOVA showed that control participants (M = 2.526°, SD = .834) and dancers (M = 2.510°, SD = .880) did not show a significant difference between joint angle errors when averaged across joint ($F(1,32) = .006$, $p = .939$) (Table 3-1). However, there was a significant main effect of joint ($F(1,32) = 7.87$, $p = .008$, $\eta^2 = .197$) such that the errors in joint angle matching at the ankle joint (M = 2.869°, SD = .758) were significantly greater than the errors at the knee joint (M =

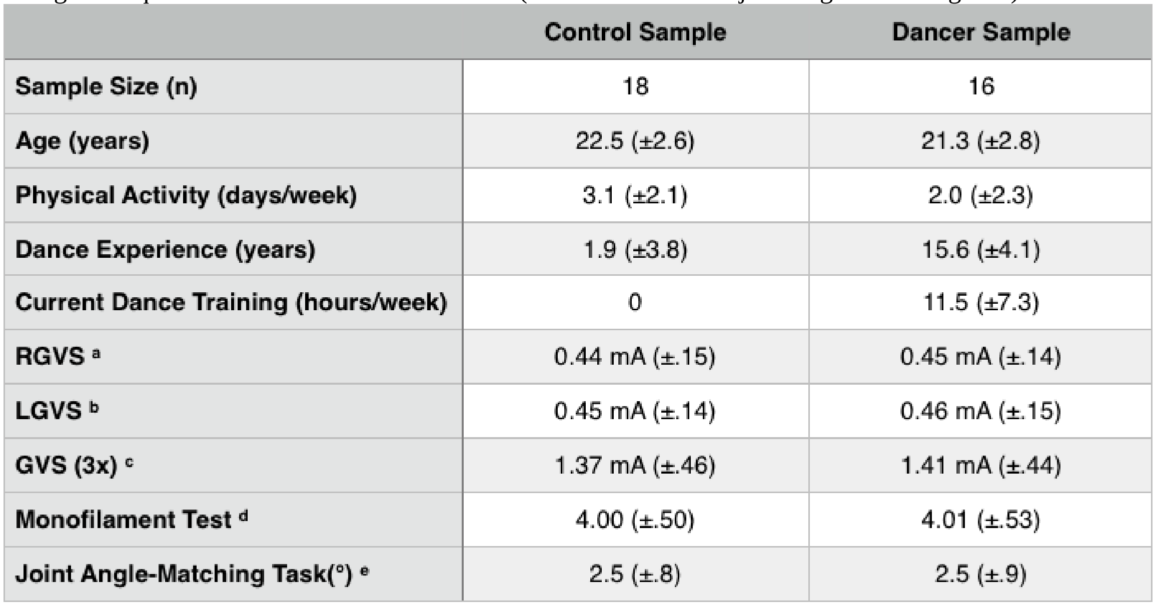
2.168°, SD = 1.10). There was no significant interaction between location and group (F(1,32) = .003, p = .960).

3.2 Triangle Completion Task

Based on the small sample size of each group, assumptions were verified prior to running the statistical analysis. Box plots showed that there were very few outliers across conditions, and no single participant was a consistent outlier across the twelve conditions. Thus, all values were included in the analysis. The assumption of normality is not met based on the sizes of the sample ($n_{control}$= 18, n_{dancer} = 16). Since the majority of the twelve conditions produced non-significant values in both the Shapiro-Wilk and Kolmogorov-Smirnov tests for each dependent variable, all values were included in the analysis and normality was assumed. Both P-P and Q-Q plots produced patterns that were consistent with the homogeneity of variance. All values of Levene's Test for equality of variance were insignificant for each condition for each separate analysis. Thus, equal variances across conditions and between groups were assumed.

Prior to analyzing the triangle completion task data, the values of GVS used in the study (3 times the participant's threshold) were submitted to an independent samples T-test comparing control participants and dancers. This analysis showed that there was no significant difference in the GVS thresholds (t(32) = -.274, p = .786) between the control participants (M = 1.3661mA, SD = .458) and dancers (M = 1.4081mA, SD = .435) (Table 3-1).

Table 3-1. Participant Demographics and Results: A display of the mean values and standard deviations comparing controls subjects (n = 18) and dancers (n = 16) based on the results from the participant background questionnaire and the baseline tests (monofilaments and joint angle-matching task).



	Control Sample	Dancer Sample
Sample Size (n)	18	16
Age (years)	22.5 (±2.6)	21.3 (±2.8)
Physical Activity (days/week)	3.1 (±2.1)	2.0 (±2.3)
Dance Experience (years)	1.9 (±3.8)	15.6 (±4.1)
Current Dance Training (hours/week)	0	11.5 (±7.3)
RGVS [a]	0.44 mA (±.15)	0.45 mA (±.14)
LGVS [b]	0.45 mA (±.14)	0.46 mA (±.15)
GVS (3x) [c]	1.37 mA (±.46)	1.41 mA (±.44)
Monofilament Test [d]	4.00 (±.50)	4.01 (±.53)
Joint Angle-Matching Task(°) [e]	2.5 (±.8)	2.5 (±.9)

[a] RGVS: GVS threshold of rightward current (anode right).
[b] LGVS: GVS threshold of leftward current (anode left).
[c] GVS (3x): Participant's larger GVS threshold multiplied by 3.
[d] Monofilament test scores displayed in evaluator size.
[e] Joint angle-matching scores displayed as an absolute angular error.

All dependent variables were then submitted to a 3 x 2 x 2 mixed model repeated ANOVA comparing GVS conditions and triangles between groups. The analysis showed that there was no significant difference between control participants (M = 82.200cm, SD = 27.201) and dancers (M = 77.729cm, SD = 28.852) on arrival error (F(1,32) = .432, p = .516). However, the results showed a significant main effect of GVS (F(2,64) = 8.273, p = .001, $\eta^2 = .205$) such that GVStoward (M = 85.953cm, SD = 19.685) had significantly greater arrival errors (p = .000) than NGVS (M = 74.631cm, SD = 21.761), as well as significantly greater arrival errors (p = .016) than GVSaway (M = 79.310cm, SD = 24.175) (Figure 3-1). There was no significant main effect of triangle (F(1,32) = 3.608, p = .067) when comparing triangle 1 (M = 75.655cm, SD = 26.933) and triangle 2 (M = 84.274cm, SD = 20.268). Mauchley's test of sphericity stated that the assumption of sphericity had been violated for GVS*Triangle, □^{2}(2) = 9.68, p = .008, therefore the degrees of freedom were corrected using Huynh-Feldt estimates of sphericity (ϵ = .848). There were no significant two-way interactions between GVS and group (F(2,64) = .921, p = .403), triangle and group (F(1,32) = .079, p = .780) or GVS and triangle (F(1.697,54.298) = 2.765, p = .080). There was no significant three-way interaction between GVS, triangle and group (F(1.697,54.298) = .213, p = .772).

