THE ROLE OF CENTRAL AND PERIPHERAL OPTIC FLOW IN THE CONTROL OF UPRIGHT POSTURE

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Several studies have examined the influence of optic flow presented in the central and peripheral fields of view on postural sway, but they have yielded diverging results. Early reports suggested that movement in the periphery was associated with increased sway. Later studies have argued that central movement is equally important. The primary objective of this set of experiments was to further investigate the influence of central and peripheral optic flow on postural equilibrium. The postural sway of 20 healthy subjects (ages 21-30 years) was measured while they viewed moving visual stimuli in a computer-generated immersive environment encompassing their entire horizontal field-of-view (FOV). Two main studies were conducted. In the first, optic flow was presented at different FOVs, but the motion contained only one frequency component during each trial. In the second, the central and peripheral regions of the visual stimulus moved simultaneously but at different frequencies.

In the first experiment, the location of the optic flow stimulus significantly affected the number and size of significant postural responses. There were twice as many significant postural responses to the peripheral optic flow condition compared to the central optic flow. In addition, the magnitude of the response to the peripheral optic flow was 6.5 times greater than the response to the central flow. The number and magnitude of significant responses were also greater for higher-frequency stimuli, after accounting for quiet-stance sway components.

In the second experiment, there were 3.5 times as many significant postural responses to the peripheral optic flow stimulus as there were to the central optic flow. Likewise, the amount of sway was greater in response to the peripheral stimulus.

The results of both experiments suggest that the postural system is more sensitive to anterior-posterior optic flow in the peripheral FOV, regardless of stimulus frequency. These findings have implications for the use of virtual environments, showing that head-mounted displays with a limited central FOV do not provide the visual information most important for postural control. Furthermore, the results suggest that rehabilitation therapists should incorporate peripheral movement cues in treatment to enhance balance retraining.

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1.0 BACKGROUND AND SIGNIFICANCE

1.1 INTRODUCTION

The primary objective of this research was to investigate the effects of motion in the central and peripheral visual fields on the upright postural sway of young adults. Postural control is a complex mechanism involving the integration of the visual, vestibular, and somatosensory systems, and numerous studies over the past several decades have investigated how these systems contribute to the maintenance of postural stability. The majority of postural research has focused on the influence of visual cues in controlling upright stance. For example, it is known that subjects' sway amplitudes when their eyes are closed are about twice as large as when they view a stationary illuminated environment. Furthermore, experiments using various sinusoidally moving visual environments have reported a marked increase of sway amplitude in response to the stimulus, and this response is particularly prominent for stimulus frequencies less than 0.2 Hz.

Several theories have been developed in an attempt to characterize the functional roles of central and peripheral vision in maintaining postural equilibrium. However, it is difficult to determine which theory best reflects the available data since several different methodologies have been used, thus making it difficult to directly compare the results. While some results suggest that movement in the peripheral field of view (FOV) dominates postural control, others suggest that the central FOV is equally important in the perception of self-motion. Still another theory argues that the relative influences of the central and peripheral FOVs are dependent upon the structure of the optical information presented in the environments. Given these diverging results, further research is needed to clarify this issue.

1.2 SUMMARY OF EXPERIMENTAL METHODS AND RESULTS

The primary objective of this set of experiments was to further investigate the influence of central and peripheral optic flow on postural equilibrium. To study this, the postural sway of twenty healthy subjects (9 male, 11 female; ages 21-30) was measured while they viewed moving visual stimuli in a computer-generated immersive environment encompassing their entire horizontal field-of-view (FOV). Two main studies were conducted. In the first, optic flow was presented at different FOVs, but the motion contained only one frequency component during each trial. In the second, the central and peripheral regions of the visual stimulus moved simultaneously but at different frequencies.

The first experiment was a repeated-measures ANOVA design consisting of 3 factors: (1) stimulus region of the optic flow (central FOV, peripheral FOV, and full FOV); (2) frequency of the stimulus (0.1 and 0.25 Hz); and (3) platform condition (fixed and sway-referenced). The central stimulus was a pattern of alternating black-and-white concentric rings, and the peripheral stimulus consisted of black-and-white squares (i.e., checkerboard). For the central FOV, only the concentric rings were seen; for the peripheral FOV, only the squares were seen; for the full FOV, both were present. The peak-to-peak (p-p) stimulus amplitude was 16 cm in the anterior-posterior (AP) direction. Head and center-of-pressure (COP) position were recorded during the 90-second trials. A statistical test, used to detect the presence of a tone in white noise, determined whether there was a significant response at the stimulus frequency. Subjects who had significant responses during at least 7 of their 12 trials were considered "consistent responders." Root-Mean-Square (RMS) amplitudes of the consistent responders' AP sway were calculated at the stimulus frequency using a bandpass filter, and then normalized to their quiet-stance sway.

Head and COP movements were highly correlated with each other; therefore, analysis was restricted to the subjects' AP head motion. There were more significant postural responses to the full and peripheral optic flow (52/80 and 53/80, respectively), than there were to the central optic flow (27/80). Ten subjects were classified as consistent responders. The normalized sway amplitudes while viewing the full and peripheral optic flow were 6.5 times greater than the sway while viewing the central stimulus. The central-peripheral differences during sway-referencing were 4 times greater than when the platform was fixed. Furthermore, the normalized sway at 0.25 Hz was almost double the normalized sway at 0.1 Hz.

In the second experiment, optic flow was presented in the central and peripheral FOVs at the same time, but at different frequencies. In one stimulus the central optic flow moved at 0.1 Hz while the peripheral optic flow moved at 0.25 Hz; in the other, the frequencies were reversed. The p-p stimulus amplitude was again 16 cm, and the platform conditions were fixed and sway-referenced. A statistical test determined whether there was a significant response at either stimulus frequency. Subjects who had significant responses during ¾ of the trials were considered consistent responders. RMS sway of the consistent responders' data was calculated at both stimulus frequencies using a bandpass filter, and then normalized to their quiet-stance sway. Within each visual/platform condition, the normalized sway at the peripheral frequency was compared to the normalized sway at the central frequency using paired t-tests.

There were more significant responses to the peripheral optic flow stimulus (58/80) than there were to the central optic flow (16/80). Thirteen subjects were consistent responders. In 3 of the 4 visual/platform conditions, the normalized RMS sway at the peripheral frequency was significantly greater than the normalized sway at the central frequency.

The results of both experiments suggest that the postural system is more sensitive to anterior-posterior optic flow in the peripheral FOV, regardless of stimulus frequency. These findings have implications for the use of virtual environments, showing that head-mounted displays with a limited central FOV do not provide the visual information most important for postural control. Furthermore, the findings suggest that rehabilitation therapists should incorporate peripheral movement cues in treatment to enhance balance retraining.

1.3 SENSORY SYSTEMS INVOLVED IN POSTURAL CONTROL

Postural control is maintained by the integration of information from three sensory systems: the visual, vestibular, and proprioceptive systems. There is some redundancy between these systems, but each works optimally within a certain frequency range. Vision has been shown to be most sensitive at frequencies of sway less than 0.2 Hz (Dichgans et al. 1976; Lestienne et al. 1977; Berthoz et al. 1979). The vestibular system has two main components: the semicircular canals and otoliths. The semicircular canals function above 0.1 Hz while the otoliths work below 0.5 Hz (Nashner et al. 1989). Furthermore, the proprioceptive system is functionally important at frequencies above 1 Hz (Diener et al. 1984).

In healthy subjects natural stimulation of the vestibular system results in an actual perception that the head is moving (Paulus et al. 1984). However, stimulation of the visual system can lead to two perceptions: (1) that the self is moving through the environment, and (2) that the environment is moving around the self. A classic example of this is when you are sitting in a stationary car, and a car next to you moves forward. This motion can result in two sensations: First, you may perceive that you are moving backward and that the car beside is stationary; alternatively, you may correctly perceive that you are stationary and that the other car is moving. A similar vection phenomenon can result if you stand in a forward-moving visual environment. You may perceive that you are moving backward in stationary surroundings, which will cause a notable compensatory postural adjustment in the forward direction. Alternatively, if you realize that only the environment is moving, your postural response will be minimal.

1.3.1 The Influence of Vision on Posture During Quiet Stance

When subjects view a stationary stimulus (i.e., quiet stance sway), their upright postural sway is less than when their eyes are closed. Lee and Lishman (1975) showed this when they asked subjects to stand for 80 seconds in the presence and absence of visual inputs. During the eyes-open condition, in which they viewed a stationary room lined with a mesh structure, their sway velocity was significantly less than when their eyes were closed (Lee and Lishman 1975). Furthermore, Dornan et al. (1978) conducted a study in which healthy subjects were asked to remain upright and as still as possible for a period of three minutes (60 seconds with the eyes open, 60 seconds with the eyes closed, 60 seconds eyes open). The authors did not describe any specific visual environment for the eyes-open condition, but the mean length of the subjects' loci of postural sway was less during this condition than when their eyes were closed. This resulted in a mean Romberg ratio (sway during eyes open/sway during eyes closed) of 0.8 (Dornan et al.

1978). Other studies have shown that postural sway in the dark is about twice as large as in a illuminated environment that is viewed binocularly (van Asten et al. 1988a; van Asten et al. 1988b; Paulus et al. 1989) or monocularly (Redfern and Furman 1994).

1.3.2 Postural Sway Responses to Moving Visual Environments

Postural sway responses to moving visual scenes have been intensively studied for several years. Several experiments have used a “moving room” paradigm (Lee and Aronson 1974; Lee and Lishman 1975; Lestienne et al. 1977; Dichgans and Brandt 1978; Berthoz et al. 1979; Dijkstra et al. 1994a) in which the subject stands quietly in a fixed inertial frame while the room moves relative to this inertial frame. Such motion can be achieved by actually moving the walls of a mock room, or by providing changing visual displays that simulate such movement. By measuring the body position in the presence and in the absence of visual motion, the influence of vision on postural sway can be detected.

One of the earliest studies using the moving-room paradigm was conducted by Lee and Aronson (1974), in which they investigated the visual proprioceptive control of standing in infants (Lee and Aronson 1974). The subjects, who ranged in age from 13 to 16 months, stood in a room that was 3.6 m long x 1.8 m wide x 2 m high, facing the front wall. During each 2.5-second trial, the room moved 94 cm in the forward or backward AP direction, with a maximum velocity of 40 cm/sec. In 82% of the responses, the infants moved in the direction of the room’s motion, and in 33% of these cases they fell. It was concluded that human infants learning to stand use visual proprioceptive information about body sway in order to maintain stable posture. In addition, the visual system of infants appears to be more influential than their mechanical proprioception, which would produce a compensatory torque about their ankles, in the direction opposite of body sway.

Lee and Lishman (Lee and Lishman 1975) showed that vision functions as an integral component of the control system for maintaining stance. They placed subjects in a moving room, with the subjects facing the end wall, to which was attached a wire mesh structure to give added visual contrast. For some trials the room was driven sinusoidally in the AP direction, with an average velocity of 1.5 mm/s. For other trials the room moved irregularly back and forth within a range of 50 mm. It was found that the room's motion gives the subjects misleading visual proprioceptive information that they are swaying in the opposite direction. As a result, the subjects correct their posture by swaying in the direction of the room's motion. Lestienne et al. presented black-and-white checkered patterns to their subjects using a front screen (1.8 m x 2.4 m) and mirrors that encompassed their peripheral and inferior visual fields. The visual environment moved in the AP direction, and its velocity was constant (linear) in some trials and sinusoidally modulated in others. In response to the linear motion, the subjects increased the amplitude of their postural sway, especially at low frequencies (0.02-0.2 Hz), and in response to the sinusoidal motion, their sway decreased with increasing stimulus frequency (Lestienne et al. 1977).

van Asten et al. (1988) studied how visual information processing of a rotating visual scene affected postural responses. The subjects wore diving goggles that limited the viewing angle to about 80 degrees rotationally symmetric about the left eye, and the right eye was completely covered. Since the subject's viewing angle was limited, the visual stimulus always covered his entire visual field. The visual stimulus was a windmill pattern consisting of eight black and eight white sectors of equal size positioned alternately. In the middle a dark circular spot (diameter, 2.1 degrees) was presented to serve as a fixation point for the subject. Rotation of the scene induced postural sway movements involving medial-lateral (ML) rotations in the ankle joint. For modulation frequencies of rotation below 0.3 Hz, a clear correlation was found between the visual stimulus and postural movements in the lateral direction. The amplitude of postural movements appeared to be independent of the angular velocity of the rotation of the scene if the angular velocity exceeded 5 degrees/second for sinusoidally modulated rotations or 10 degrees/second for randomly modulated rotations (van Asten et al. 1988b).

Dijkstra et al. (1994) conducted a set of experiments in which subjects stood in front of a large translucent screen displaying a uniform density of small dots that oscillated in the AP direction. In one experiment the screen moved at 0.2 Hz with a peak-to-peak amplitude of 8 cm. In another, the screen moved at one of six frequencies within the range 0.05-0.5 Hz; the amplitude was covaried with frequency so as to keep the mean Root-Mean-Square (RMS) velocity of the wall constant at 2.22 cm/second. In both experiments, the response amplitude was close to the stimulus amplitude (i.e., the gain was close to 1) for most subjects. In the latter experiment, the gain was generally independent of the frequency (Dijkstra et al. 1994b).

1.3.3 The Influence of Somatosensory and Vestibular Inputs on Posture

In addition to examining the influence of visual motion, other studies have investigated the contribution of somatosensory and vestibular inputs on upright posture. For example, Berthoz et al. (1979) studied people's sway as they stood on a moving platform. In their experiment subjects stood erect in a mobile cart that was enclosed on all sides. They wore lightweight cardboard blinders that blocked the lateral and inferior aspects of their visual field and permitted only restricted views of the cart's ceiling. The visual scene projected in front of them consisted of a black-and-white checkerboard pattern. Three conditions of visual surround motion were used, and in each case the cart moved in the backward direction with a peak velocity of 0.5 m/sec and a peak acceleration of 0.05 m/sec^2. In the control condition, the visual surround and the cart moved at the same velocity relative to the ground, i.e. the surround was stationary relative to the cart's motion. In the first experimental condition, the visual scene motion was opposite to the cart velocity and therefore stationary relative to the ground (as in "natural" motion). In the second experimental condition, the visual surround moved relative to the cart velocity but in the same direction as the cart; relative to the ground, the image velocity was twice the cart velocity. This provided an "unnatural" condition in which visual and proprioceptive information conflicted. In both of the experimental conditions, there was a significant increase in body pitch (compared to the control condition), and the direction of sway was in the direction of image motion. Calculations of peak body pitch revealed that the effect of visual surround was about twice as great when visual surround was combined with body motion. The frequency spectrum of cart and image velocity stimuli given in this series of experiments did not exceed about 0.2 Hz, thus supporting the general idea that vision is sensitive to low frequency motion (Berthoz et al. 1979).

Ring et al. (1989) also studied the effects of visual and somatosensory deprivation on the postural sway of healthy adults. Anterior-posterior and medial-lateral sway was measured in the following conditions: (1) Standing on a force platform with eyes open and fixating on a visual target on the wall; (2) Same floor condition as in 1, with eyes closed; (3) Standing with eyes open on polyurethane foam placed over the platform, so that somatosensory inputs were less reliable; and (4) Same floor conditions as in 3, with eyes closed. In all experimental conditions (2, 3, and 4), the increase in sway was greater in the AP direction than in the ML direction.