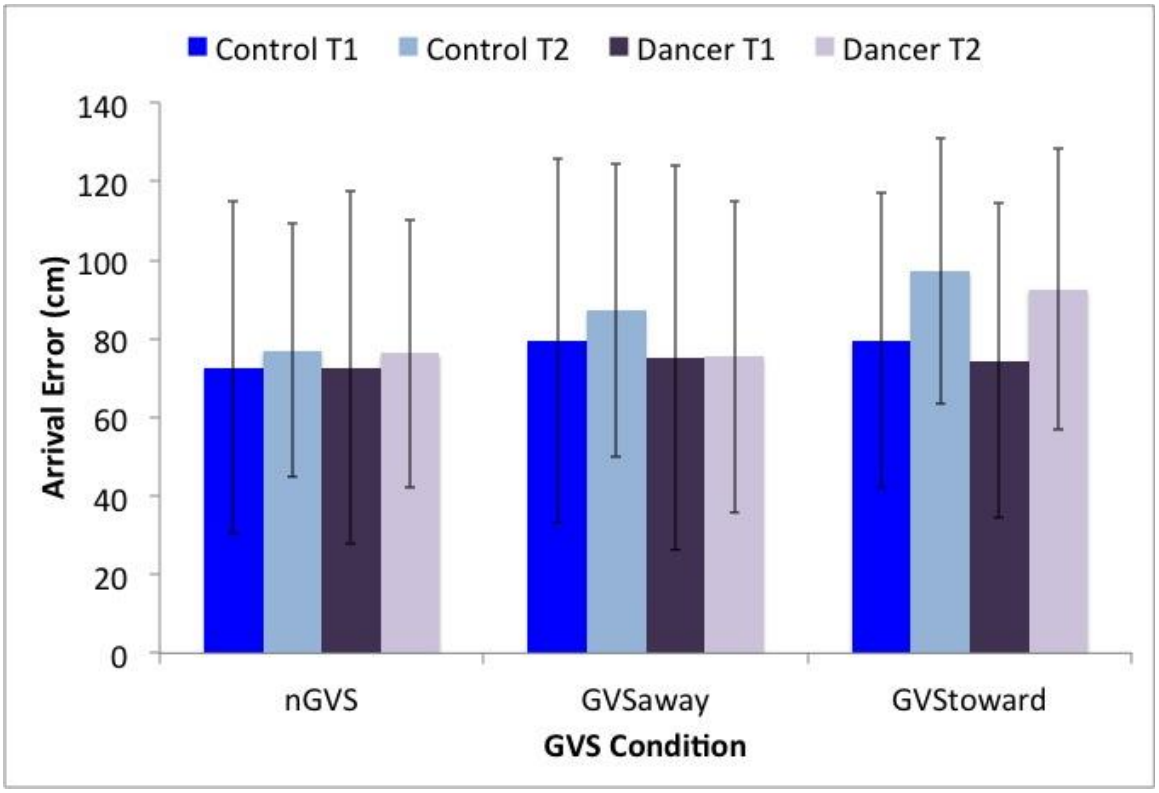


Figure 3-1. Arrival Error: The average arrival error compared within triangle (triangle 1 vs. triangle 2) and GVS (No GVS, GVS away from direction of turn, GVS towards direction of turn) conditions, and between groups (control vs. dancer). Results show a main effect of GVS (F(2,64) = 8.273, p = .001, η^2 = .205) such that GVStoward had significantly greater arrival errors than NGVS (p<.001) and GVSaway (p = .016). Error bars represent the variability for each condition.

With respect to angular error, the 3 x 2 x 2 mixed model repeated measures

ANOVA showed that there was no significant difference between control participants (M = 9.058°, SD = 3.697) and dancers (M = 7.820°, SD = 3.918) when comparing the actual angle of projection to the ideal angle (F(1,32) = 1.796, p = .190). However, the results showed a significant main effect of GVS (F(2,64) = 6.340, p = .003, η^2 = .165) such that NGVS (M = 7.430°, SD = 2.682) had significantly smaller error (p = .025) than GVSaway (M = 8.629°, SD = 3.236), as well as significantly smaller error (p = .003) than GVStoward (M = 9.258°, SD = 3.656) (Figure 3-2). There was no significant main effect of triangle (F(1,32) = 2.206, p = .147) when comparing errors between triangle 1 (M = 7.811°, SD = 3.248) and triangle 2 (M = 9.067°, SD = 4.012). Mauchley’s test of sphericity stated that the assumption of sphericity had been violated for GVS*Triangle, □^{2}(2) = 15.38, p < .001, therefore the degrees of freedom were corrected using Huynh-Feldt estimates of sphericity (ϵ = .767). There were no significant two-way interactions between GVS and group (F(2,64) = .153, p = .859) or triangle and group (F(1,32) = .097, p = .758). However, there was a significant two-way interaction between GVS and triangle (F(1.534,49.086) = 3.783, p = .040, η^2 = .106) in the GVStoward condition between triangle 1 (M = 7.911°, SD = 4.152) and triangle 2 (M = 10.604°, SD = 5.452). There was no significant three-way interaction between GVS, triangle and group (F(1.534,49.086) = .175, p = .782).