Furthermore, the increase in sway was greater during somatosensory deprivation than with visual deprivation, and greatest when both modalities of sensory input were diminished concurrently (Ring et al. 1989).

Redfern and Furman (1994) investigated standing postural sway of healthy adults and patients with vestibular disorders in response to optic flow in the central field. The visual conditions included: sinusoidal expansions/contractions of a radially checkered stimulus, sinusoidal movements of a checkered tunnel in the AP direction, constant linear movement of the tunnel toward the subject, and vertical sinusoidal flow of a rectangular checkerboard. Each of the scenes was viewed monocularly with a 60-degree viewing field. Patients with vestibular disorders swayed significantly more than control subjects while viewing central optic flow stimuli. Sinusoidally expanding and contracting optic flow induced postural sway at the stimulus frequency for both controls and vestibular patients; however, patients showed a much larger increase in sway at the stimulus frequency. This suggests that vestibular patients are particularly sensitive to optic flow stimuli in the central region of the visual field (Redfern and Furman 1994).

Peterka and Benolken (1995) further studied how visual, vestibular, and somatosensory cues contribute to postural equilibrium. Postural sway was induced by full-field, sinusoidal visual surround rotations about an axis at the level of the ankle joints. The front of the visual scene consisted of a circular target pattern of concentric 6.5-cm-wide rings of alternating black and white sectors. The right and left sides of the scene consisted of a checkered pattern of alternating black and white rectangles, 6.3 by 20.3 cm. The influences of vestibular and somatosensory cues were characterized by comparing postural sway in normal and bilateral vestibular-absent subjects in conditions that provided either accurate (i.e., fixed-platform) or inaccurate (i.e., sway-referenced-platform) somatosensory information. It was found that in normal subjects, the amplitude of visually induced sway reached a saturation level as stimulus amplitude increased, and the saturation amplitude decreased with increasing stimulus frequency. The vestibular patients did not exhibit any saturation in their responses, suggesting that vestibular cues were responsible for the saturation phenomenon. For visually induced sways below the saturation level, the stimulus response curves for both normal subjects and vestibular patients were nearly identical. Given these results, Peterka and Benolken concluded that control subjects were not using vestibular information to attenuate their visually induced sway, and that subjects with vestibular loss did not utilize visual cues to a greater extent than control subjects. Lastly, it was found that for both subject groups, the amplitude of visually induced sway was four times greater in tests where somatosensory cues provided inaccurate versus accurate orientation information (Peterka and Benolken 1995).

Borger et al. (1999) used a visual scene based on the exact specifications followed by Peterka and Benoken (1995) in order to compare postural sway responses of healthy elderly subjects to those of young subjects. The motion of the visual environment was in the AP direction, and it varied according to four amplitudes (2.5, 5, 7.5, and 10 degrees peak-to-peak) and two visual frequencies (0.1 and 0.25 Hz). Each visual condition was tested with a fixed and sway-referenced support surface. Results showed that elderly subjects swayed more than younger subjects during all visual/platform conditions. Sway-referencing affected the elderly more than the young, and the differences between the two age groups were greater at increased amplitudes of scene movement. The results suggest that the elderly are more influenced by dynamic visual information than the young, especially when the support surface is compliant (Borger et al. 1999).

Peterka (2002) further investigated sensorimotor integration in human postural control by evoking AP body sway. He used pseudorandom rotation of the visual surround and /or support surface about an axis collinear with the subjects' ankle joints (amplitudes 0.5 – 8 degrees peak-to-peak). The visual surround had a half-cylinder shape (70-cm radius) and was lined with a complex checkerboard pattern consisting of white, black, and three gray levels. Both normal subjects and subjects with severe bilateral vestibular loss observed six conditions offering different combinations of available sensory information. The subjects' responses were highly correlated to the stimulus motion for all conditions and amplitudes. However, overall behavior in normal subjects was nonlinear because the increase in sway amplitude lessened with increasing stimulus movement. A reweighting of sensory inputs could account for this nonlinear behavior with subjects showing more reliance on vestibular cues as stimulus amplitudes increased. Since vestibular patients could not perform this reweighting, their stimulus-response behavior remained quite linear, meaning that their sway responses continued to increase in proportion to stimulus amplitude (Peterka 2002).

1.4 THE INFLUENCE OF PERIPHERAL AND CENTRAL VISION ON POSTURAL EQUILIBRIUM

Several postural control studies have focused their investigations on the functional roles of movement in the central and peripheral FOVs in the perception of self-motion and stabilization of posture. However, it is difficult to directly compare the results of these studies since they have used a wide variety of methodologies. For example, there is no standard designation for central and peripheral vision, but researchers generally agree that central vision is approximately a 30-degree viewing diameter, and peripheral is the viewing region beyond this (Brandt et al.

1973; Paulus et al. 1984; Bardy et al. 1999). Bardy and colleagues (1999) divided the theories of the role of central and peripheral vision in the control of posture into three categories: peripheral dominance, retinal invariance, and functional sensitivity.

1.4.1 Studies Supporting the Peripheral Dominance Hypothesis

The peripheral dominance hypothesis states that peripheral vision is most important in the perception of self-motion. One of the earliest studies to support this hypothesis was conducted by Brandt et al. (1973). In this experiment subjects sat in a chair located in the center of a closed cylinder that rotated about its long axis at various constant speeds ranging from 10-360 degrees/sec. The visual stimulus was comprised of vertical black and white stripes subtending 7 degrees of visual angle. It was found that with the periphery blocked, exposures up to 60 degrees of visual angle of flow to the central retina and fovea produced little or no perceived self-motion. In the periphery (with the center blocked out) even much smaller exposures yielded strong sensations of rotation (Brandt et al. 1973).

Johansson (1977) also supported the peripheral dominance paradigm. In his experiment, subjects viewed a vertically moving random pattern of black dots on a white background. The size of the dots was about 2 degrees of visual angle, and the black-to-white ratio was about 1:4. In one experiment subjects viewed a flow of vertical motion presented to limited areas of their peripheral retina (45-90 degrees) while their central visual field viewed a stationary wall. Most subjects perceived themselves as sitting in an elevator moving upward or downward. Johansson concluded that peripheral motion stimulation over a few percent of the retina determines movement perception even though the rest of the retina observes a stationary stimulus. When the moving stimulus was presented to the central part of the retina, the subjects perceived object motion but did not feel like they were moving (Johansson 1977).

Amblard and Carblanc (1980) suggested that peripheral vision is dominant in controlling postural stability during quiet stance. They measured the magnitude of postural sway as subjects viewed a stationary scene with full, peripheral, and foveal vision. The subjects stood on a balance support of thick foam rubber, which was placed in the center of a vertical cylinder completely covering their lateral visual field. The visual pattern consisted of horizontal black and white stripes 1.2 cm wide, with a spatial frequency of 0.4 cycles/degree. For the foveal condition, only a circular spot with a 1.2-degree diameter was visible, and for the peripheral condition, the area excluding this spot was visible. They observed that balance was significantly impaired with foveal vision compared to full or peripheral vision, and thus concluded that foveal vision plays only a supplementary role in the maintenance of postural equilibrium. However, considering that the foveal area was so small, it is possible that the greater postural stability observed during the full and peripheral conditions resulted merely from a greater amount of retinal stimulation, regardless of the specific regions of stimulation (Amblard and Carblanc 1980).

1.4.2 Studies Supporting the Retinal Invariance Hypothesis

The second hypothesis describing the roles of central and peripheral vision in controlling posture is retinal invariance. This theory states that both central and peripheral vision are equally sensitive to the perception of self-motion. For example, Crowell and Banks (1993) examined the ability to use optic flow to judge heading at different retinal eccentricities and at different heading directions. Retinal eccentricity was defined as the angle between the fovea and the center of the stimulus, while heading eccentricity was defined as the angle between the specified heading and the center of the stimulus. Subjects were presented with two optic flow stimuli simulating translation (straight-line motion) through a cloud of random dots. The cloud was limited to a circular region 10 degrees in diameter. The mean speed of the translation was constant at 200 cm/sec when the focus of expansion was visible, but it decreased with increased head eccentricities (ranging from 0 to 70 degrees), so that the angular velocity at the center of the stimulus was constant. The subjects verbally reported whether the perceived direction of the heading in the second sequence was to the left or the right of the direction of the first sequence. Judgments were much more accurate with radial flow fields (small heading eccentricities) than with lamellar fields (large heading eccentricities), regardless of the region of the retina being stimulated. Furthermore, when radial flow was presented, judgments were more accurate when the stimulus was presented near the fovea. They concluded that the visual system is equally efficient at processing radial and lamellar flow fields, and that this efficiency is reasonably constant at all retinal eccentricities (Crowell and Banks 1993).

In addition, Andersen and Dyre (1989) found that lamellar and radial flow significantly affected postural stability when stimulation was restricted to the central visual field. Displays simulated observer motion through a volume of randomly positioned points that moved sinusoidally in either the medial-lateral (ML) or AP direction. The displays were observed binocularly through a circular aperture that limited the FOV to a 15-degree diameter. The velocity of each display varied according to the sum of four sine functions, and the average number of points visible in a display was 500. A frequency analysis of postural sway indicated that increased sway occurred at the frequencies of motion simulated in the display for both lamellar and radial optic flow (Andersen and Dyre 1989).

Bardy et al. (1999) also supported the retinal variance theory. He found that subjects walking on a treadmill while viewing a moving visual display at different retinal eccentricities had generally equivalent postural responses in the direction of the stimulation. During this experiment a front screen (22 degrees in diameter) oscillated sinusoidally in front of the subjects, displaying either radial, lamellar (horizontal), or intermediate flow patterns. These different patterns were presented at various retinal eccentricities (angles) by rotating the treadmill with respect to the front screen, and the angle of the treadmill was held constant for each trial. The subjects responded with large amplitudes of postural sway that were similar across the various flow patterns and retinal eccentricities of the stimulus (Bardy et al. 1999).

Nakamura (2001) argued that the effects of central and peripheral presentations of a moving visual pattern are equivalent. He conducted a study similar to that of Brandt et al. (1972; discussed above in support of the peripheral dominance hypothesis). The visual stimuli were two random patterns of dots (presented in the central and peripheral FOVs), which moved at the same linear speed but in opposite medial-lateral directions. The radius of the central stimulus varied between 10–45 degrees on a screen subtending 90 x 60 degrees (vert. X horiz.). In addition, the speed of visual motion varied between the FOVs in one of the experiments. The subjects held a button in each hand, and were instructed to press the one corresponding to the direction of perceived self-motion. It was concluded that vection strength is determined by the stimulus size and speed but not by its eccentricity (Nakamura 2001). These results corroborate the findings of analogous experiment in which the central and peripheral FOVs were stimulated individually (Nakamura and Shimojo 1998). However, the author acknowledged that stimulus eccentricity could be confounded with stimulus size, since a larger stimulus inevitably stimulates more of the peripheral region of the observer's visual field. Other researchers have proposed that central and peripheral vision are equally effective in stabilizing posture in a stationary visual environment, once one accounts for the size of the representation in the visual cortex (Straube et al. 1994).

1.4.3 Studies Supporting the Functional Sensitivity Hypothesis

The third paradigm describing the influence of central and peripheral vision in the perception of self-motion is the functional sensitivity hypothesis, which proposes that the peripheral retina is maximally sensitive to lamellar flow, while the central retina is maximally sensitive to radial flow. Stoffregen (1985) provided support for this theory when he used a moving room that was textured with a marble pattern of various FOVs. He observed a stronger sway response to optic flow having a largely lamellar structure presented to the retinal periphery than to more radially structured flow in the center. In a separate experiment, radial flow was presented to the peripheral retina and lamellar flow to the central retina. The result was that radial flow presented to the retinal periphery caused no compensatory sway, while lamellar flow in the central retina produced some sway (Stoffregen 1985).

In addition, the findings of Andersen and Braunstein (1985) opposed the conclusion from previous research that visual induction of self-motion requires a large area of peripheral stimulation. They demonstrated that perceived linear self-motion can be elicited by exposures of radially expanding AP flow limited to the central retina. In this study each display simulated motion of an observer through an area uniformly filled with randomly positioned dots. The visual angle subtended by the display varied between 7.5 and 21 degrees, but the change in angle generally did not influence the duration of reported self-motion (Andersen and Braunstein 1985).

van Asten et al. (1988) offered further evidence supporting the functional sensitivity theory. They presented subjects with radial and lamellar checkered patterns that moved sinusoidally in the AP direction. Postural responses were recorded while the scenes were viewed monocularly through goggles that limited the FOV to about 80 degrees rotationally symmetric about the left eye. The right eye was completely covered. They included conditions in which the stimulus patterns were covered by a 15 x 30 degree mask (horiz. x vert.). It was found that masking the central portion of a scene containing a large central radial expansion almost eliminates correlated postural responses, whereas the central masking of a moving tunnel with a large peripheral shear component had only a minimal effect. These findings suggest that both peripheral and central vision can significantly contribute to the control of postural balance (van Asten et al. 1988a).

Furthermore, Warren and Kurtz (1992) found that central vision accurately extracts radial, rotary, and lamellar flow, whereas peripheral vision extracts lamellar flow but is less sensitive to radial and rotary flow. Subjects observed unidirectional radial flow patterns of dots and dashes under three FOV conditions: 1) full, in which the entire 40 degree screen was visible; 2) central, in which only an inner circle was shown (diameter varied between 10-25 degrees); and 3) peripheral, in which only an outer ring was visible. The direction (or eccentricity) of radial flow varied between 0 to ± 4 degrees off-center, and during each trial the subjects were instructed to press one of two buttons to indicate whether it looked as if they would pass to the left or right of the target if they continued on their current path. They found that the subjects more accurately sensed the direction of the radial motion during the central condition than with the peripheral displays. Performance dropped rapidly as the eccentricity of the focus of outflow increased, indicating that the periphery does not accurately extract radial flow patterns.

Therefore, Warren and Kurtz argued that central stimulation is sufficient for the perception of self-motion, and that central and peripheral stimulation yield comparable effects when they are equated for retinal area (Warren and Kurtz 1992).

1.4.4 Limitations of Central-Peripheral Studies

The preceding literature review indicates that the conclusions drawn from central-peripheral studies are quite divergent. Several of the initial experiments seemed to support the peripheral dominance hypothesis, but more recent findings argue that central vision is influential as well, particularly in detecting radial flow. It is difficult make direct comparisons between the studies since they have used a wide variety of methodologies. There are several sources of variation, including the structure of the visual environment, the direction of the optic flow, the trajectories of the stimuli, the outcome measures, and the sizes of the FOVs.

Of the experiments cited in the central-peripheral literature, few have provided an immersive environment subtending 180 degrees of the horizontal FOV (Brandt et al. 1973; Amblard and Carblanc 1980; Stoffregen 1985), and therefore little is known regarding the relative sensitivities of the retinal regions under these conditions. Of the studies not providing an immersive environment, few employed eccentricities as great as 90 degrees (Johansson 1977; van Asten et al. 1988a; Straube et al. 1994; Bardy et al. 1999), while others restricted their stimulation to much narrower regions (Andersen and Braunstein 1985; Andersen and Dyre 1989; Warren and Kurtz 1992; Crowell and Banks 1993; Nakamura and Shimojo 1998; Nakamura 2001).