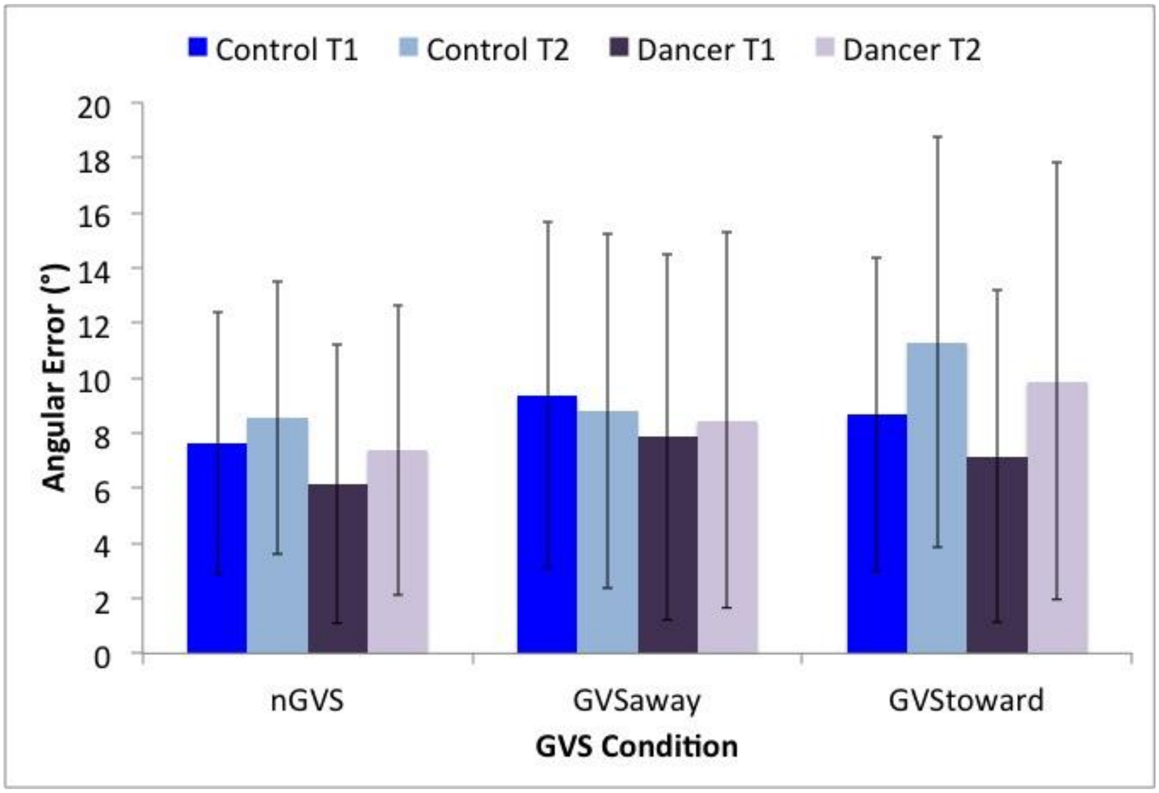


Figure 3-2. Angular Error: The average angular error compared within triangle (triangle 1 vs. triangle 2) and GVS (No GVS, GVS away from direction of turn, GVS towards direction of turn) conditions, and between groups (control vs. dancer). Results show a main effect of GVS (F(2,64) = 6.340, p = .003, η^2 = .165) such that NGVS had significantly smaller error than GVSaway (p = 0.25) and GVStoward (p = .003). Error bars represent the variability for each condition.

The same 3 x 2 x 2 mixed model repeated measures ANOVA was run on the coefficient of variation values for the instantaneous angles of each participant to determine path variability (Figure 3-3). This analysis showed that there was no significant difference between control participants (M = .139, SD = .052) and dancers (M = .135, SD = .052) when comparing the CoV values of path trajectory (F(1,32) = .121, p = .730). There was no significant main effect of GVS (F(2,64) = 1.937, p = .153) when comparing NGVS (M = .122, SD = .052), GVSaway (M = .146, SD = .058), and GVStoward (M = .143, SD = .064) conditions. There was no significant main effect of triangle (F(1,32) = .256, p = .616) when comparing variability between triangle 1 (M = .134, SD = .047) and triangle 2 (M = .140, SD =.058). There were no significant two-way interactions between GVS and group (F(2,64) = 1.086, p = .344), triangle and group (F(1,32) = 1.256, p = .271), or GVS and triangle (F(2,64) = 1.079, p = .346). There was no significant three-way interaction between GVS, triangle and group (F(2,64) = 1.924, p = .154).

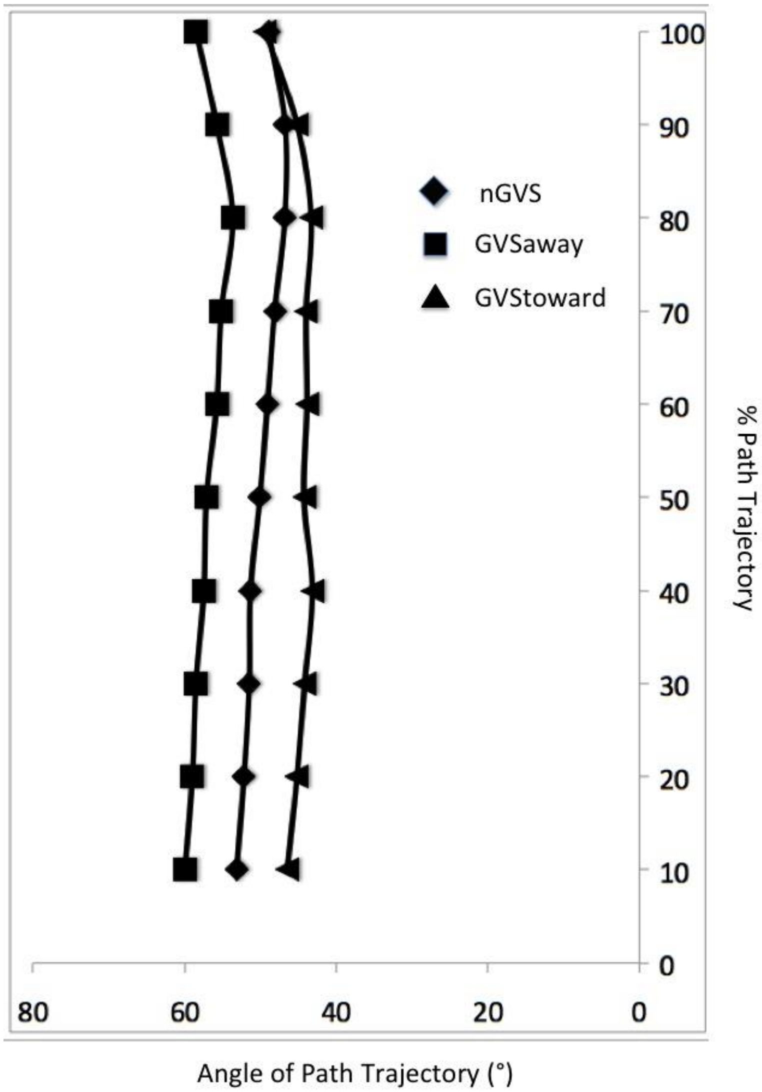


Figure 3-3. Path Trajectory: Path angle data from one participant during the return phase of each GVS condition (nGVS, GVSaway, GVStoward) for triangle 1. The target final body rotation for triangle 1 was 56.3° (Figure 2-4A). Instantaneous angles were recorded and averaged across the three trials at ten equally distributed time points (0-100%) during the final path trajectory.

Coefficient of variation (CoV) values were also calculated for both arrival error and angular error to determine if there were any significant differences in variability between groups. Error values for both variables were submitted separately to the 3 x 2 x 2 mixed model repeated measures ANOVA. This analysis showed no significant differences between control participants (M = .431, SD = .163) and dancers (M = .428, SD = .174) in arrival error (F(1,32) = .006, p = .941), and no significant differences between control participants (M = .620, SD = .146) and dancers (M = .630, SD = .152) in angular error (F = (1,32) = .078, p = .782). There was no significant difference between GVS conditions NGVS (M = .456, SD = .169), GVSaway (M = .434, SD = .157) and GVStoward (M = .399, SD = .152) in arrival error (F (2,64) = 1.692, p = .192) as well as no significant difference between GVS conditions NGVS (M = .634, SD = .145), GVSaway (M = .648, SD = .157) and GVStoward (M = .593, SD = .181) and angular error (F(2,64) = 1.160, p = .320). Lastly, there were no main effect of triangle when comparing triangle 1 (M = .430, SD = .157) and triangle 2 (M = .429, SD = .134) in arrival error (F(1,32) = .002, p =.963), as well as no significant main effect of triangle when comparing triangle 1 (M = .647, SD = .152) and triangle 2 (M = .603, SD = .152) in angular error (F(1,32)= 1.421, p = .242).

A post-hoc power analysis was conducted for each of the main effects on all three of the dependent variables in SPSS. The power calculation was based on the size of the sample, the statistical significance, and the effect size of each dependent variable. The observed powers for the main effect of GVS were: arrival error = .954, angular error = .886, and path variability = .387. The observed powers for the main effect of triangle were: arrival error = .453, angular error = .302, and path variability = .078. And lastly, the observed powers for the main effect of dance training (between groups) were: arrival error = .098, angular error = .255, and path variability = .063.