A limitation in studies using a narrow FOV is that they cannot fully assess the validity of any of the central-peripheral theories. For example, studies showing that central stimulation causes notable postural responses do not exclude the possibility that peripheral stimulation would cause even greater responses. Therefore, it is misleading to support the retinal invariance hypothesis on the basis of experiments not using an immersive environment. The experiments described in this thesis used an environment encompassing 180 degrees x 70 degrees (horiz. x vert.) FOV, thus providing the effect of a “moving room” paradigm. Such an environment is necessary to accurately assess the relative influences of central and peripheral vision in the perception of self-motion.

1.5 CORTICAL MECHANISMS OF VISUAL PERCEPTION

1.5.1 The Ventral and Dorsal Streams of the Primate Visual Cortex

Within the last thirty years, several electrophysiological, anatomical, and behavioral studies have indicated that visual information is divided into two different cortical streams. The ventral stream located in the inferior temporal cortex is mainly responsible for the identification of an object’s shape and color, while the dorsal stream in the posterior parietal cortex modulates spatial and motion vision (Ungerleider and Mishkin 1982; Van Essen and Maunsell 1983). The proposed functions of these two streams were inferred largely from behavioral evidence gathered from lesion studies. Monkeys with lesions of the inferior temporal cortex were profoundly impaired in visual pattern discrimination and recognition (Gross 1973), but less impaired in solving ‘landmark’ tasks, in which the location of a visual cue determines which of the alternative locations is rewarded. An opposite pattern of results was observed in monkeys with posterior parietal lesions (Pohl 1973; Milner et al. 1977; Ungerleider and Brody 1977; Goodale and Milner 1992).

The information coming from the two major types of retinal ganglion cells is processed differently. Parvocellular (small-diameter) ganglion cells are more prevalent near the fovea, while magnocellular (large-diameter) ganglion cells are more prevalent in the periphery (Wright and Ikeda 1974). Different ganglion cell-types project to different parts of the lateral geniculate nucleus (LGN) (Wiesel and Hubel 1966; Schiller and Malpeli 1978; Leventhal et al. 1981; Perry et al. 1984). Furthermore, stimulation of the central and peripheral retina activates the parvocellular and magnocellular layers of the LGN, respectively (Schiller and Malpeli 1978). Although these findings are mainly derived from research on non-human primates, a few studies have shown visual perception to be similar in humans and monkeys (De Valois and Jacobs 1968; Merigan 1989).

Parvocellular cells generally send information to the ventral stream visual areas, including the striate cortex (V1), the extrastriate cortex (V2), the inferior occipito-temporal cortex, and the ventral anterior striate region (V4) (Livingstone and Hubel 1987). Area V4 is retinotopically organized, and it receives information from extrastriate regions (V2 and V3), as well as the medial temporal area. From V4, shape recognition is conveyed to the inferior temporal cortex (Perrett et al. 1979; Hasselmo et al. 1989; Perrett et al. 1991).

Magnocellular neurons relay information to the dorsal stream visual areas, including V1, V2, the medial temporal region (MT), the medial superior temporal area (MST), the ventral intraparietal area (VIP), and higher regions of the partietal cortex (Livingstone and Hubel 1987). Interestingly, Ungerleider and colleagues have shown that central retinal stimulation causes activation of the ventral stream while peripheral retinal stimulation causes activation of the dorsal stream (Ungerleider and Desimone 1986b; Desimone and Ungerleider 1989; Boussaoud et al. 1990; Baizer et al. 1991; Boussaoud et al. 1991). Although magno- and parvo-cellular information separates into two cortical streams (Shipp and Zeki 1985; Tootell et al. 1988; Maunsell et al. 1990), other results suggest that there is still significant cross-talk between the visual areas comprising the two streams (Maunsell et al. 1990; Merigan and Maunsell 1993; Ferrera et al. 1994; Levitt et al. 1994a; Levitt et al. 1994b). Nevertheless, since the dorsal cortical regions play the dominant role in processing optic flow, the remainder of this section will briefly summarize their functional characteristics.

1.5.2 Neuronal Processing of Optic Flow in Primate Visual Cortex

The neuronal processing of optic flow has been investigated both through physiological studies in monkeys and psychophysical studies in humans. Information from the striate cortex (V1) passes through the extrastriate cortex (V2 and V3) and onto the medial temporal (MT) and medial superior temporal (MST) areas, also referred to as V5/V5a (Zeki 1971, 1974, 1978; Van Essen et al. 1981; Albright 1984; Albright et al. 1984). From there, the motion information travels to cortical regions in the parietal cortex as part of an analysis of spatial relationships between objects in the environment and the viewer (Andersen 1995, 1997; Colby 1998). We will first describe the cortical areas responsible for visual motion processing in the macaque monkey and then give a brief review of imaging studies that have led to the identification of homologous areas in the human visual cortex. For a detailed discussion of these respective topics, refer to the following chapters: “Stages of Self-Motion Processing in Primate Posterior Parietal Cortex” (Bremmer et al. 2000), and “Human Cortical Areas Underlying the Perception of Optic Flow” (Greenlee 2000), both found in Neuronal Processing of Optic Flow.

1.5.3 Cortical Areas Responsible for Optic Flow Processing in Macaque Monkeys

Motion information from the retinae travels via the thalamus to area V1 of the macaque visual cortex (Figure 1.1). Information is sent directly from there or via a further processing stage (area V2) to the medial temporal area (MT), located in the posterior bank of the superior temporal sulcus (STS) (Ungerleider and Desimone 1986b, a; Shipp and Zeki 1989; Andersen 1995, 1997; Colby 1998). The vast majority of cells in area MT (or V5) are tuned for the direction and speed of a moving visual stimulus (Albright 1984; Mikami et al. 1986a, b; Lagae et al. 1993). Cells with similar preferred directions are clustered in columns (Albright 1984), and the directions are uniformly distributed (Albright 1989). Information in area MT is sent to the medial superior temporal (MST) and ventral intraparietal (VIP) areas. Electrophysiological studies indicate that the MST region responds selectively to visual stimuli simulating forward (expansion) or backward (contraction) motion, translational movements, as well as rotational and spiral stimuli (Saito et al. 1986; Tanaka et al. 1986; Tanaka et al. 1989; Tanaka and Saito 1989; Duffy and Wurtz 1991b, a; Graziano et al. 1994; Lagae et al. 1994; Duffy and Wurtz 1995; Lappe et al. 1996; Bremmer et al. 1999). Neurons in area VIP are also involved in the processing of self-motion information (Bremmer et al. 1995; Schaafsma and Duysens 1996; Bremmer et al. 1997; Schaafsma et al. 1997), showing specific responses for the direction and speed of optic flow (Duhamel et al. 1991; Colby et al. 1993).

The motion-sensitive part of the dorsal visual stream continues beyond areas MST and VIP in the macaque visual cortical system, as both areas send feed-forward connections to area 7a. Some neurons in 7a exhibit the classical tuning for the direction of optic flow (e.g., they prefer expansion over contraction stimuli), while others are tuned for classes of optic flow [e.g., they prefer radial optic flow (expansion and contraction) over rotational optic flow (clockwise and counterclockwise)] (Bremmer et al. 1994; Read and Siegel 1997; Siegel and Read 1997). Although visual information is largely segregated between the ventral and the dorsal pathways, the anterior part of the macaque superior temporal polysensory area (STPa) is a region where signals from both cortical streams converge. STPa receives input from the inferotemporal area (TEO) in the ventral stream and from areas MST and 7a in the dorsal stream (Boussaoud et al. 1990), and it has been reported that most STPa neurons respond only to visual motion originating from movements of external objects rather than to retinal stimulus motion caused by a movement of the animal (Hietanen and Perrett 1996a, b).

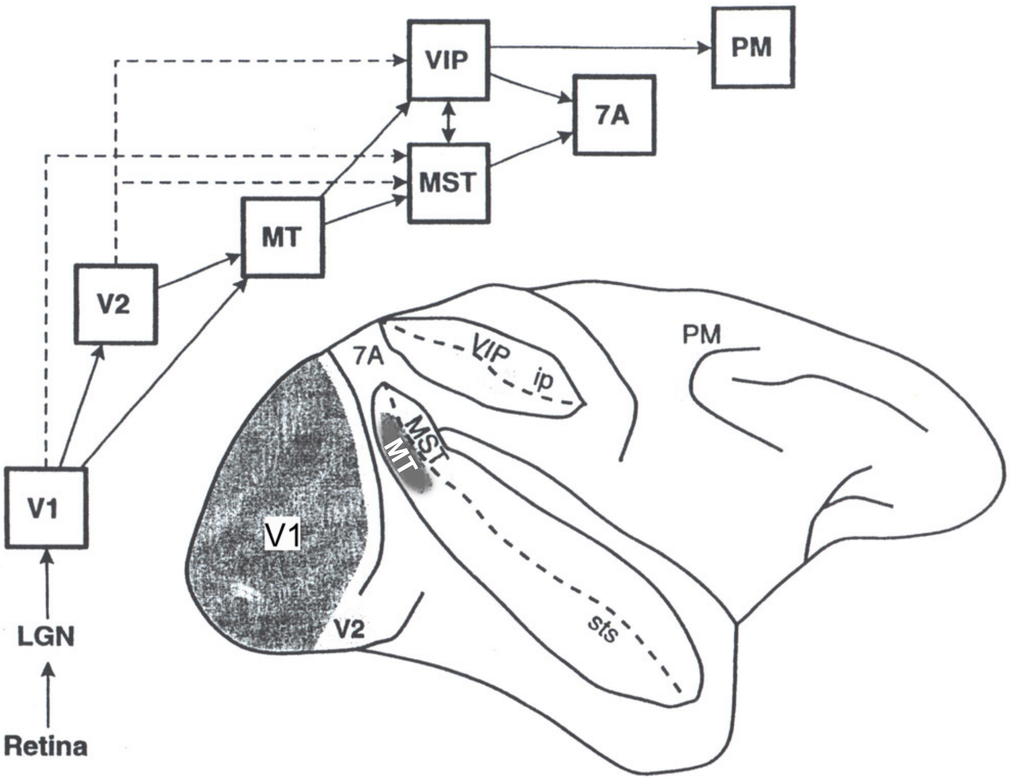


Figure 1.1. Adapted from: Bremmer, F. (2000). Stages of Self-Motion Processing in Primate Posterior Parietal Cortex. Neuronal Processing of Optic Flow. M. Lappe. San Diego, Academic Press: 175. Motion sensitive areas in the dorsal part of the visual cortical system in monkeys. The panel in the lower right shows a lateral view of a right cerebral hemisphere. The superior temporal sulcus (sts) and the intraparietal sulcus (ip) are unfolded to show the location of areas buried within the sulcus. The panel in the upper left depicts schematically the information flow from the retina via the lateral geniculate nucleus (LGN) to the primary visual (or striate) cortex (V1) and extrastriate areas (V2). From there, visual information travels to higher-order motion-sensitive regions, including the medial temporal (MT), medial superior temporal (MST), and ventral intraparietal (VIP) areas, as well as Brodmann's area 7a and the premotor cortex (PM). Arrows indicate existing connections between areas, while dashed lines indicate weak connections.

1.5.4 Cortical Areas Responsible for Optic Flow Processing in Humans

Various neuroimaging studies have allowed for the non-invasive investigation of cortical responses to optic flow in humans. Through the use of such methods, it has been shown that the human visual cortical system contains two functionally specialized parallel pathways, which are separated topographically into a more ventral and dorsal region (Haxby et al. 1991; Zeki et al. 1991; Tootell et al. 1996). Studies using muultichannel electroencephalography (EEG) (Probst et al. 1993), magnetoencephalography (MEG) (Anderson et al. 1996), positron emission tomography (PET) (Zeki et al. 1991; Watson et al. 1993; Dupont et al. 1994), and functional magnetic resonance imaging (fMRI) (Tootell et al. 1995) have observed significant activation of the occipitotemporal and/or temporoparietooccipital junction (TPO) while subjects viewed optic flow stimuli. These cortical regions are considered to be human homologues of areas V5/V5a; however, they do not appear to be selectively active during the presentation of optic flow stimuli (de Jong et al. 1994). Instead, three other regions may form a specific optic flow processing network in the higher parietal areas of humans: the right area V3/V3a (Reppas et al. 1997; Tootell et al. 1997), a region in the right superior parietal lobule (de Jong et al. 1994; Cheng et al. 1995), and the bilateral occipitotemporo ventral surface (also known as the kinetic occipital cortex) (Dupont et al. 1994).

Lastly, Stephen et al. (2002) conducted a human imaging study that is specifically relevant to this thesis. They observed a significant difference in ventral versus dorsal stream activation in response to central and peripheral field stimulation. This was shown by a faster onset time for two dorsal stream areas - the superior lateral occipital gyrus (putative MT) and the intraparietal sulcus – in response to the initial onset of the peripheral visual stimulus. There was also a larger prevalence of dorsal stream areas active during peripheral stimulation than during central stimulation. Similar areas were active during the initial visual response as during the later sustained visual activity, with a small change in distribution form lower to higher visual areas (Stephen et al. 2002).

1.6 SIGNIFICANCE OF THIS RESEARCH

The purpose of this thesis is to investigate the role of central and peripheral optic flow in the control of upright posture. Given the inconclusive results of previous central-peripheral studies, further research is needed to clarify this issue. A limitation in many previous studies is that they did not incorporate a full FOV and therefore could not accurately assess the influence of the visual fields within immersive environments. In contrast, the experiments of this thesis utilized an immersive visual stimulus encompassing 180 degrees x 70 degrees (horiz. x vert.) of the subjects' FOV, but before they are discussed, we will describe a statistical method by which we distinguished subjects who consistently responded to the optic flow stimuli from those who did not.

2.0 DETECTING POSTURAL RESPONSES TO SINUSOIDAL SENSORY INPUTS: A STATISTICAL APPROACH

2.1 ABSTRACT

A common way for understanding sensory integration in postural control is to provide sinusoidal perturbations to the sensory systems involved in balance. However, not all subjects exhibit a response to the perturbation. Determining whether or not a response has occurred is usually done qualitatively, e.g. by visual inspection of the power spectrum. In this paper we present the application of a statistical test for quantifying whether or not a postural sway response is present. The test uses an F-statistic for determining if there is significant power in postural sway data at the stimulus frequency. Twenty subjects viewed sinusoidal anterior-posterior optic flow at 0.1 and 0.25 Hz. while their anterior-posterior head translation was measured. Application of the test showed that significant postural responses were detected at the stimulus frequency in 12/20 subjects at 0.1 Hz and 13/20 subjects at 0.25 Hz.