4.0 Discussion

The purpose of this research was to examine the effect of vestibular perturbation (GVS) on path trajectory and body rotation during spatial navigation in control participants and dancers. It was hypothesized that there would be a significant difference in the arrival error, angular error, and path variability between groups such that dancers would show significantly less error, demonstrating a main effect of training on performance.

4.1 Effects of GVS and Triangle Size

Path integration is the strategy of spatial navigation in the absence of vision involving two parameters: perception of distance and direction of locomotion (Bredin et al., 2005). Both of these parameters are measured in the triangle completion task as arrival error and angular error, respectively. When navigating throughout the environment, individuals constantly use idiothetic information from non-visual sensory organs, such as the vestibular system, in order to update their spatial location as a product of movement. Thus, it would be expected that a perturbation of the vestibular system would alter the spatial accuracy of movements and increase the errors produced during path integration. It was hypothesized in the current study that during experimental trials in which GVS was administered, there would be increased arrival and angular errors and greater path variability when completing a task of spatial navigation in the absence of visual cues. Results revealed a significant main effect of GVS on both arrival error (Figure 3-1) and angular error (Figure 3-2) across participants, but no significant effect on path variability (Figure 3-3).

Previous literature has determined that, in the absence of vision, our central nervous system (CNS) attributes a higher weight to the vestibular system in tasks of spatial navigation (Frissen et al., 2011). So in the absence of visual cues, in a task of path integration such as the triangle completion task, individuals are likely to increase the gain of the vestibular input during sensory integration. Since the vestibular system was perturbed via GVS, the CNS may have been unable to down-regulate its reliance on vestibular information (inaccurate information) to complete the task, which in turn affected the motor output. In this case, the reliance on inaccurate sensory input has caused an increase in both arrival and angular error. This explanation is further supported by the research by Campos and colleagues (2012), which demonstrated that vestibular information contributes to distance perception in the absence of visual input by estimating the distance travelled (Campos et al., 2012). It is possible that arrival error in the current study was significantly worse when GVS was administered because vestibular input, which is normally used to estimate the distance travelled and help guide individuals back to their initial position, was inaccurate due to the perturbation of GVS. In the absence of vision, vestibular information is an important source of input that greatly contributes to our spatial navigation abilities. Thus, when this sensory input is perturbed, it reduces an individual's ability to accurately navigate throughout their environment.

With regards to angular error, our hypotheses line up with the results, such that there was a significant difference between the control condition without GVS (NGVS) and both experimental conditions with GVS (GVSaway, GVS toward) (Figure 3-2). However, the results of arrival error showed that when GVS was administered towards the direction of the turn, performance was significantly different from both the condition with no GVS and when GVS was administered away from the direction of the turn (Figure 3-1). Since the effects of GVS on spatial navigation have not been thoroughly discussed in previous literature, it is difficult to postulate why arrival error was significantly greater in conditions when GVS was administered in the direction towards the turn compared to away from the turn. One possible explanation for this difference could be generated from the previous research stating that there is an additive effect of visual and vestibular perturbations during locomotion (Carlsen et al., 2005; Kennedy et al. 2003). When vestibular and visual perturbations were applied at the same time in a congruent direction, the resulting perturbation was approximately equal to the summation of the independent perturbations. When they were applied in opposing directions, the visual and vestibular perturbations counteracted each other, producing smaller deviations in path trajectory. Although a body rotation is not a visual perturbation, the movement is still perturbing the body while the individual attempts to maintain stability. It is possible that the additive effect of visual and vestibular perturbations could also be applied during physical and sensory perturbations. This would explain why, when the body rotation was in the same direction as the GVS current, there was a larger arrival error during the task. The combination of the physical and sensory perturbation could be producing an additive effect on the distance estimation of path trajectory, causing greater errors when the perturbations are congruent. Future studies should aim to further understand how physical and sensory perturbations work together to control locomotor trajectory, specifically in tasks of spatial navigation.

The results of this study have also shown a difference in the effect of GVS on performance with respect to the dependent variable. When looking specifically at the experimental conditions administering GVS (GVSaway, GVStoward), there was a significant difference between conditions in arrival error (Figure 3-1), but not angular error (Figure 3-2). Previous research has indicated that during tasks of path integration, distance and angular components are processed by separate mechanisms (Berthoz et al., 1999; Smith et al., 2010; Worsley et al., 2001). Worsley and colleagues (2001) further explored this declaration by conducting a study that observed the arrival and angular errors during a triangle completion task comparing individuals with lesions in the right hemisphere, left hemisphere, and control participants. Although results showed that all three groups had equal absolute measures of distance estimation (no significant differences in arrival error), patients with lesions in the right hemisphere had significantly greater angular errors. This allowed the researchers to determine that heading angle is represented in the right hippocampus. Thus, differences between arrival and angular errors during GVS conditions could be attributed to the different mechanisms responsible for distance and heading. GVS may have a greater effect on the site (right hippocampus) or the processing of the angular component of path trajectory, that resulted in a greater error during path integration in the current study. This is further supported by the prior research by Berthoz and colleagues (1999), who made the distinction between distance and heading mechanisms, stating that the information is separately coded in the human brain. The researchers were one of the first to verify the activation of the hippocampus by vestibular perturbation in humans (Berthoz et al., 1999). This connection of the vestibular perturbation with the area of the brain responsible for determining heading during spatial navigation supports that GVS would have a substantial effect on the angular error during the triangle completion task. These particular studies were unable to identify the exact neural structure responsible for the processing of distance information during spatial navigation, however, more recent research has revealed that vestibular input contributes to the estimation of distance travelled (Campos et al., 2012). Thus, GVS may directly affect the distance error in the triangle completion task because it perturbs the vestibular input used for distance perception. One final possible explanation for the difference between results in arrival and angular error is the timing of the delivery of the GVS. Since the stimulus was administered prior to the final body rotation, it could have had a different effect on the angular error as opposed to the distance error. The effect of GVS on both arrival error and even path variability may have been different if the GVS was delivered after the final body rotation and just prior to the initiation of the final path trajectory. The administration of the GVS in the current study may have had more of an effect on angular error based on the delivery just prior to the final body rotation, possibly affecting the heading of the trajectory more than the distance or variability. Although more research is needed to completely understand the neural mechanisms behind the processing of distance and heading during spatial navigation, the distinction between the two mechanisms as independent of each other is enough to explain why there are differences between the two components in the results of the current study.

Since the results showed no significant effect of variability in the path trajectory of the final leg of the triangle (Figure 3-3), it can be assumed that once participants began the return to their initial position, they maintained their initial heading angle. Their path trajectory did not significantly deviate in any given direction once they began the final leg of the triangle, such that there were no significant corrections in their direction of travel. Two particular factors could have contributed to this finding: the timing of the administration of GVS and the short distance of the return. The stimulation was applied once the participants reached the second target pole, approximately 100ms prior to their final body rotation. Since the vestibular system detects angular and linear acceleration of the head, it may be possible that once the head position reached a constant velocity, the GVS did not have as significant of an effect on the variability of path trajectory. This could be due to the fact that the inaccurate vestibular input affected the final body rotation, and then the participant's deviation was actually constant once they began their path trajectory; the vestibular input remained constant and so did the angular of path trajectory. This lack of variability in path trajectory can also be seen in the findings of previous studies such as that of Fitzpatrick, Wardman and Taylor (1999) that show participants producing path trajectories that deviate from the intended direction of travel, but do not show variability within the path trajectory that was elicited (Fitzpatrick et al., 1999). This explanation supports the findings of the current study since there was a significant effect of GVS on angular error. The stimulation clearly affected the final body rotation that determined the heading angle, but once the participant began their final path trajectory, the participants generally continued in their intended direction without significant variability.