2.2 INTRODUCTION

A common method for assessing the sensory integration of posture is to provide sinusoidal perturbations to the different sensory modalities subserving balance. For example, the contribution of the peripheral vestibular system to the control of posture has been examined using sinusoidal galvanic vestibular stimulation (GVS) (Coats 1972; Benson and Jobson 1973; Hlavacka and Njiokiktjien 1985, 1986; Storper and Honrubia 1992; Petersen et al. 1994; Latt et al. 2003). Likewise, the influence of vision on posture has been examined using sinusoidal optic flow stimuli (Lestienne et al. 1977; Berthoz et al. 1979; van Asten et al. 1988a; van Asten et al. 1988b; Dijkstra et al. 1994a; Dijkstra et al. 1994b; Redfern and Furman 1994; Peterka and Benolken 1995; Loughlin et al. 1996; Kay and Warren 2001; Loughlin and Redfern 2001; Keshner 2003). The role of somatosensory inputs, transduced using both upper and lower extremities, has also been examined (Diener et al. 1982; Jeka et al. 1997; Jeka et al. 1998; Buchanan and Horak 1999). Typically, postural sway responses occur at the stimulus frequency, and these responses are evaluated using some outcome measure, such as the spectral power. However, not all subjects respond to these stimuli, and rarely does an individual subject respond to all stimuli (Dijkstra et al. 1994a; Kay and Warren 2001). For instance, Kay and Warren have reported that visually-induced postural responses consistently occur in 1/2 to 2/3 of subjects (Kay and Warren 2001). Despite this observation, rarely is the ability of the subjects to respond to the stimulus noted.

Clearly, a method is needed to quantitatively determine if a postural response has occurred at the stimulus frequency. It is possible that greater insight about postural control mechanisms may be reached if differences between “significant” and “insignificant” responses to any given stimulus are examined. Furthermore, recent experiments have explored the use of multi-modal, multi-frequency stimuli (Oie et al. 2002). In these cases, it would be desirable to determine if a significant response occurred at any or all of the stimulus frequencies.

The use of a statistical-based method for detecting a sinusoid in the presence of noise is well known in the signal processing literature (Percival 1994). The purpose of this report is to describe the technique and to apply this method to postural sway data elicited by sinusoidal optic flow.

2.3 METHODS

2.3.1 Statistical Test

In order to evaluate if a signal, $x(t)$, has a significant tone, $s(t)$, embedded in noise, $w(t)$, consider the following model (Percival 1994):

$$x(t) = s(t) + w(t), \quad t = 1/f_s, \dots, n/f_s \qquad (1)$$

$$s(t) = A\cos(2\pi f_k t + \phi) \qquad (2)$$

where A, f_k, and ϕ are the amplitude, frequency, and phase of the sinusoid, t is a time vector, f_s is the sampling frequency, n is the number of samples, and $w(t)$ is zero-mean Gaussian white noise. Assume that $0 < f_k < f_N$, where f_N is the Nyquist frequency ($f_s/2$). The null hypothesis is that there is not a significant component at the stimulus frequency f_k (i.e., $A = 0$).

A periodogram of the signal $x(t)$ results in a spectral density function $X(f)$. Let $j = 1, \dots, J$ form a set of non-zero frequencies such that $J < f_N$. If the null hypothesis is true and $w(t)$ is Gaussian white noise, then the $X(f_j)$ are independent random variables from a χ_2^2 distribution, multiplied by the variance term: $\sigma_{w(t)}^2/2$. An F-statistic that tests whether there is a significant component at the stimulus frequency can be constructed simply by forming the ratio of the power at the stimulus frequency to the average power at all other frequencies:

$$F_{2,2(J-1)} = \frac{(J-1)X(f_k)}{\sum\limits_{\substack{j=1,\ldots,J \\ j\neq k}} X(f_j)} \qquad (3)$$

If the ratio of the power at the stimulus frequency to the average power at the other frequencies is greater than the critical $F_{2,2(J-1),1-\alpha}$, then the null hypothesis that $A=0$ must be rejected and it is concluded that a tone is present. The critical $F_{2,2(J-1),1-\alpha}$ is explicitly known by the following equation:

$$F_{2,z,1-\alpha} = \frac{z\left(1-\alpha^{2/z}\right)}{2\alpha^{2/z}} \qquad (4)$$

where z is the denominator degrees of freedom. For reference, the critical F is tabulated for some standard data lengths and levels of α (Table 2.1). As can be seen, the critical F is more highly dependent on α than on the sample size.

Table 2.1. Critical F-value as a function of sample size (length of time series) and level of significance, α . J is the number of frequency bins obtained from the periodogram, excluding 0 and the Nyquist frequency. z is the denominator degrees of freedom.

$F_{2,2(J-1),1-\alpha}$			α						
Data length	J	$z=2(J-1)$	**0.1**	**0.05**	**0.025**	**0.01**	**0.005**	**0.025**	**0.001**
64	63	124	2.3469	3.0693	3.8008	4.7805	5.5313	6.2905	7.3073
128	127	252	2.3238	3.0316	3.7434	4.6904	5.4113	6.1362	7.1006
256	255	508	2.3131	3.0135	3.7158	4.6472	5.3540	6.0627	7.0025
512	511	1020	2.3078	3.0045	3.7023	4.6260	5.3259	6.0268	6.9547
1024	1023	2044	2.3052	3.0001	3.6955	4.6156	5.3121	6.0091	6.9312
2048	2047	4092	2.3039	2.9979	3.6922	4.6104	5.3052	6.0002	6.9194
4096	4095	8188	2.3032	2.9968	3.6905	4.6078	5.3017	5.9959	6.9136
8192	8191	16380	2.3029	2.9963	3.6897	4.6065	5.3000	5.9937	6.9107
16384	16383	32764	2.3027	2.9960	3.6893	4.6058	5.2992	5.9926	6.9092
32768	32767	65532	2.3027	2.9959	3.6891	4.6055	5.2987	5.9920	6.9085
65536	65535	131068	2.3026	2.9958	3.6890	4.6053	5.2985	5.9917	6.9081
131072	131071	262140	2.3026	2.9958	3.6889	4.6053	5.2984	5.9916	6.9079

Another case involves determining if there are postural responses at each of several stimulus frequencies, f_{k_m}. Consider the following model:

$$x(t) = \sum_{m=1,\ldots,M} A_m \cos\left(2\pi f_{k_m} t + \phi_m\right) + w(t), \quad t = 1/f_s, \ldots, n/f_s \quad (5)$$

First, one can test the null hypothesis that there are no significant components at any of the stimulus frequencies, i.e. $A_1 = \ldots = A_M = 0$. An F-statistic can be constructed by forming the ratio of the average power at the stimulus frequencies to the average power at the non-stimulus frequencies.

$$F_{2M,2(J-M)} = \frac{(J-M) \sum\limits_{m=1,\ldots,M} X\left(f_{k_m}\right)}{M \sum\limits_{\substack{j=1,\ldots,J \\ j \neq k_m}} X\left(f_j\right)} \quad (6)$$

If the ratio is greater than the critical $F_{2M,2(J-M),1-\alpha}$, then the null hypothesis is rejected and the alternative hypothesis that at least one A_m is greater than 0. Unfortunately, it cannot immediately be determined which of the multiple frequency components is greater than zero. In order to discern this, it is recommended to perform a post-hoc test using Equation 1.3 for the individual frequency components, with the following modifications:

1) f_j is not equal to any of the stimulus frequencies

2) the denominator degrees of freedom equal $2(J-M)$

2.3.2 Experimental Procedure

As noted in the Introduction, subjects may not always have a postural sway response at the same frequency as the sensory stimulus. Consequently, the technique was applied to postural sway data collected from human subjects as they viewed optic flow stimuli in a full field of view (180 deg horizontal, 70 deg vertical) immersive environment (Figure 2.1). Optic flow consisted of alternating black and white squares (15 cm x 15 cm) that moved sinusoidally in the anterior-posterior direction. Trials were conducted at stimulus frequencies of 0.1 and 0.25 Hz. In all cases, the amplitude of the movement was 16 cm peak-to-peak, and movement occurred for 90 seconds.

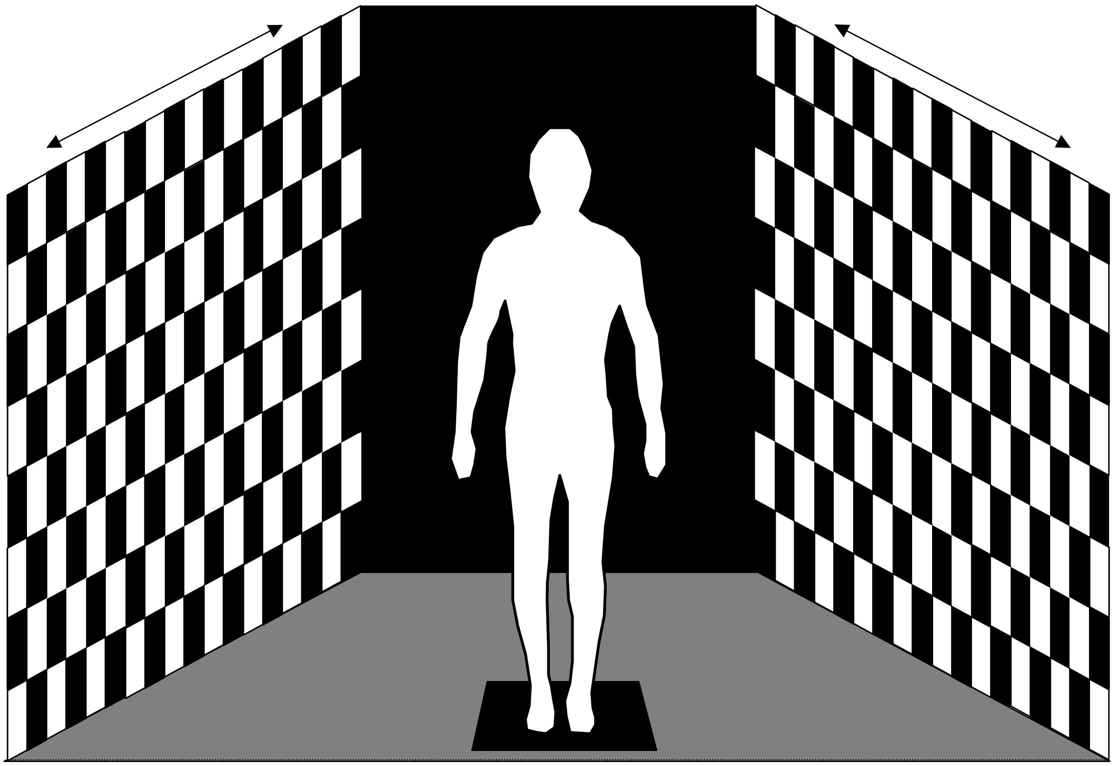


Figure 2.1. Experimental set-up of optic flow conditions in which subject is standing in an immersive environment that encompasses a field of view of 180 degrees horizontally and 70 deg vertically. The movement of the optic flow is in the anterior-posterior direction.

Twenty healthy young subjects (9 male and 11 female, mean age = 24 years, range 21 to 30) participated after providing informed consent. They were instrumented with 6-degree of freedom electromagnetic sensors (Polhemus Fastrak) placed on top of their head and around their waist. All data were digitized at 5 Hz and stored for subsequent analysis. While viewing the moving scenes, subjects were instructed to stand in a relaxed manner, looking straight ahead, with their arms crossed in front of their chest.

2.3.3 Data Analysis

The first and last 5 seconds of the trial were discarded. After applying a digital lowpass filter (Butterworth, order 4, zero phase, cutoff frequency 2.0 Hz), periodograms of the data were examined. For example, postural sway data obtained from a subject while viewing a peripheral optic flow stimulus moving at 0.25 Hz is presented in Figure 2.2. The time series demonstrates a strong response at the stimulus frequency, although the amplitude is quite variable. In the power spectrum, a peak at 0.25 Hz can clearly be seen approximately 20 dB above the floor of the noise. However, there is a 50 dB rolloff in signal power from 0 to 1.5 Hz. Because the spectrum cannot be assumed to be zero-mean Gaussian white noise, the signal must be conditioned in some way prior to applying the statistical test. Therefore, a pre-whitening filter was applied to the data (See Appendix). Figure 2.3 demonstrates the spectrum of optic flow sway data after the pre-whitening filter was applied to the data in Figure 2.2. Observe the flatness of the spectrum, which can now be modeled as zero-mean white noise. Furthermore, the peak at 0.25 Hz is preserved.

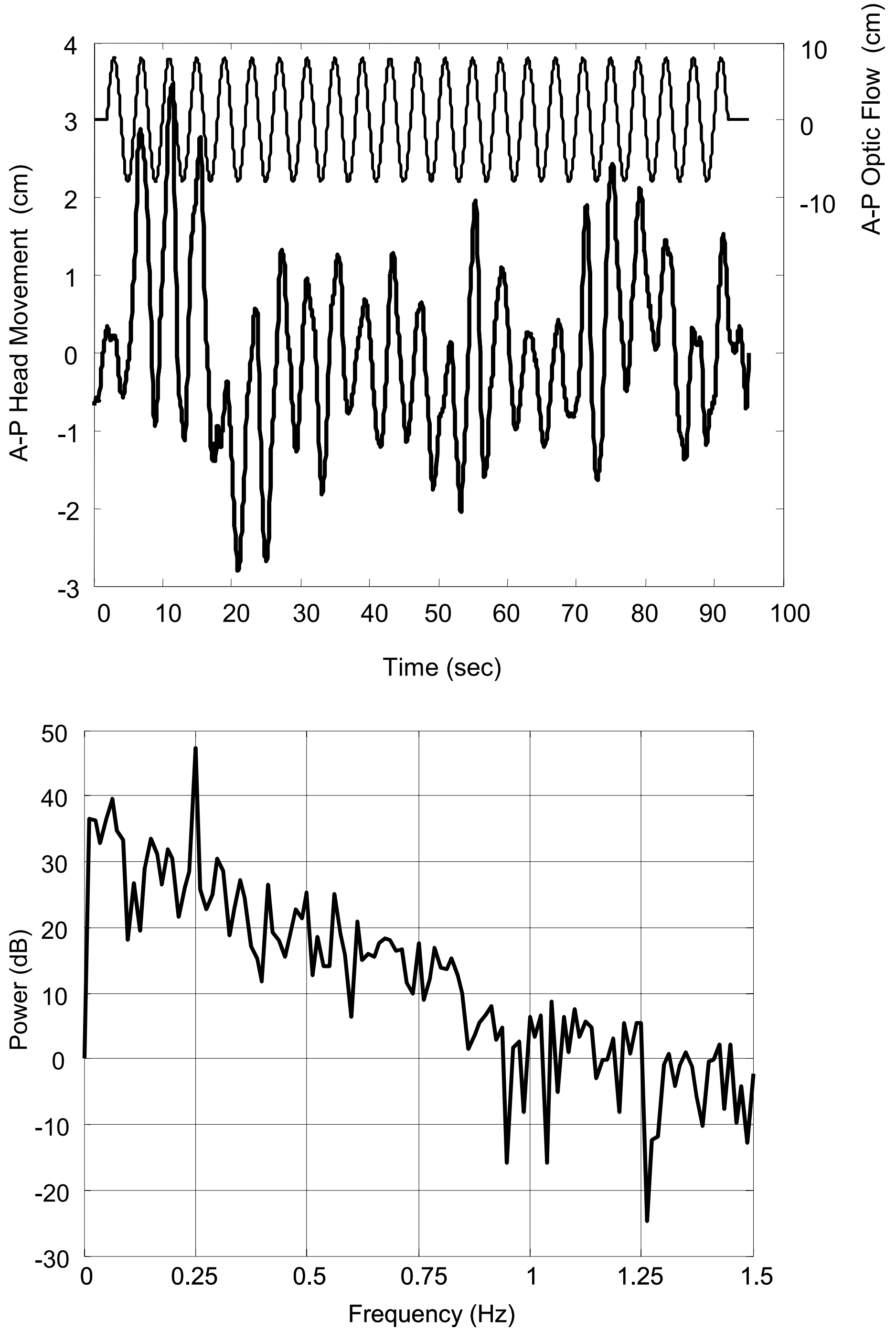


Figure 2.2. Anterior-posterior (A-P) head translation of subject A obtained while viewing the optic flow stimulus at 0.25 Hz. *Top*: Time series showing head translation (thick line) and optic flow stimulus (thin line). *Bottom*: Periodogram of head translation, before pre-whitenting filter was applied. Observe peak at 0.25 Hz.