On the other hand, another explanation for a lack of significant variability in path trajectory across the conditions could be due to the short distance (approximately 3.6 metres) of the final leg of the triangle. Bent and colleagues (2002) demonstrated that after the initial onset of GVS, there were no deviations in the execution of a forward voluntary step. An effect of GVS on path trajectory was not observed until the participants reached a dynamic phase of locomotion (Bent, 2002). Since the final leg of the triangle was only 3.6m long, it is possible that the participants did not spend enough time in their constant dynamic phase of locomotion in order to exhibit any significant variability in trajectory. Participants appeared to exhibit more instability at the final body rotation, the end of the trajectory, and step termination compared to their step initiation and locomotion prior to a constant dynamic phase. However, this could not be quantified based on the fact that the camera volume was not large enough to encompass the foot markers at the end of the trajectory and at the point of gait termination. It is possible that a pathway of greater distance would have exhibited a greater variability in path trajectory that resulted in significant variability during the GVS conditions. However, the current study was limited by both the size of the lab space and camera volume, and triangles larger than 3m x 2m did not fit within the available area of data collection.

One final explanation for the lack of path variability found across conditions and participants could be related to the dependent variables and how they were quantified. Although arrival and angular error are two values that have been frequently used to determine the ability of an individual to navigate throughout space during the triangle completion task (Berthoz et al., 1999; Loomis et al., 1993; Smith et al., 2010; Worsley et al., 2001), these values are not necessarily a good representation of the effects of GVS during the task. Although an effect of GVS was expected based on the vestibular system’s contributions to tasks of path integration (Campos et al., 2012; Frissen et al., 2011), these values do not completely encompass how the body is responding to the perturbation. Using a weighted COM value in order to determine the trajectory of each participant gives a general idea of how the individual moved throughout the environment, but it is not report how GVS affected the trajectory and body kinematics of the individual. Previous literature using GVS as a vestibular perturbation have analyzed the body's response based on variables such as head roll and foot placement. A particular study by Bent and colleagues (2004) used these variables to quantify the effects of GVS when delivered across different phases of gait initiation (Bent et al., 2004). Both of these dependent variables have been shown to be significantly affected by GVS, and thus could have been a better value to measure during the current study. Head roll could have been more precisely measured by adding digitized points at each of the participant's ears, and gait kinematics could have been determined by the foot markers. However, the main focus of the rigid body on the head was the visibility of the markers in the camera volume, in order to maintain a constant visual flow in the virtual environment to avoid causing motion sickness in the participants. In addition, foot marker data was collected in the current study, but was not clean enough to generate and study specific gait kinematics of each participant due to the limited lab space and camera volume. Even so, both of these values could have given more insight of the effects of GVS on gait kinematics and body trajectory during a task of spatial navigation in the absence of visual cues. These limitations could also have affected both arrival and angular error, even though there was still a significant main effect of GVS simply based on a weighted COM value. However, the focus of the current research was to study the general path trajectory of the individuals, and a weighted COM value was still sufficient in demonstrating a main effect of GVS on both arrival and angular error. Clearly, future research should consider studying the effects of GVS during the triangle completion task by analyzing the head roll and gait kinematics (specifically foot placement) of the participants in order to develop a better understanding of the vestibular system’s contribution to spatial navigation.

Fitzpatrick and colleagues (2006) conducted a study that further supports the benefits of additional dependent measures. Researchers observed the path trajectories of individuals during blindfolded walking towards a previously seen target during a vestibular perturbation. A vestibular stimulus was applied when the head was in an upright position, tilted backwards 20-30°, and tilted forwards 20-30°. Results of the study demonstrated that when subjects received the vestibular stimulus when the head was tilted backwards or forwards, there was a greater deviation in path trajectory towards the anode compared to when the head was held upright. However, when the head was upright, there were significantly greater lateral body movements and irregular foot placement compared to the other two head conditions (Fitzpatrick et al., 2006). Since in the current study, the head was placed in an upright position in order to obtain clear visibility of the head markers within the camera volume, it would be expected that GVS would have had a more significant effect on lateral body movements and foot placement as opposed to path trajectory. It would be expected that, if there were a way to navigate throughout the virtual environment with the head pitched forwards or backwards, there would be an even greater effect of GVS on path trajectory. Thus, further supported by the research conducted by Fitzpatrick and colleagues (2006), future research should aim to either study head roll and foot placement during the upright head position, or manipulate the orientation of the head by pitching it forwards or backwards 20-30° to analyze the effects of GVS on path trajectory during a task of spatial navigation in the absence of visual cues.

The second within-subject factor assessed the difference in arrival error, angular error, and path variability between two different triangles. The reasoning behind altering the pathway that the participants travelled was to analyze the effects of different angles of final body rotation and how they were affected by GVS, as well as to reduce learning effects of the spatial parameters of the study. It was predicted that there would be no significant difference between triangle conditions in all three dependent variables. The results supported this hypothesis, such that there was no effect of triangle on error or variability of spatial navigation in the absence of visual cues. This finding is most likely because the distance travelled during the final leg of the triangle was always the same (3.6 metres) regardless of the triangle. In addition, the angles of final body rotation (56.31° or 33.69°) were close enough in magnitude that the difficulty of the sharper turn (triangle 2) did not produce significantly greater errors. If the lab space and camera volume would have been large enough to allow for triangles with side lengths that created final angles of body rotation that were more extreme, there potentially would have been a significant main effect of triangle, and it is predicted that the smaller angle (triangle 2) would have produced greater angular errors during the task.

4.2 Control Participants vs. Dancers

Although there is no current research focusing specifically on quantifying the spatial navigation abilities of dancers, previous literature suggests that expert dancers have special embodied representations of movement, and this information includes spatial parameters in an egocentric reference frame. Dancers with expert training were better able to match a specific ballet movement to an associated spatial parameter

(Blasing & Schack, 2012; Cortese and Rossi-Arnaud, 2010). Thus, it was predicted that these special representations of movement would reduce the errors demonstrated by the sample of dancers in the triangle completion task, even in the absence of visual cues. This prediction was further justified based on previous studies that have supported that athletes are better able to calibrate idiothetic cues of self-motion to more successfully navigate through space in the absence of vision (Bredin et al., 2005). However, there was no significant difference between groups in any of the dependent variables in the current study. Dancers did not perform significantly better than control participants in the triangle completion task, regardless of the GVS condition.