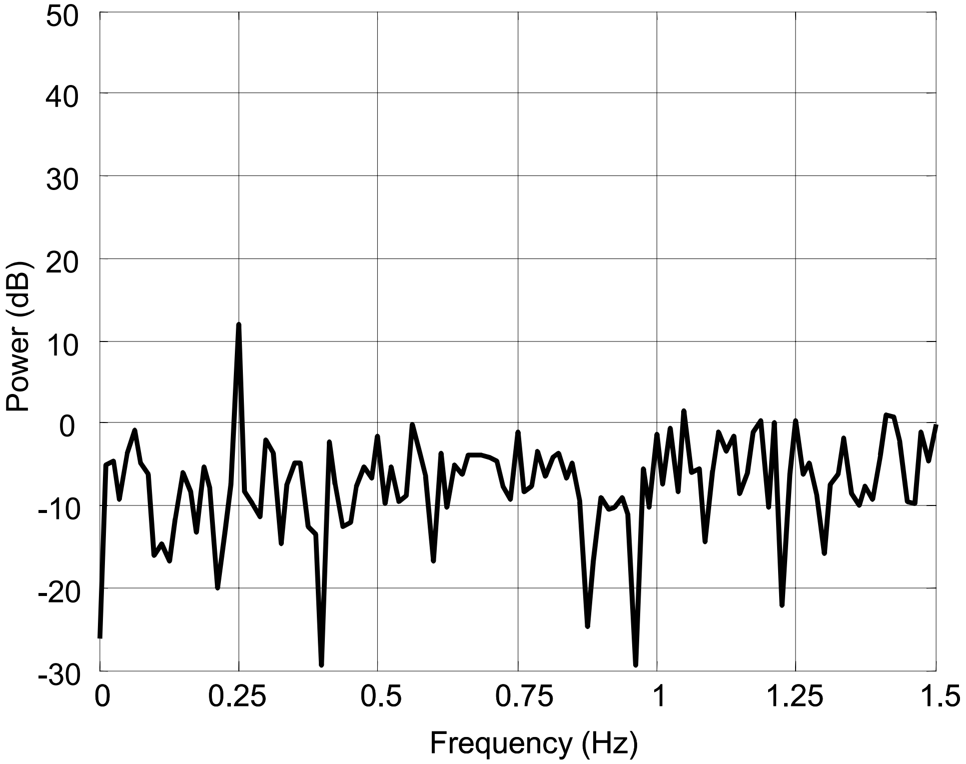


Figure 2.3. Frequency spectrum of postural sway data shown in Figure 2 (0.25 Hz optic flow). Periodogram of postural sway data after pre-whitening filter was applied. Observe flatness of spectrum with peak at 0.25 Hz maintained.

F-statistics were then computed, using the frequency range of 0.05 – 1 Hz. These were compared to a critical value of F with $\alpha = 0.05$. The number of trials that passed the threshold was counted as a function of stimulus frequency.

2.4 RESULTS

The application of this technique to data that had an obvious component at the stimulus frequency was demonstrated in Figures 3.2 and 3.3. In this example, the F-statistic was 65.6, compared to a critical F value of 3.056. In order for the method to be useful, it should also reject responses that do not appear to have a component at the stimulus frequency. Consider a different subject's response to the same stimulus (Figure 2.4). The time series appears to have significant low and high frequency components, but does not have a strong response at 0.25 Hz. The pre-whitened spectrum reflects this assertion, as there is no discernible peak at 0.25 Hz. The F-statistic for this trial was 1.8, which is less than the critical F value of 3.056.

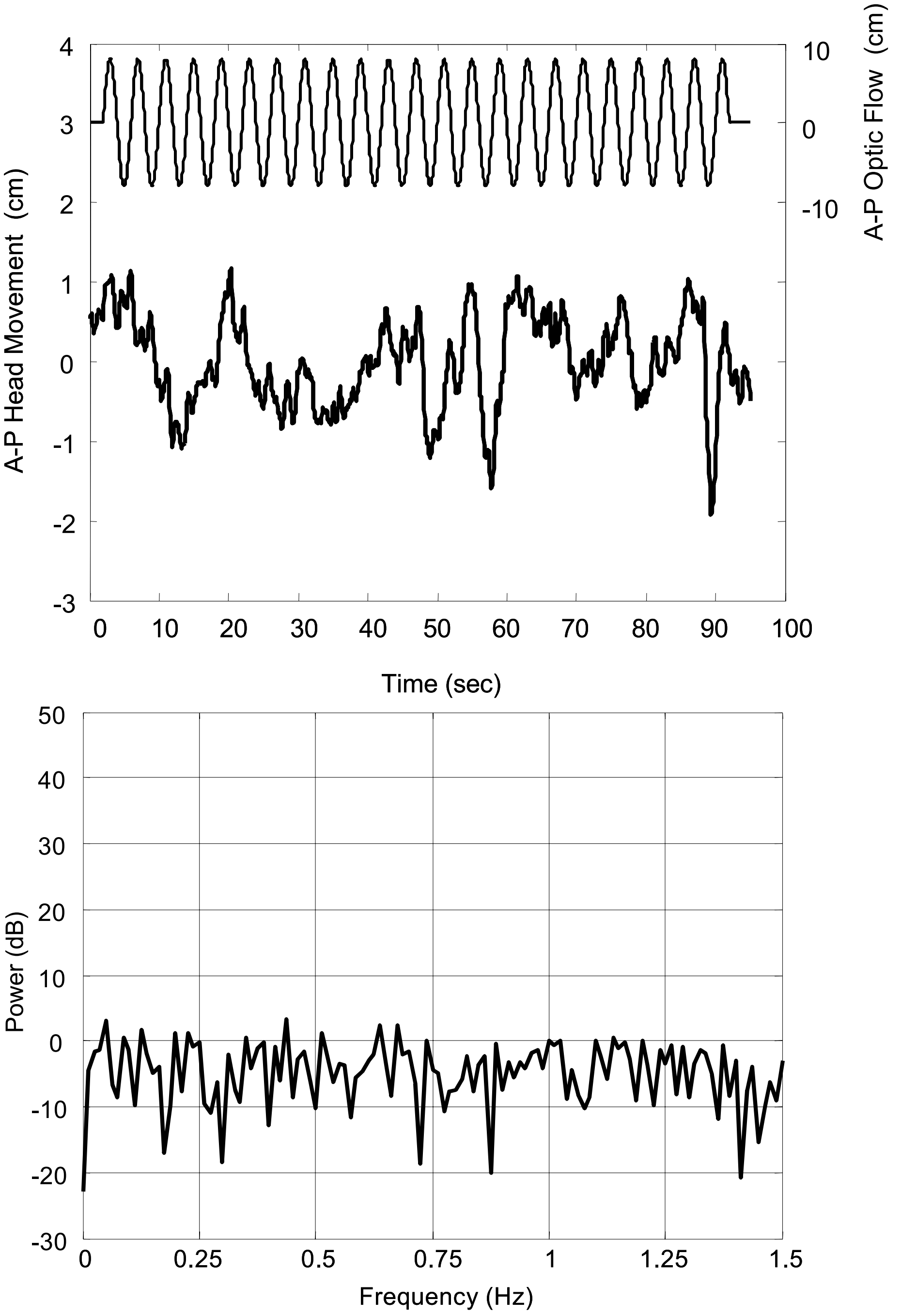


Figure 2.4. Anterior-posterior (AP) head translation of subject B obtained while viewing 0.25 Hz optic flow. *Top*: Time series showing head translation (thick line) and optic flow stimulus (thin line). *Bottom*: Periodogram of head translation, after pre-whitenting filter was applied. No observable peak at 0.25 Hz is present.

Averaged periodograms of the postural sway data (all 20 subjects) for the 2 frequency conditions are shown in Figure 2.5. Note how greater signal power is apparent at 0.25 Hz compared with 0.1 Hz. Twelve of the 20 subjects' responses were significant at 0.1 Hz, and 13/20 of the responses were significant at 0.25 Hz. In addition, the average power spectra are shown for the significant and non-significant responses, demonstrating a clear difference in how subjects respond to the optic flow.

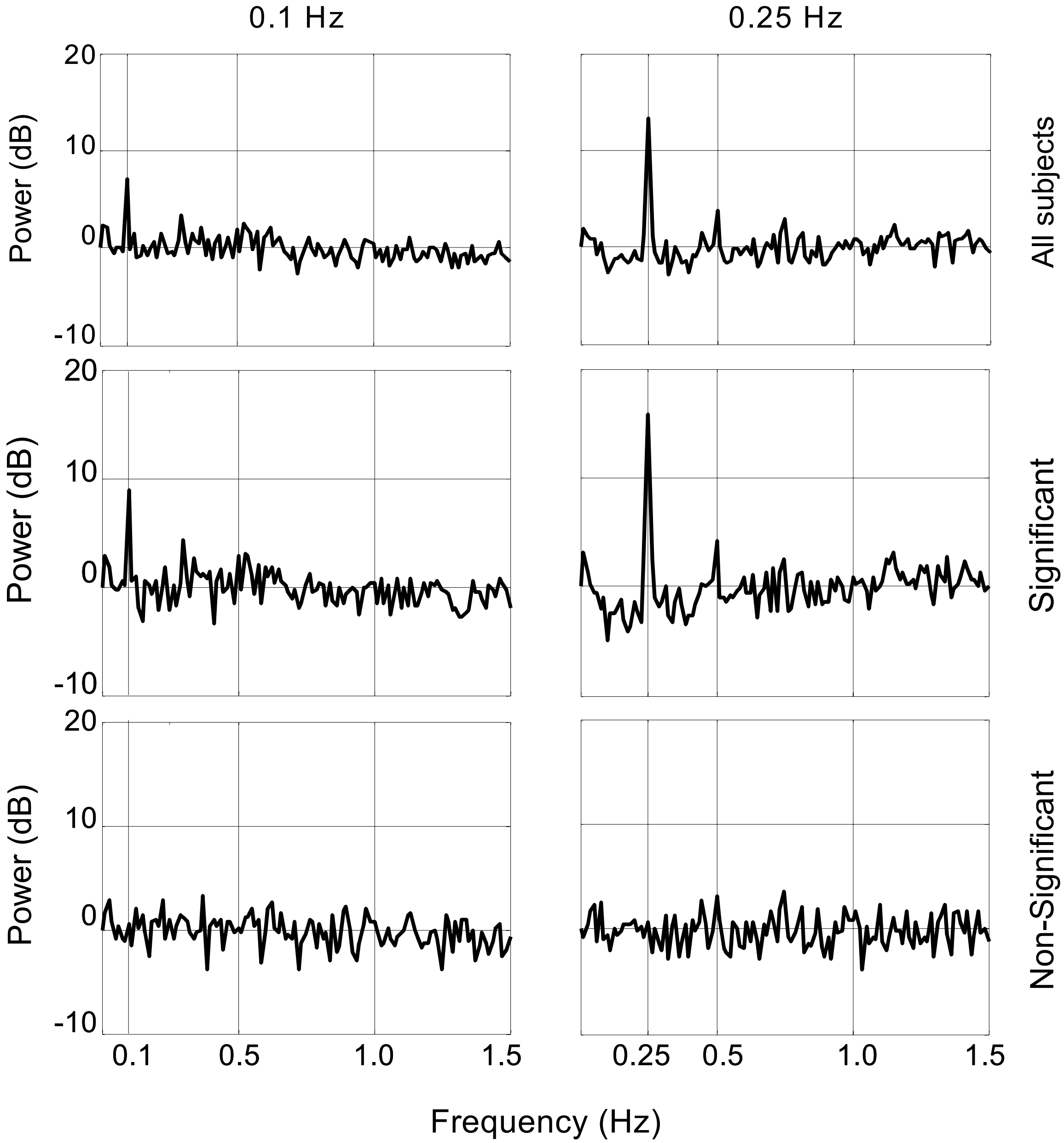


Figure 2.5. Average frequency spectra of anterior-posterior head translation, as a function of frequency. *Top*: Average spectra for all 20 subjects. A larger peak at the stimulus frequency is seen at 0.25 Hz. *Middle*: Average spectra for significant responses only (n=12 at 0.1 Hz and n=13 at 0.25 Hz). *Bottom*: Average spectra for non-significant responses only (n=8 at 0.1 Hz and n=7 at 0.25 Hz).

2.5 DISCUSSION

A reason for applying this method to postural sway data came from the authors' observations that not all subjects responded to optic flow stimuli. This experience was corroborated by the findings of Kay and Warren (Kay and Warren 2001), who were not able to elicit visually-induced postural responses in 1/3 of their subjects. The current findings are similar, given that 15/40 (38%) of the responses were not significant. In other studies examining postural responses to visual perturbations, there have been reports of subjects not responding to all stimuli (Dijkstra et al. 1994a), and reports of excluding data from subjects who did not respond to the stimuli (Delorme and Martin 1986). Consequently, fundamental questions arise regarding the use of such stimuli. 1) Is it appropriate to include response measures from data sets in which there is no apparent response to the stimulus? 2) Should the number of data sets in which a significant response was not detected be reported? 3) Can different conclusions be made if one includes non-significant responses versus not including these data?

Two viewpoints can now be considered. The first assumes that all subjects are homogeneous in that they constitute a random sample of a larger population of similar individuals (healthy controls or some clinical population). All data are included in statistical analysis. A downside to this view is that inclusion of datasets in which no response is detected may prevent a significant finding from being made by minimizing differences between groups, or by increasing variability. The second view suggests that some subjects may inherently respond differently. For example, 5 of the 20 subjects did not respond to optic flow stimuli at either frequency. Immediately one may question why these subjects did not respond. Examination of these subject differences may lead to greater insight about postural control, but also may lead to less generalizability of the findings.

One of the requirements for using this technique is that the sinusoid be embedded in white noise, i.e. has a flat spectrum in the region of interest. However, postural sway data routinely demonstrate a low-pass spectrum in which the power decreases with increasing frequency. Therefore, in order to apply this method, a pre-whitening filter was applied that flattened out the spectral response (See Appendix for details of the pre-whitening filter). In 88% of the 40 trials, linear regression confirmed that the spectra were flat in the range from 0.05 to 1.0 Hz.