Previous work by Bredin and colleagues (2005) supported that, particularly at fast velocities, athletes were more accurate at performing a task of path integration. However, this task was simply straight-line walking in the absence of vision towards a previously seen target. The purpose of the current study was to determine if these previous findings carried over when the athletes were trained specifically in dance and when the task was more difficult than straight-line walking. Since the current results found that dancers were not more accurate than control participants during tasks of spatial navigation in the absence of vision, we can attempt to explain these results based on the factors discussed above: training or task difficulty. Smith and colleagues (2010) assessed the type of athletic training individuals were exposed to and how this influenced their performance in tasks of path integration. When comparing large to small spatial-scale athletes (rugby vs. martial arts) during a triangle completion task, their results revealed that rugby players were more accurate when selecting their heading angle than martial artists, but there was no difference in arrival error between groups. The results from Smith and colleagues

(2010) demonstrate that training at different spatial scales affects an individual's accuracy of path integration, and also that the distance and heading parameters can be dissociated. There is also evidence that the improvements in accuracy of path integration in larger-scaled athletes carry over to a more difficult task. Smith and colleagues (2010) attributed their findings to the fact that larger-scale athletes have greater experience calibrating idiothetic cues during locomotion and are required to make greater inferences on spatial location in the absence of visual input. Dancers are required to not only focus on their own idiothetic cues, but must also take into account what is going on simultaneously around them (i.e., infer spatial parameters of the other dancers around them), which is why dancers can be considered both large and small spatial-scale athletes. Thus, if the large spatial scale training further improves the ability of rugby players to accurately perform a task of path integration, then it is reasonable to believe that dance training would cause significantly less errors in the triangle completion task compared to non-athletes. Since this was not the case in the current study, it is possible that task difficulty was not the reason for a lack of difference between groups, but rather the type of dance training experienced by the dancers in the current sample. However, based on the current study, it is unknown as to what specific element of dance training differentiates the ability of dancers and field athletes to accurately navigate throughout space in the absence of visual cues.

Not only were the dancers expected to have reduced arrival and angular errors during the triangle completion task because of their improved path integration abilities, but it was believed that dancers rely more heavily on their somatosensory information when producing a motor output. Many studies have identified dancers as being less reliant on visual input than non-dancers when producing the appropriate motor output (Mouchnino et al., 1992). This reduced reliance on vision implies that dancers use other forms of sensory input (vestibular and somatosensory) in order to accurately produce a desired motor output. This fuelled the hypothesis in the current study that, at least in conditions without GVS, the removal of visual cues during a task of spatial navigation should have less of an effect on dancers than control participants (i.e., smaller errors in accuracy). In addition, previous research has demonstrated that during tasks of dynamic balance, dancers shift their sensorimotor reliance from vision to somatosensory input (Golomer et al., 1999; Golomer & Dupui, 2000; Simmons, 2005). In the current study, there was no manipulation of somatosensory input; in the absence of vision and with the manipulation of vestibular information via GVS, somatosensory information was the only accurate source of information available to guide locomotion. Since dancers are thought to rely more on their somatosensory input when producing a motor output, it was predicted that they would have smaller arrival and angular errors in the spatial navigation task compared to controls, regardless of GVS condition, because their dominant sensory input was still accurate. However, results from the current study did not support this hypothesis, because there was no significant difference in arrival error (Figure 3-1) or angular error (Figure 3-2) between control participants and dancers. The lack of significance in accuracy between the groups may be due to the variability in the structure and intensity of the training regimen the dancers experienced.

The limited body of research in this particular field makes it more difficult to speculate why dancers were not significantly more accurate in navigating throughout the environment. However, a study by Israel and colleagues (2005) could provide a possible explanation as to why dancers did not demonstrate smaller angular error during the triangle completion task. Researchers tested both dancers and non-dancers in a study of whole-body return in the absence of vision to analyze both egocentric and exocentric methods of return. Participants were passively rotated 90, 180 or 270°, and instructed to return to the starting position, indicated by a previously seen target. Participants had the option of using egocentric cues by inverting the rotation and retracing the pathway, or using exocentric cues by completing the rotation and continuing the direction of the turn to the full 360°. Egocentric cues included vestibular and somatosensory input (particularly proprioceptive cues) that participants gained from the initial rotation, whereas the exocentric cue was the previously seen visual target. Results of the study showed that both control and dancer participants were more likely to use egocentric cues (invert the rotation) in order to find their starting position, supporting that vestibular and proprioceptive input largely contribute to navigational tasks in the absence of vision. However, there was no significant difference between groups with respect to the accuracy of the task (Israel et al., 2005). Dancers were not significantly more accurate than untrained participants in using egocentric cues from the vestibular and somatosensory system to complete a task of whole-body return in the absence of vision. It is possible that there was no significant difference between the control group and the dancers in the current study because dancers are not any more efficient at using vestibular or proprioceptive input to update their movement throughout space than untrained individuals. Israel and colleagues suggest that there is a deficiency in the integration of vestibular information for updating one's egocentric representation with respect to an external visual target during these passive whole-body rotations (Israel et. al, 2005).

Although previous research supports that active navigation increases the amount of idiothetic information received and improves spatial learning (Chrastil & Warren; Grant & Magee, 1998), this proposed deficiency in passive body rotations could still affect the integration of information during active body rotations, and may have influenced the lack of significant difference between the control participants and dancers in the current study. If dancers are not sufficiently better at integrating vestibular information to update their position in space with respect to body rotations, then this justifies why dancers did not have significantly less angular error during the triangle completion task.

Prior to the triangle completion task, baseline testing was conducted in order to analyze any possible difference in somatosensory inputs between control participants and dancers. These tests were completed in order to potentially explain any possible group differences based on dance training. Dancers have been found to rely more heavily on their somatosensory input during locomotion (Golomer et al., 1999; Golomer & Dupui, 2000; Simmons, 2005), but very few studies have actually teased out if this shift in reliance on somatosensory information is a product of enhanced cutaneous mechanoreceptor or proprioceptive inputs. However, a particular study by Simmons (2005) controlled for cutaneous sensitivity between samples, and demonstrated that dynamic balance in dancers was more affected by proprioceptive perturbations than the control participants. These findings support the idea that when dancers shift their reliance to their somatosensory input, they are more specifically relying on proprioceptive input from their joint receptors to produce the appropriate motor output for the task at hand (Simmons, 2005). In addition, Kiefer and colleagues demonstrated that dancers have superior proprioceptive awareness compared to control participants at the hip, knee, and ankle joints (Kiefer et al., 2013).

In order to examine if improved proprioception was in fact the reason that dancers were expected to demonstrate greater accuracy in spatial navigation, two tests were conducted measuring both cutaneous mechanoreceptor sensitivity and proprioceptive awareness. These tests were meant to determine not only if somatosensory differences existed between control participants and dancers, but whether those differences were due to mechanoreceptors and/or proprioceptive inputs. The monofilament test was used to quantify the cutaneous receptor sensitivity of the participants on the plantar surface of the feet. Previous research has revealed that dancers do not significantly differ from control participants with respect to cutaneous sensitivity (Simmons, 2005). Likewise, it was expected that dancers in the current study would not demonstrate more sensitive mechanoreceptor thresholds compared to the control participants. Results of the current study were in agreement with Simmons (2005), showing no difference between groups in average plantar cutaneous sensitivity (Table 3-1), suggesting that this particular sample of dancers did not have increased cutaneous mechanoreceptor input compared to the control group during the spatial navigation task.

The second somatosensory baseline test was conducted in order to quantify the proprioceptive awareness of both the dancers and control participants. Dancers were expected to have increased proprioceptive awareness based on their training alone. The essence behind dance is to produce movements and positions of the body that have extremely specific joint placement, particularly in the legs. Dancers must constantly use their awareness of the location of their limbs in space, without visual input, to manipulate their bodies into the required joint positions. There is even an emphasis when performing in a group that your movements and joint positions must match the other dancers around you. Based on these demands, and the fact that dancers have these experiences during both training and performance, it would be expected that they would have increased awareness of where their joints were positioned in space. To assess this hypothesis, the joint angle-matching task was used to determine the proprioceptive awareness of participants by measuring their error in reproducing a target joint position in the absence of vision, similar to the task conducted by Kiefer and colleagues (2013). As previously stated, their results revealed that dancers were more accurate in reproducing joint angle positions than non-dancers, and this difference was the most pronounced at the ankle joint, indicating that dancers are better able to use proprioceptive information to sense and reproduce specific limb positions (Kiefer et al., 2013). Therefore, it was predicted that dancers would have improved proprioceptive awareness compared to control participants, demonstrating smaller errors in estimating the target joint position. However, results of the current study showed no significant difference between control participants and dancers in the joint-angle matching task, suggesting that the two groups have similar proprioceptive awareness of their ankle and knee joint positions in space (Table 3-1). This lack of significance in baseline somatosensory testing of cutaneous sensitivity and proprioception could explain why there was no significant difference between control participants and dancers during the task of spatial navigation. If the reduction of arrival and angular errors was expected based on differences in somatosensory input (cutaneous mechanoreceptor or proprioceptive) between the two groups, then we would expect that there would be no significant main effect of training when there was no difference between groups during baseline testing.

This overall lack of significance between groups during the triangle completion task could be directly related to the sample of dancers used in the study. The dancer group was a convenience sample selected based on available dancers in the appropriate age group that fit the inclusion criteria and lived in Waterloo, Ontario. This limited the sample of dancers to individuals in an area where there is no option of a standard professional training regimen. Thus, the variability in training technique, intensity, quality, and style of the dancers in the sample most likely nullified any group effects with respect to their performance in both the baseline tests and the triangle completion task. The sample group of dancers was heterogeneous with respect to the characteristics of their training regimen. In addition, all of the dancers in the current sample trained at a competitive level; no participant in the current study trained professionally, which is at a much higher intensity than competitive dance training. Thus, the quality of training may not have been at a high enough level to elicit a significant difference between groups as expected.

Another explanation as to why the current study did not find a significant main effect of training could be related to the power of the study. A post-hoc power analysis between groups generated power values of .098, .255, and .063 for arrival error, angular error and path variability, respectively. It is possible that there is limited statistical power between groups because of the sample sizes in this study ($n_{control}$= 18, n_{dancer} = 16), and this may have influenced the statistical significance of the main effect of training. A higher sample size for each group would most likely improve the power of the analysis, and increase the statistical significance between groups. The current study may not demonstrate a significant effect of dance training on the performance of the triangle completion task, but this does not necessarily mean a difference does not exist. It is possible that a greater sample size may have generated the power necessary to create statistical significance between groups with respect to the task in the current study. Future research should aim to include larger sample sizes, of dancers in particular, with increased homogeneity in order to study the main effects of training on tasks of spatial navigation in the absence of visual cues.

5.0 Conclusion

The current experiment combined spatial navigation, galvanic vestibular stimulation, and virtual reality (VR) to determine if dance training improves an individual’s ability to overcome vestibular perturbation in the absence of vision during spatial navigation tasks.

Regardless of training experience, galvanic vestibular stimulation significantly decreased the accuracy of spatial navigation in the absence of visual cues in all participants. The effect of GVS on spatial accuracy can be attributed to the fact that vestibular system plays a major role in locomotion, particularly in estimating the distance travelled in the absence of vision. Thus, GVS caused this navigational sensory input to become inaccurate, which produced an increase in both the arrival and angular errors in the triangle completion task. However, GVS did not significantly increase variability of the path trajectory during the return to the initial position. A larger data collection space and camera volume would allow for larger triangles of greater distances to be studied, which would allow individuals to reach a constant dynamic phase of movement that might be more strongly affected by the vestibular perturbation. A larger camera volume would also allow for better data collection of the foot kinematics, which would allow for the investigation of how GVS affects gait characteristics such as step length, width, variability, etc. during a task of spatial navigation. This application of the methodology would allow for a better understanding of how GVS affects the gait of an individual as they are navigating throughout the environment in the absence of visual cues.

Although it was expected that dancers would be more accurate at navigating through the environment in the absence of visual cues, there were no significant differences between their results and those of the control participants. This demonstrated that there was no effect of dancer training on the performance of the triangle completion task, with or without vestibular perturbation. However, this does not necessarily mean that dance training does not influence spatial navigation or sensory reweighting abilities. This methodology could replicate findings that support previous research on dancers increased reliance on the somatosensory system as well as their specialized spatial parameters when applied to a different experimental group. These results could simply have been due to the variability in training characteristics of the selected sample of dancers. This study could produce different findings if it were tested on a professional group of dancers with uniform ability, structure, and style. Future studies should aim to recruit dancers from a professional company, such as the National Ballet of Canada, in order to study the effects of training on expert dancers and without any confounding factors. It is also a possibility that the effects of dance training on spatial navigation are not beneficial until a later age. Older adults who have experience in dance and are still currently participating in dance training may have maintained their spatial awareness and sensory reweighting abilities across their lifespan, which could result in significantly better accuracy in the current study than a group of older adults that are non-dancers. If these findings prove true, it would be beneficial to further investigate if these qualities would reduce falls in older adults, thus stressing the importance of dance training programs across the lifespan. Future studies should aim to replicate the methodology of the current study, but apply it to a sample of professional dancers with increased homogeneity in characteristics of their training regimen, or explore the findings it produces in older adults.

The current study has given major insight into the effects of GVS on spatial navigation when visual input from the environment is removed. Future studies should aim to further analyze the training effects of professional populations on the accuracy of navigating throughout the environment, as well as the effect of GVS on gait characteristics during a task of spatial navigation. This methodology has potential to be applied to other samples and populations in order to expand the current body of knowledge and further understand the process of sensory reweighting during tasks of spatial navigation.