A question may arise as to how much signal power is needed in order to significantly detect a response at the stimulus frequency. Therefore, simulations were performed in order to quantify what percentage of signals with a nominal signal-to-noise ratio (SNR) would pass critical F thresholds at given values of α. Pure-tone signals (0.25 Hz) with added white noise were generated in the frequency range considered to be typical for postural sway (bandwidth 0.05 – 2.0 Hz). The amplitude of the noise was adjusted in order to achieve the desired SNR. One thousand realizations were generated for the following SNRs: 0, -3, -6, -9, -12, -15, -18, -21 dB. F-statistics were computed for each of these realizations in the range of 0.05 – 1.0 Hz, and compared with the critical F values for various values of α (0.10, 0.05, 0.025, 0.01, 0.005, 0.0025, 0.001).

The percentage of signals (60 sec duration, .05 – 1.0 Hz bandwidth) that passed the critical F values for different levels of α are tabulated as a function of the SNR for a 60 sec signal (Table 2.2). Given a standard $\alpha = 0.05$, signals with a SNR greater than or equal to –9 dB pass all of the time. At an SNR of approximately –15 dB, 2/3 of the signals pass the critical threshold at $\alpha = 0.05$. Consequently, the test can detect relatively small signal power. If the criterion for detection was set at a more stringent level ($\alpha = 0.01$), then a signal with an SNR of approximately -12 dB would pass the same amount of time. Objective criteria (such as SNR and significance level) can be used to establish what constitutes a significant postural response.

Table 2.2. Percentage of simulated signals that have an F-statistic greater than the critical F-value, as a function of signal to noise ratio (SNR) and level of significance, alpha. 1000 realizations of a signal were generated for each SNR.

	Alpha						
SNR (dB)	**0.1**	**0.05**	**0.025**	**0.01**	**0.005**	**0.0025**	**0.001**
0	100	100	100	100	100	100	100
-3	100	100	100	100	100	100	100
-6	100	100	100	100	100	100	100
-9	100	100	100	99	98	98	95
-12	97	93	88	78	70	62	51
-15	75	66	57	43	32	24	18
-18	53	38	27	18	11	7	4
-21	30	18	11	6	4	3	1

Postural sway is a complex biological signal, which makes it difficult, at times, to discern if a significant response has occurred due to some stimulus. The proposed statistical-based method provides an objective rule for determining if significant postural responses occur as a result of sinusoidal sensory stimuli. Consequently, the use of such a rule could form the basis of a hypothesis test that examines if a response depends upon some experimental condition. For example, the effect of optic flow stimulus frequency on the ability to detect a significant response would have been found to be not significant using the χ^2 statistic. Given the widespread use of sinusoidal perturbations in the postural control literature, this method can be an important tool for understanding the sensory control of posture.

3.0 THE ROLE OF CENTRAL AND PERIPHERAL OPTIC FLOW IN THE CONTROL OF UPRIGHT POSTURE WITHIN SINGLE-FREQUENCY VISUAL ENVIRONMENTS

3.1 INTRODUCTION

Over the past several decades, numerous studies have investigated how the integration of the visual, vestibular, and somatosensory systems contributes to the maintenance of postural stability. Much of the research has focused on the influence of visual cues in controlling upright stance. For example, it has been reported that subjects' sway amplitudes when their eyes are closed are 1.25 to 2 times as large as when they view a stationary environment (Dornan et al. 1978; van Asten et al. 1988a; van Asten et al. 1988b; Paulus et al. 1989; Redfern and Furman 1994). In addition, postural sway responses to optic flow have been studied through the use of various "moving room" paradigms (Lee and Aronson 1974; Lee and Lishman 1975; Lestienne et al. 1977; Dichgans and Brandt 1978; Berthoz et al. 1979; Dijkstra et al. 1994a), in which the subjects stand upright while the room moves relative to their inertial frame. Within these environments, subjects' sway amplitudes increase markedly, especially if their somatosensory inputs are attenuated or if they suffer from a vestibular deficit (Redfern and Furman 1994; Peterka and Benolken 1995; Borger et al. 1999; Peterka 2002).

It is important to note that stimulation of the visual system can lead to two perceptions: (1) that the self is moving through the environment, and (2) that the environment is moving around the self. A classic example of this is when you are sitting in a stationary car, and a car next to you moves forward. This motion can result in two sensations: First, you may perceive that you are moving backward and that the car beside is stationary; alternatively, you may correctly perceive that you are stationary and that the other the car is moving. A similar vection phenomenon can result if you stand in a forward-moving visual environment. You may perceive that you are moving backward in stationary surroundings, which will cause a notable compensatory postural adjustment in the forward direction. Alternatively, if you realize that only the environment is moving, your response will be much smaller. The goal of most optic flow studies is to provide a visual motion that is large enough to induce a sway response, but also subtle enough to convince the subjects that they are moving in a stationary environment. If the amplitude or velocity of the optic flow is too large, the subjects realize that only the environment is moving, in which case their postural adjustment is minimal (Stoffregen 1986).

Several optic flow studies have focused their investigations on the functional roles of central and peripheral vision in the perception of self-motion and the stabilization of posture. As a result, three main theories have developed regarding the relative influences of the different fields-of-view (FOVs) on postural control (Bardy et al. 1999). First, the peripheral dominance theory states that peripheral vision is most important in the perception of self-motion, and this has been supported by several early studies. For example, it has been reported that rotational flow presented to the central retina and fovea produces little or no perceived self-motion, while much smaller exposures to the periphery (with the center blocked out) yields strong sensations of rotation (Brandt et al. 1973). Furthermore, vertical motion presented to limited areas of the peripheral FOVs (45-90 degrees) seems to cause a strong sense of vertical vection. However, when the same motion was presented to the central part of the retina, subjects perceived object motion but do not feel like they were moving (Johansson 1977). Lastly, a study examining QS sway in response to a stationary stimulus revealed that balance was significantly impaired with foveal vision compared to full or peripheral vision (Amblard and Carblanc 1980).

In contrast to the peripheral dominance theory, the retinal invariance theory states that both central and peripheral vision are equally sensitive to the perception of self-motion; support for this hypothesis has been gained largely from experiments utilizing radial optic flow patterns. For example, heading judgments were shown to be much more accurate with radial flow fields (small heading eccentricities) than with lamellar fields (large heading eccentricities), regardless of the region of the retina being stimulated (Crowell and Banks 1993). In addition, subjects walking on a treadmill while viewing a moving visual display at different retinal eccentricities had generally equivalent postural responses in the direction of the stimulation (Bardy et al. 1999). Moreover, studies using random patterns of dots (presented in the central and peripheral FOVs), seemed to indicate that vection strength is determined by the stimulus size and speed but not by its eccentricity (Nakamura and Shimojo 1998; Nakamura 2001).

The third paradigm describing the influence of central and peripheral vision in motion-perception is the functional sensitivity hypothesis. It argues that peripheral vision is maximally sensitive to lamellar flow, while the central retina is maximally sensitive to radial flow. For instance, lamellar optic flow presented to the retinal periphery has caused greater postural sway than a more radially structured flow presented in the center. However, radial flow presented to the retinal periphery caused no compensatory sway, while lamellar flow in the central retina produced some sway (Stoffregen 1985). In another experiment, the central masking of a scene containing a large central radial expansion almost eliminated correlated postural responses, whereas the central masking of a moving tunnel with a large peripheral shear component had only a minimal effect. These findings suggest that both peripheral and central vision can significantly contribute to the control of postural balance (van Asten et al. 1988a). Lastly, the central FOV has been shown to extract radial flow patterns more accurately than the peripheral FOV (Warren and Kurtz 1992).

Experiments using sinusoidal visual environments have shown a marked increase of sway in response to stimulus frequencies ranging between 0.1 and 0.5 Hz, and within this range the response amplitude decreased with increasing frequency (van Asten et al. 1988a; van Asten et al. 1988b; Peterka and Benolken 1995). These results have led to the general conclusion that the visual system is more sensitive to lower frequencies. However, a confounding factor in this analysis is that quiet-stance (QS) sway typically exhibits low-pass characteristics, resulting in prominent low-frequency components even in the absence of a moving stimulus. Therefore, the greater moving-stance (MS) sway at lower frequencies may simply be due to typical sway components; it is not necessarily indicative of greater visual sensitivity to lower-frequency motion. In order to gauge how much subjects reacted to the visual environment, most studies also performed QS trials to compare the frequency spectrum of the subjects' QS sway with their frequency response during the moving stimulus, and some normalized the responses with respect to the stimulus amplitude (van Asten et al. 1988a; van Asten et al. 1988b). However, few studies normalized the subjects' sway responses at the stimulus frequencies with respect to their QS sway at these frequencies; this method was implemented in the present experiment.

In summary, several of the initial central-peripheral experiments seemed to support the peripheral dominance hypothesis, but more recent findings argue that central vision is influential as well, particularly in detecting radial flow. It is difficult make direct comparisons between the studies since they have used a wide variety of methodologies. There are several sources of variation, including the structure of the visual environment, the direction of the optic flow, the trajectories of the stimuli, the outcome measures, and the sizes of the FOVs. Given the diverging results regarding the roles of central and peripheral vision in affecting postural sway, further research needs to be conducted in order to clarify this issue. The primary purpose of the current study was to investigate how anterior-posterior (AP) optic flow in the central and peripheral FOVs influences upright posture. A secondary purpose was to examine whether central-peripheral effects are influenced by the frequency of an oscillating stimulus.

3.2 METHODS

3.2.1 Subjects

Twenty healthy subjects (9 males; 11 females; mean age: 24 years; range: 21-30 years) who were naïve to the specific purposes of the experiment participated after providing informed consent.

3.2.2 Study Design

The experimental protocol was approved by the Institutional Review Board of the University of Pittsburgh. The study was a repeated measures design consisting of three main factors: (1) the field of view (FOV) of the moving stimulus (of which there were three levels); (2) the frequency of the moving stimulus (two levels); and (3) the platform (two levels). This resulted in twelve visual/platform conditions. The dependent variable used in the analysis was the Root-Mean-Square (RMS) of the subjects' anterior-posterior (AP) head sway.

3.2.3 Equipment

Postural sway data of the subject's head and pelvis were acquired in the anterior-posterior (AP) direction using the Polhemus Fastrak™ system. The head transducer was attached to the crown of the subject's head by an adjustable strap, and the pelvis transducer was attached by an adjustable velcro belt and positioned at the height of the subject's iliac crest. The data from the Polhemus transducers were digitized at a rate of 20 Hz and stored on a computer for subsequent analysis. Center-of-pressure (COP) data were also recorded at 100 Hz from a moveable NeuroTest™ force platform, which could rotate about an axis collinear with the subject's ankles.

The subjects were surrounded by three contiguous screens encompassing 180 degrees horizontal and 70 degrees vertical FOV (Figure 3.1). Thus, the effect of the stimulus was quite similar to an immersive "moving room" paradigm (Lee and Aronson 1974; Lee and Lishman 1975; Lestienne et al. 1977; Dichgans and Brandt 1978; Berthoz et al. 1979). The images were back-projected using three VREX Stereoscopic projectors (model VR-2210), with a resolution of 1024 (vert.) x 768 (horiz.). Each of the projectors was interfaced to a computer, and movement across the three screens was synchronized to a fourth computer responsible for coordinating the moving scenes and acquiring the data.

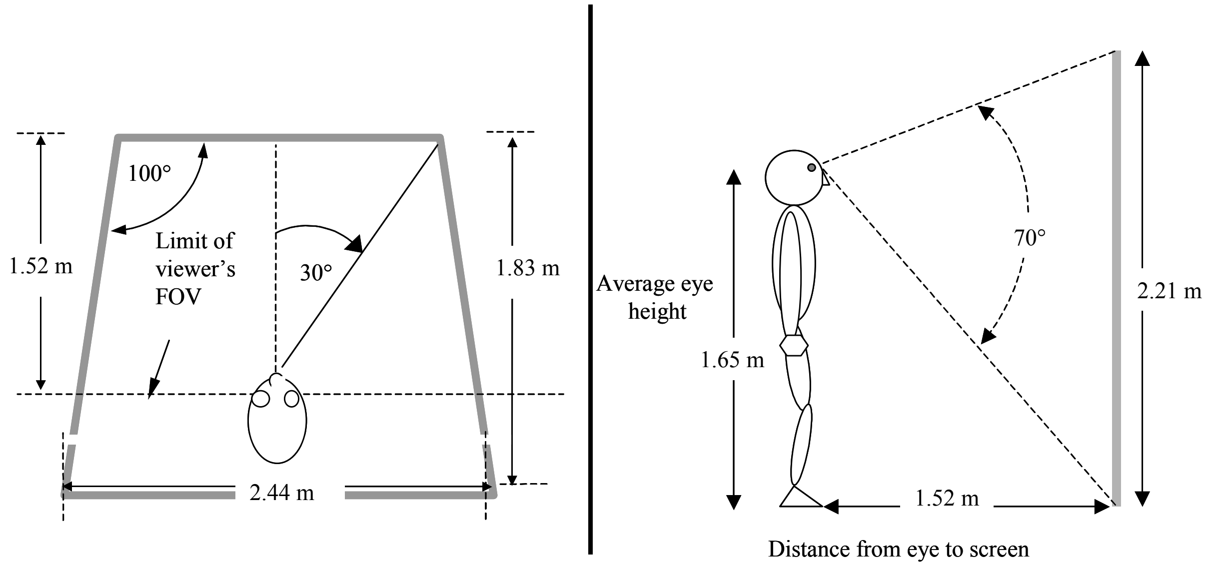


Figure 3.1. Overhead view (left) and side view (right) of experimental setup.

3.2.4 Procedure

The subjects removed their shoes and were asked to stand comfortably, looking straight ahead with their arms crossed in front of their chest. Their ankles were aligned with the platform's rotational axis. A harness system was used to prevent injury from falling during testing, but it did not impede the subjects' movement. The examiner stood directly behind the subjects to stop an impending fall, and if they became unstable and did not regain their balance within a few seconds, the trial was stopped and repeated after a momentary rest.

3.2.5 Visual Stimulus

The visual stimulus was modeled after the environment used in two previous experiments (Peterka and Benolken 1995; Borger et al. 1999). The central portion of the stimulus was a black-and-white target pattern comprised of a black center circle (5° in radius) and five alternating rings (each 5° wide), giving the entire target a diameter of 60°. The height of the target was adjusted so that its center was aligned with the subjects' eye height. The periphery of the stimulus was a pattern of black-and-white alternating squares (i.e., checkered pattern), with each square modeled to be 15 cm x 15 cm.

3.2.6 Experiment 1

For the first experiment, the visual stimuli had a peak-to-peak amplitude of 16 cm, and the initial direction of movement was always away from the subjects. The scenes varied according to two independent parameters: (1) the frequency of sinusoidal visual oscillations in the AP direction: 0.1 Hz and 0.25 Hz; and (2) the stimulus region of the optic flow: central FOV, peripheral FOV, and full FOV (Figure 3.2). For the full FOV condition, both the central and the peripheral objects were present; for the central FOV, only the target was present; and for the peripheral FOV condition, only the side checkers were present. Each subject observed all six visual stimuli for 90 seconds, during both fixed and sway-referenced platform conditions.

Sway-referencing was accomplished via the Neurotest to reduce the subjects' ability to use information from ankle proprioception to maintain upright posture. AP movements of the hip were referenced to a mean displacement that was calculated during a 30-second quiet-stance (QS) trial in which the subjects stood in the dark. The movements were converted to angular displacements and sent to the platform's rotation motor at a rate of 20 Hz. The signal was not filtered and had a lag of 0.05 seconds.

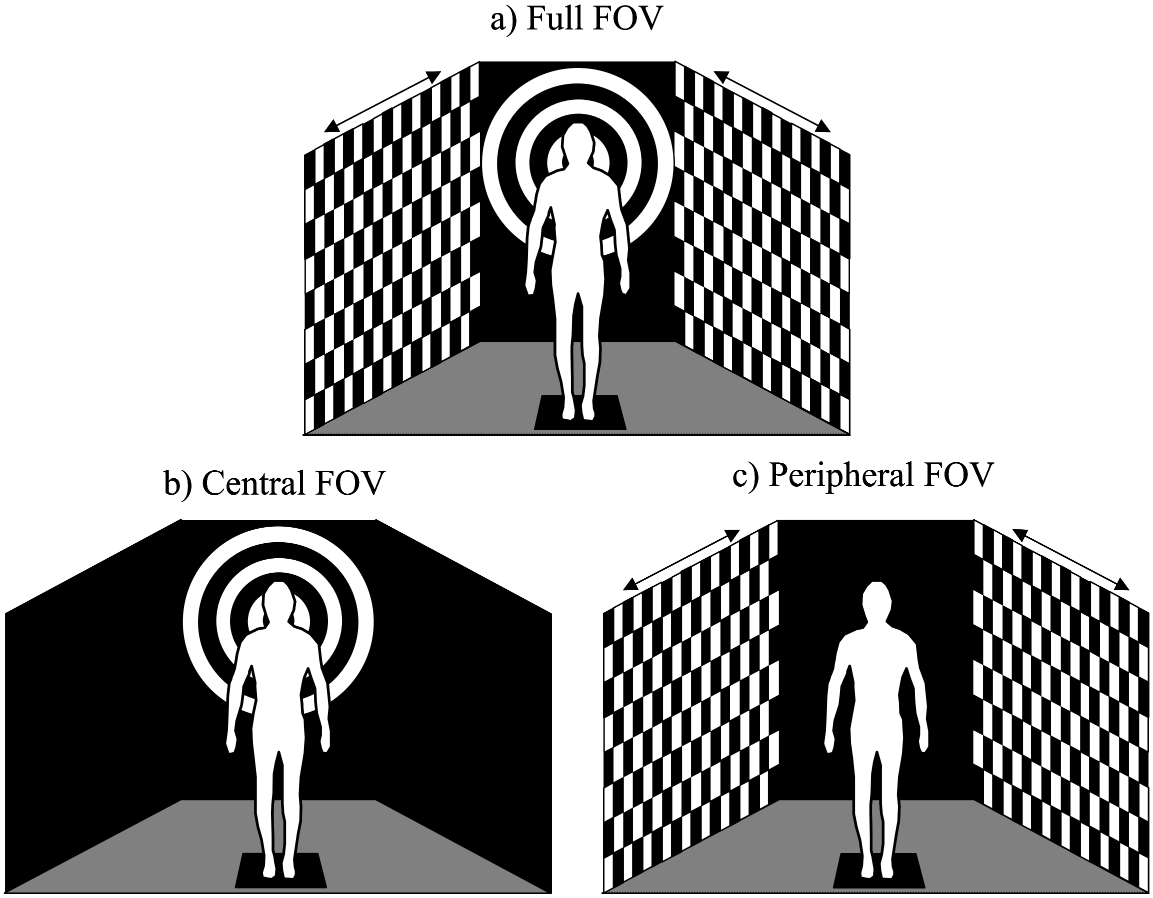


Figure 3.2. Schematics of a subject in the visual environment during the a) Full, b) Central, and c) Peripheral field-of-view (FOV) conditions. The arrows on the top of subplots a) and c) indicate the anterior-posterior direction of the oscillatory optic flow. The checkered patterns provided lamellar flow to the subjects' periphery while the concentric rings radially expanded and contracted in the subjects' central FOV.

The testing for each subject was conducted over two visits, and the trials were blocked according to platform condition. In addition to the six motion trials, three 90-second QS trials were performed during each session, in which the full, peripheral, and central FOVs were shown, but the stimulus did not move. The order of the platform conditions and the presentation of the visual scenes were randomized between subjects. After each trial the subjects rested for about a minute while still standing on the platform. They were asked to maintain the position of their feet but were free to relax their arms and bend their legs. After every three trials, they sat and rested for a few minutes, during which time their blood pressure was monitored, and they were asked to report any symptoms of motion sickness. The platform was calibrated for sway-referencing immediately preceding each set of trials. These calibrations were only necessary for the sway-referencing session, but they were performed during both sessions for the sake of consistency.

3.2.7 Data Analysis

All data analysis was performed using MATLAB (The MathWorks, Inc.). The original time series of the unfiltered head, pelvis, and COP data were highly correlated with each other; therefore, the inverted pendulum model of body motion was assumed, and analysis was restricted to the subjects' AP head movement. Root-Mean-Square (RMS) amplitudes of the zero-meaned time series were calculated before and after filtering with a 2nd-order Butterworth bandpass filter centered at the stimulus frequency (±0.05 Hz). The attenuation at the cutoff frequencies was 6 dB after the filter was implemented in the forward and backward directions to eliminate phase distortions. The magnitude responses of the filter centered at 0.1 and 0.25 Hz are plotted in Figure 3.3.

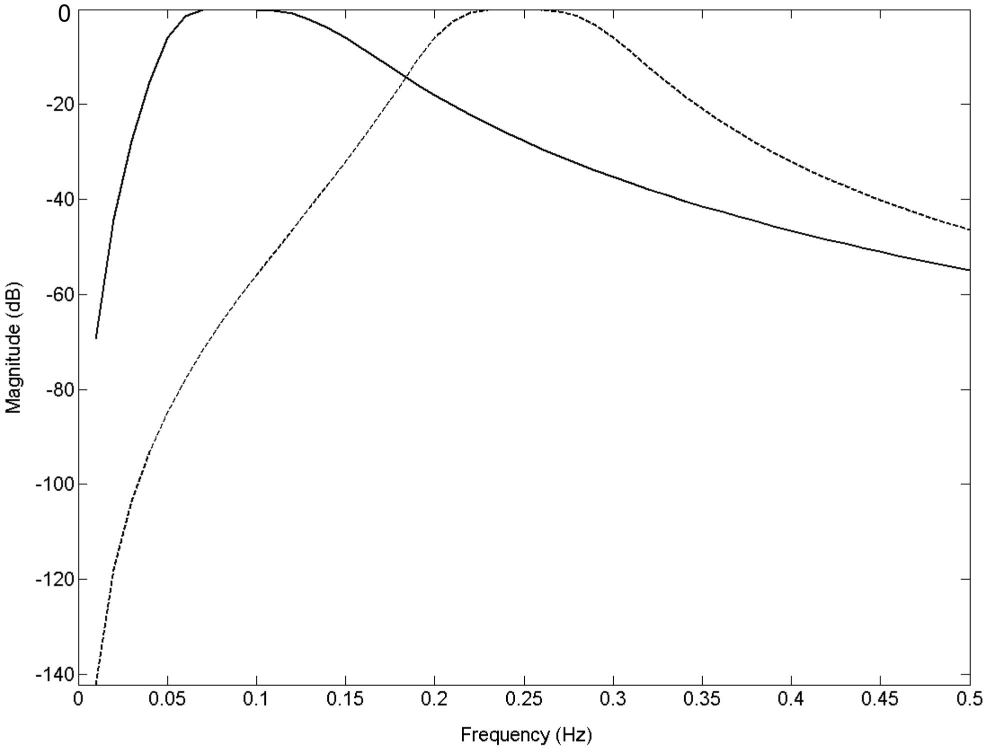


Figure 3.3. The magnitude response of the 2nd-order Butterworth bandpass filter centered at 0.1 Hz (solid) and 0.25 Hz (dashed).

3.2.8 Evaluating Subjects' Response at the Stimulus Frequency

Previous studies have shown that visual stimulation typically elicits postural responses in only one-half to two-thirds of participants (Delorme and Martin 1986; Dijkstra 1994; Warren et al. 1996). The analysis of the unfiltered RMS sway (RMS_{RAW}) included the data of all 20 subjects, even if they did not respond well to the stimulus frequency. However, before analyzing the filtered sway amplitudes (RMS_{FILT}), a statistical method was implemented to determine whether the subjects' movement contained a significant sinusoidal component at the stimulus frequency (Percival 1994). This method - referred to as the Tone Test – is described in Chapter 3, and it was applied separately to each moving-stimulus (MS) trial. Subjects who passed the Tone Test in 7 out of their 12 MS trials were considered "consistent responders," and only their data were included in the RMS_{FILT} analysis. Furthermore, the number of passes was tabulated as a function of FOV and stimulus frequency; this was done for all 20 subjects and for the consistent responders only. χ^2 statistics were used to determine whether the fixed factors affected how many subjects responded to the stimuli.

3.2.9 Normalization of RMS_{FILT} Amplitudes

Postural control mechanisms are known to collectively act as a low-pass filter, causing people to naturally sway more at lower frequencies - even in the absence of a moving stimulus (van Asten et al. 1988a; van Asten et al. 1988b; Peterka and Benolken 1995). The RMS_{FILT} amplitudes include the quiet-stance (QS) component as well as the subjects' response to the moving stimulus, but in order to evaluate how much the subjects reacted to the scenes' motion, their RMS_{FILT} values were normalized to their bandpass-filtered QS sway ($RMS_{QS,FILT}$). As already stated, the subjects viewed a stationary scene of each FOV, and from those QS trials, the $\mathrm{RMS}_{\mathrm{QS,FILT}}$ sway at the two stimulus frequencies was calculated after the data were filtered with the same bandpass filters as described above. The $\mathrm{RMS}_{\mathrm{QS,FILT}}$ amplitudes were then subtracted from the $\mathrm{RMS}_{\mathrm{FILT}}$ values calculated from the motion trials of the corresponding frequency and FOV. The result was the filtered, normalized RMS sway: $\mathrm{RMS}_{\mathrm{FILT,\ NORM}} = \mathrm{RMS}_{\mathrm{FILT}} - \mathrm{RMS}_{\mathrm{QS,FILT}}$.

3.2.10 Statistical Analysis

A 3-way repeated measures ANOVA was performed on each of the data sets - $\mathrm{RMS}_{\mathrm{RAW}}$, $\mathrm{RMS}_{\mathrm{FILT,}}$ and $\mathrm{RMS}_{\mathrm{FILT,NORM}}$ - to test for the main effects of Frequency, FOV, and Platform condition, as well as the 2-way and 3-way interactions ($\alpha = 0.05$). Lastly, twelve independent-sample t-tests were used to compare the $\mathrm{RMS}_{\mathrm{QS,FILT}}$ sway between the consistent responders and the inconsistent responders. This was done for all six of the visual/platform QS conditions, and within each condition two sets of filtered $\mathrm{RMS}_{\mathrm{QS,FILT}}$ amplitudes were compared (one for each stimulus frequency).

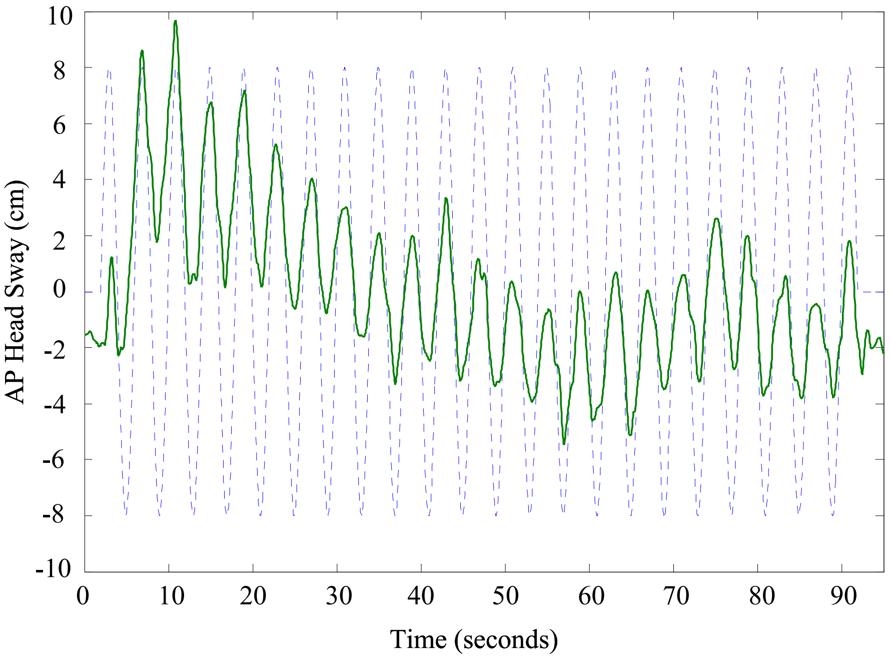
3.2.11 Calculating the Phase of the Postural Sway Response

For the trials in which the subjects showed a significant response to the stimulus, the phase difference between the sway response and the tunnel's motion – as well as the amplitude of the subjects' sway – was calculated during each cycle of the tunnel's oscillation. This was done using a least-squares regression analysis, in which a sine curve was fit to each cycle of the subjects' response. If the r^2 value computed from the regression was less than 0.5 for any cycle (indicating a poor fit), then that cycle was excluded from further analysis. If two or more cycles remained for the trial, the mean and standard deviation of the amplitude and phase were computed. In order to determine if the mean phase values were uniformly distributed within each visual/surface condition, a Rao Spacing test was performed. This test is based on the total deviation of the arcs from their expected value (Rao 1969; Batschelet 1981; Mardia and Jupp 2000; Sparto and Schor 2004). In the phase plots presented in the Results section, a positive phase shift indicates that the subject's sway response leads the stimulus, while a negative phase shift indicates that the subject's sway response lags behind the visual scene.

3.3 RESULTS

3.3.1 Unfiltered Sway Amplitudes

Figure 3.4 plots the unfiltered AP head movement of a consistent responder (top) and an inconsistent responder (bottom) superimposed onto the trajectory of the stimulus motion, during the 0.25-Hz/Peripheral-FOV/Fixed-Platform condition. Note that the consistent responder's sway is well entrained to the stimulus' motion, although the amplitude is quite variable.