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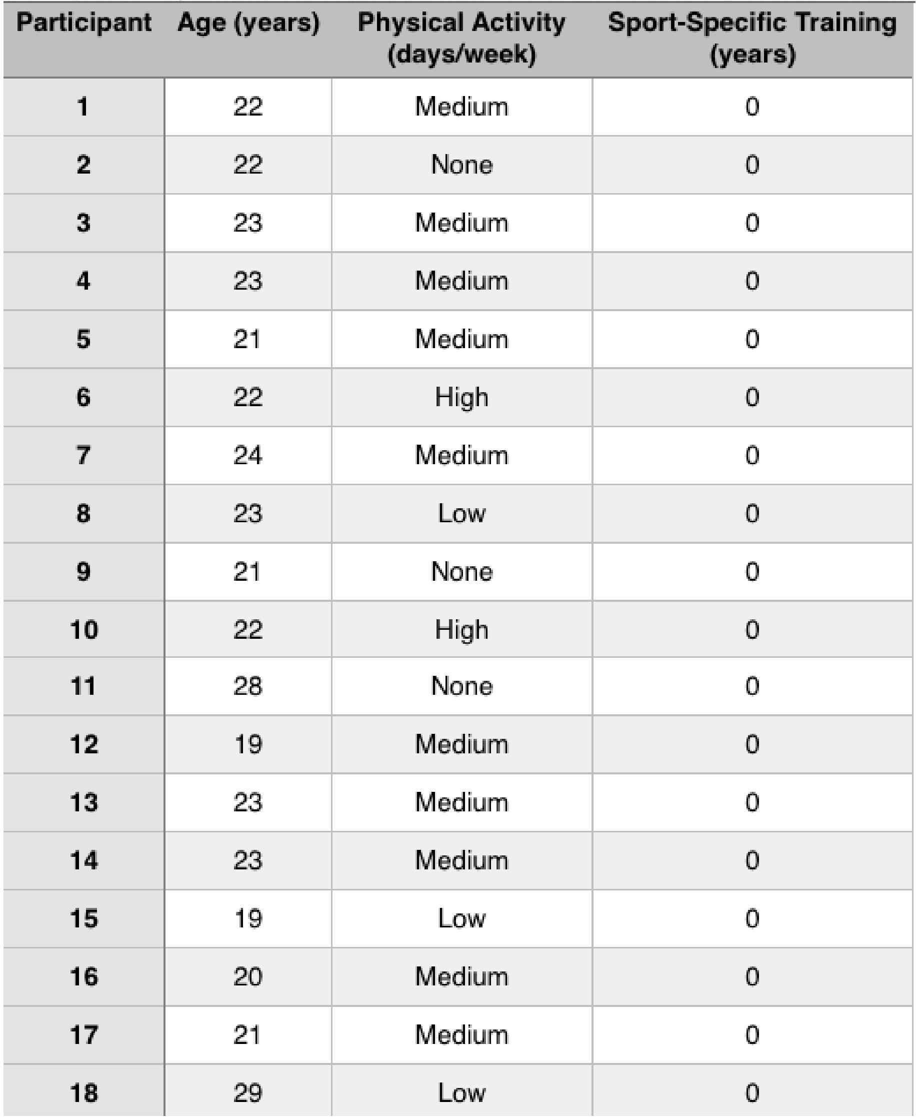
Appendices

Table A-1. Individual Participant Demographics of Control Subjects: Inclusion criteria based on the participant background questionnaire for each individual in the sample (n=18).

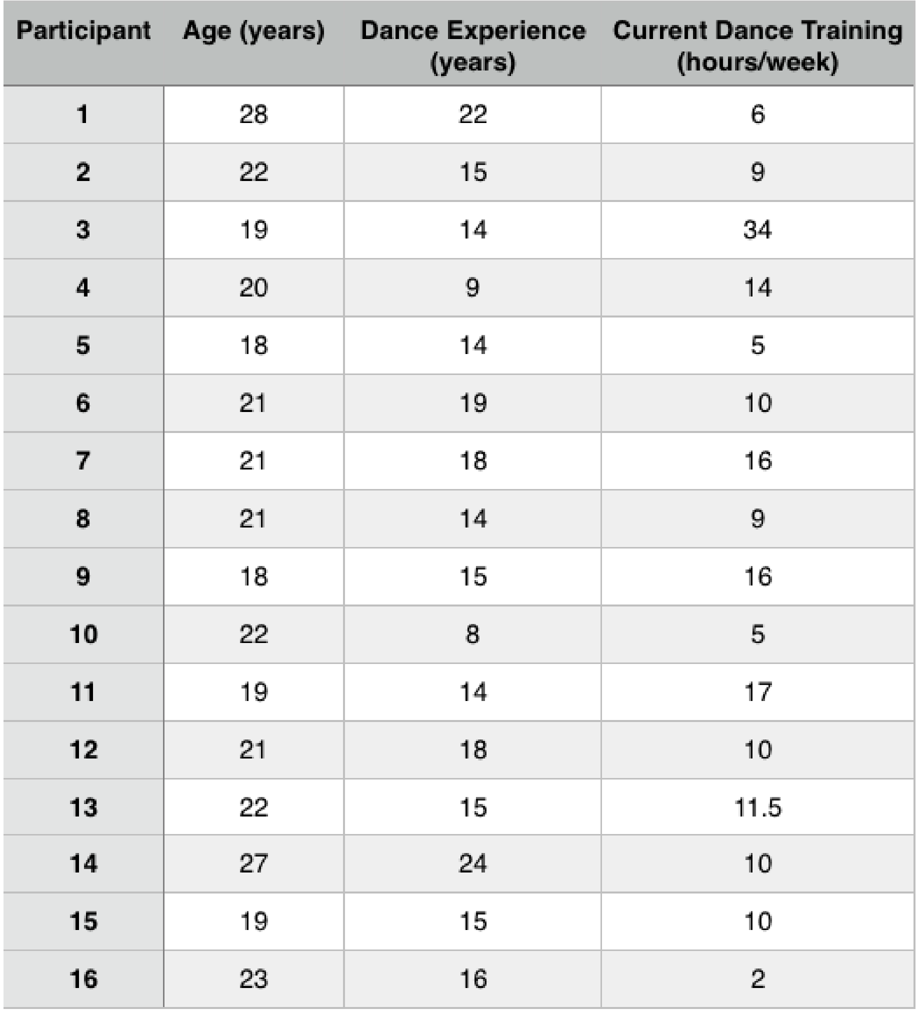


Participant	Age (years)	Physical Activity (days/week)	Sport-Specific Training (years)
1	22	Medium	0
2	22	None	0
3	23	Medium	0
4	23	Medium	0
5	21	Medium	0
6	22	High	0
7	24	Medium	0
8	23	Low	0
9	21	None	0
10	22	High	0
11	28	None	0
12	19	Medium	0
13	23	Medium	0
14	23	Medium	0
15	19	Low	0
16	20	Medium	0
17	21	Medium	0
18	29	Low	0

*Physical activity is defined as exercise that is not sport-specific: low (0-2 days/week), medium (3-5 days/week) and high (6-7 days/week) frequencies are displayed.

*Sport-specific training includes any athletic training at the varsity level or higher.

Table A-2. Individual Participant Demographics of Dancers: Inclusion criteria based on the participant background questionnaire for each individual in the sample (n=16).



Participant	Age (years)	Dance Experience (years)	Current Dance Training (hours/week)
1	28	22	6
2	22	15	9
3	19	14	34
4	20	9	14
5	18	14	5
6	21	19	10
7	21	18	16
8	21	14	9
9	18	15	16
10	22	8	5
11	19	14	17
12	21	18	10
13	22	15	11.5
14	27	24	10
15	19	15	10
16	23	16	2

*Styles of dance included in the categories dance experience and current dance training: ballet, pointe, jazz, tap, hip-hop, contemporary, acrobatics, Highland and traditional Indian dance.