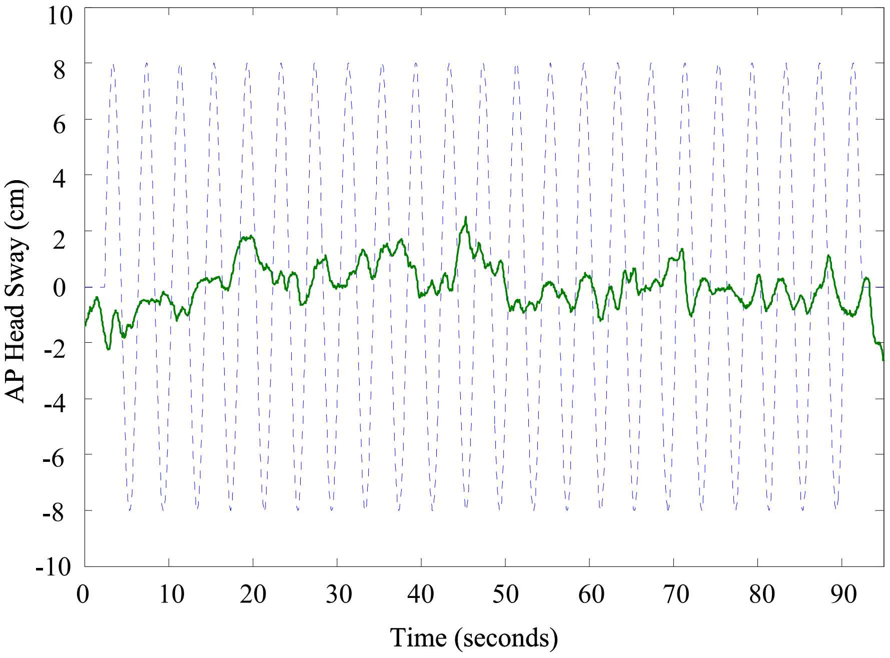


Figure 3.4. Unfiltered AP head movement (solid trace) of a consistent responder (top) and an inconsistent responder (bottom), superimposed onto the trajectory of a 0.25 Hz stimulus (dashed trace). Both time series were collected during the Peripheral-FOV/Fixed-Platform condition.

Figure 3.5 shows the mean values of the absolute unfiltered sway of all 20 subjects for all of the visual/platform conditions. The ANOVA model revealed significant effects due to all three main factors - FOV ($p = 0.01$), Platform ($p < 0.001$), Frequency ($p = 0.02$) – as well as two significant interactions: FOV*Platform ($p = 0.026$) and FOV*Frequency ($p = 0.033$). Within each platform condition, the unfiltered response to the 0.25 Hz stimuli varied across the different FOVs while the response during the 0.1 Hz movement did not (FOV*Frequency). When comparing the response to the 0.25 Hz stimulus at each platform, the drop in sway at the central condition was much greater during sway-referencing than when the platform was fixed (FOV*Platform). The unfiltered sway did not vary between the full and peripheral FOVs, but they both caused significantly greater sway than the central rings. The main Frequency effect existed because the 0.25 Hz stimulus caused a greater response than 0.1 Hz in all cases except the central/sway-referenced condition. Lastly, as would be expected, the sway-referenced condition caused greater sway than the fixed platform due to an attenuation of somatosensory inputs.

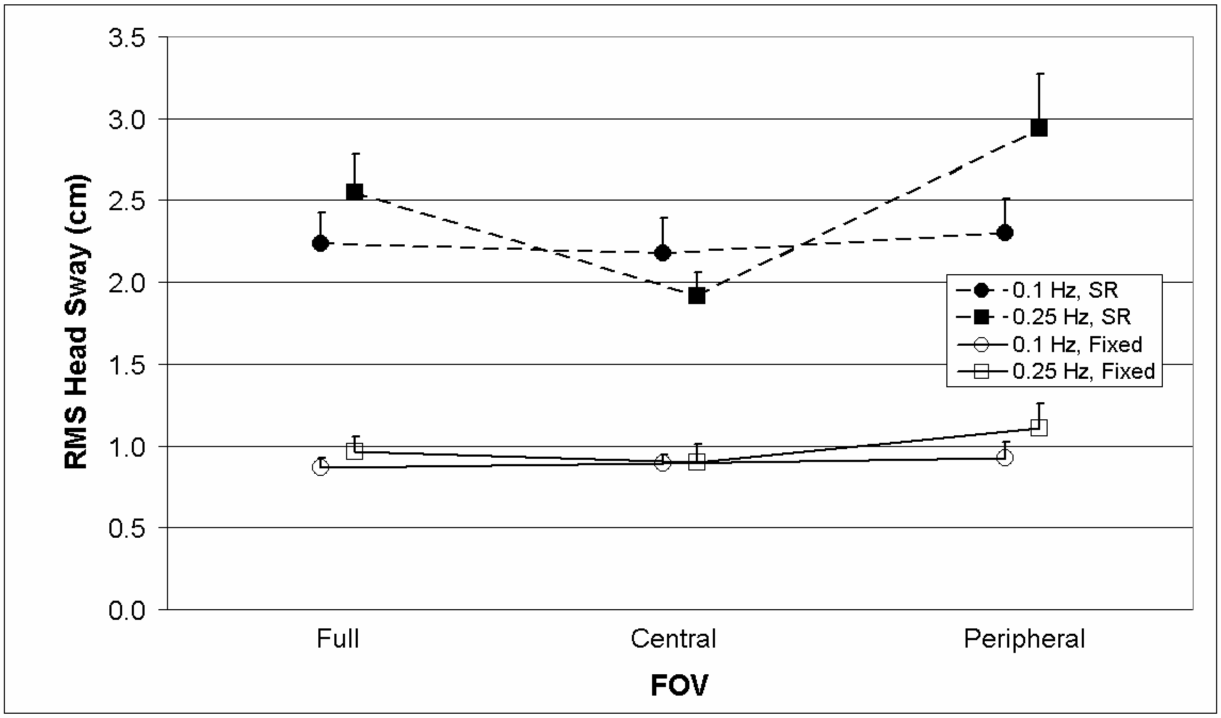


Figure 3.5. Average $\mathrm{RMS}_{\mathrm{RAW}}$ head sway during all visual/platform conditions (n = 20). Vertical bars indicate SEMs. Peak-to-peak stimulus amplitude was 16 cm. Data at 0.1 and 0.25 Hz are shifted horizontally from each other for clarity.

3.3.2 Number of Significant Responses

Table 3.1 shows the number of significant responses to the stimulus frequencies for all visual/platform conditions, as determined by the Tone Test. The number of responses varied significantly between the different FOV (χ_2^2 = 21.92, p < 0.001) and Platform (χ_1^2 = 8.15, p = 0.004) conditions, but not between the two frequencies (χ_1^2 = 3.30, p = 0.069). There were about twice as many responses to the full and peripheral FOVs, as there were during the central condition, and more subjects followed the scene during sway-referencing than during the fixed platform.

Table 3.1. Results of the Tone Test, including all 20 subjects. Number of subjects (out of 20) who passed the Tone Test in each visual/platform condition, plus the totals for the fixed factors. Each of the Platform-Frequency Totals is out of a possible 60; FOV totals, out of 80; Frequency and Platform totals, out of 120. Grand total number of trials is 240.

	Fixed		Sway-Referenced		FOV Totals
	0.1 Hz	0.25 Hz	0.1 Hz	0.25 Hz	
Full	8/20	13/20	15/20	16/20	52/80
Central	4/20	5/20	9/20	9/20	27/80
Peripheral	12/20	13/20	11/20	17/20	53/80
Platform-Frequency Totals	24/60	31/60	35/60	42/60	Grand Total: 132/240
Frequency Totals	0.1 Hz: 59/120		0.25 Hz: 73/120		
Platform Totals	Fixed: 55/120		Sway-Ref.: 77/120		

Subjects who responded to at least 7 of their 12 motion trials were designated consistent responders. Ten subjects met this criterion, and their Tone-Test results are listed in Table 3.2. For this subgroup the number of responses varied significantly with all three fixed factors: FOV ($\chi_2^2 = 25.69$, $p < 0.001$), Frequency ($\chi_1^2 = 4.10$, $p = 0.043$), and Platform ($\chi_1^2 = 4.10$, $p = 0.043$). Like the larger group, the consistently responsive subjects also attended to the full/peripheral stimulus about twice as often as they did to the central target, they were entrained to the higher frequency more often than the lower frequency, and they responded more during sway-referencing. The χ^2 results for all the subjects and for the consistent responders are summarized in Table 3.3.

Table 3.2. Results of Tone Test, only including the ten subjects who responded to the stimulus frequency during at least eight or their twelve motion trials. Number of subjects (out of 10) who passed the Tone Test in each visual/platform condition, plus the totals for the fixed factors. Each of the Platform-Frequency Totals is out of a possible 30; FOV totals, out of 40; Frequency and Platform totals, out of 60. Grand total number of trials is 120.

	Fixed		Sway-Referenced		FOV Totals
	0.1 Hz	0.25 Hz	0.1 Hz	0.25 Hz	
Full	5/10	10/10	8/10	10/10	33/40
Central	2/10	3/10	6/10	6/10	17/40
Peripheral	9/10	9/10	8/10	10/10	36/40
Platform-Frequency Totals	16/30	22/30	22/30	26/30	Grand Total: 86/120
Frequency Totals	0.1 Hz: 38/60		0.25 Hz: 48/60		
Platform Totals	Fixed: 38/60		Sway-Ref.: 48/60		

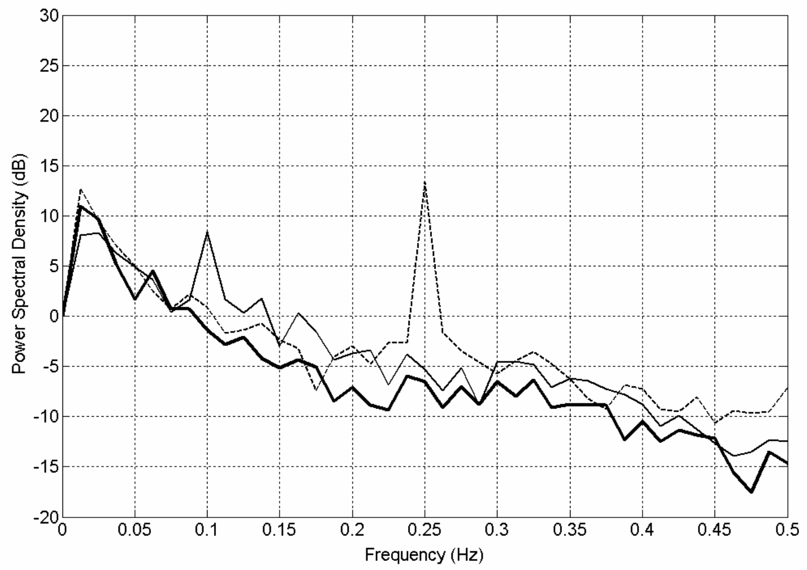
Table 3.3. χ^2 results showing whether the number of responses to the stimuli was significantly influenced by the fixed factors ($\alpha = 0.05$). Includes results for all subjects ($n = 20$) and for the consistent responders only ($n = 10$). Significant effects are indicated in **bold**.

Subject Group	Factor	Chi-Squared Value	p-value
All 20	FOV	**21.92**	**p < 0.001**
	Frequency	3.30	p = 0.069
	Platform	**8.15**	**p = 0.004**
10 Consistent Responders	FOV	**25.69**	**p < 0.001**
	Frequency	**4.10**	**p = 0.043**
	Platform	**4.10**	**p = 0.043**

The $RMS_{QS,FILT}$ sway at 0.1 and 0.25 Hz was compared between the consistent responders and inconsistent responders; this was done for all the FOV/platform conditions of the QS trials. Independent-sample t-tests did not reveal significant differences for any of the conditions ($0.084 \leq p \leq 0.978$).

3.3.3 Power Spectra of the Consistent Responders' Sway

Figure 3.6 plots the averages of the consistent responders' power spectral densities during the fixed (*top*) and sway-referenced (*bottom*) platform conditions. Each graph contains the average spectra from the following Full FOV conditions: QS, 0.1 Hz visual movement, and 0.25 Hz visual movement. Postural sway data routinely exhibit a low-pass spectrum in which the signal power decreases with increasing frequency. This was observed in the QS spectra of both platforms (thick line), although for sway-referencing the QS spectrum remained roughly flat from 0 to 0.2 Hz. The spectral floors of the moving scene (MS) averages also followed a low-pass trend, with a 20-25 dB rolloff in signal power from 0 to 0.5 Hz. Each of the MS spectra contained a strong peak at the stimulus frequency. Note that the power at 0.25 Hz was slightly greater than the peak at 0.1 Hz during both platforms, but the QS sway at 0.1 Hz was roughly 5 dB greater than the QS sway at 0.25 Hz during both platforms. Therefore, the increase in power from QS to MS sway was far greater for 0.25 Hz than for 0.1 Hz. For the fixed platform, the increase in power was about 10 dB at 0.1 Hz and 20 dB at 0.25 Hz; during sway-referencing, the increase was 14 dB at 0.1 Hz and 23 dB at 0.25 Hz.



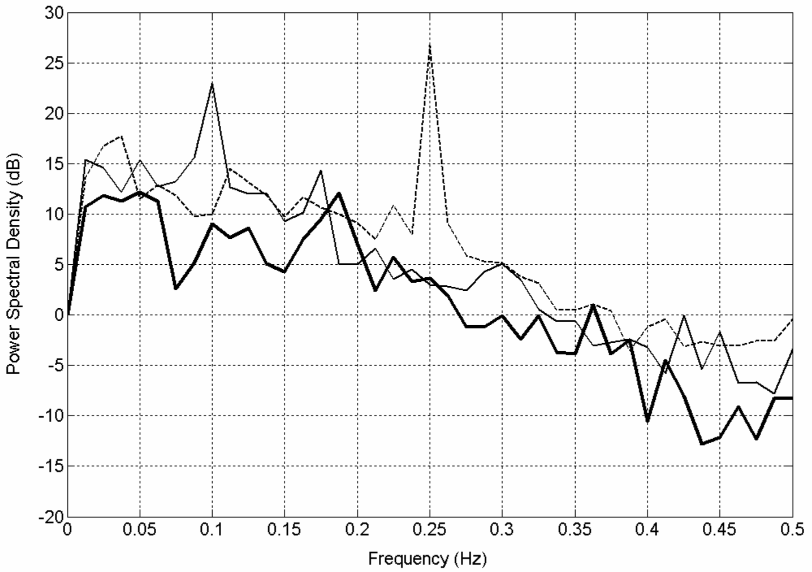


Figure 3.6. Averages of the consistent responders' power spectral densities during the fixed (top) and sway-referenced (bottom) platform conditions. Each graph contains the average spectra from the following Full FOV conditions: quiet stance (thick solid line), 0.1 Hz visual movement (thin solid line), and 0.25 Hz visual movement (thin dashed line). Note that the power of the quiet-stance spectra decreases as a function of increasing frequency, and that the spectral floors of the moving scene averages followed this trend.

3.3.4 Filtered-Absolute Sway Amplitudes

A repeated-measures ANOVA was performed on the consistent responders' RMS_{FILT} amplitudes, and the means are plotted in Figure 3.7. There was a significant FOV effect ($p = 0.001$), in which the central stimulus caused less sway than the full and peripheral scenes, but the difference between the latter two was not significant. The decrease in sway at the central FOV – which was especially drastic at 0.25 Hz during sway-referencing – was consistent with the small number of responses given by the Tone Test. The central target had very little influence on the subject's sway response under these amplitude and frequency conditions. When averaging across the FOV and platform conditions, the difference between the two frequencies was minimal ($p = 0.585$). There were significant FOV*Platform ($p = 0.019$) and FOV*Frequency ($p = 0.014$) interactions. Both of these were mainly due to the drastic drop in sway at 0.25 Hz during the central/sway-referenced condition; the attenuation at the corresponding fixed-platform condition was not nearly as severe. For both platform conditions, the decrease in the filtered sway response during the 0.1 Hz-central FOV was relatively small.

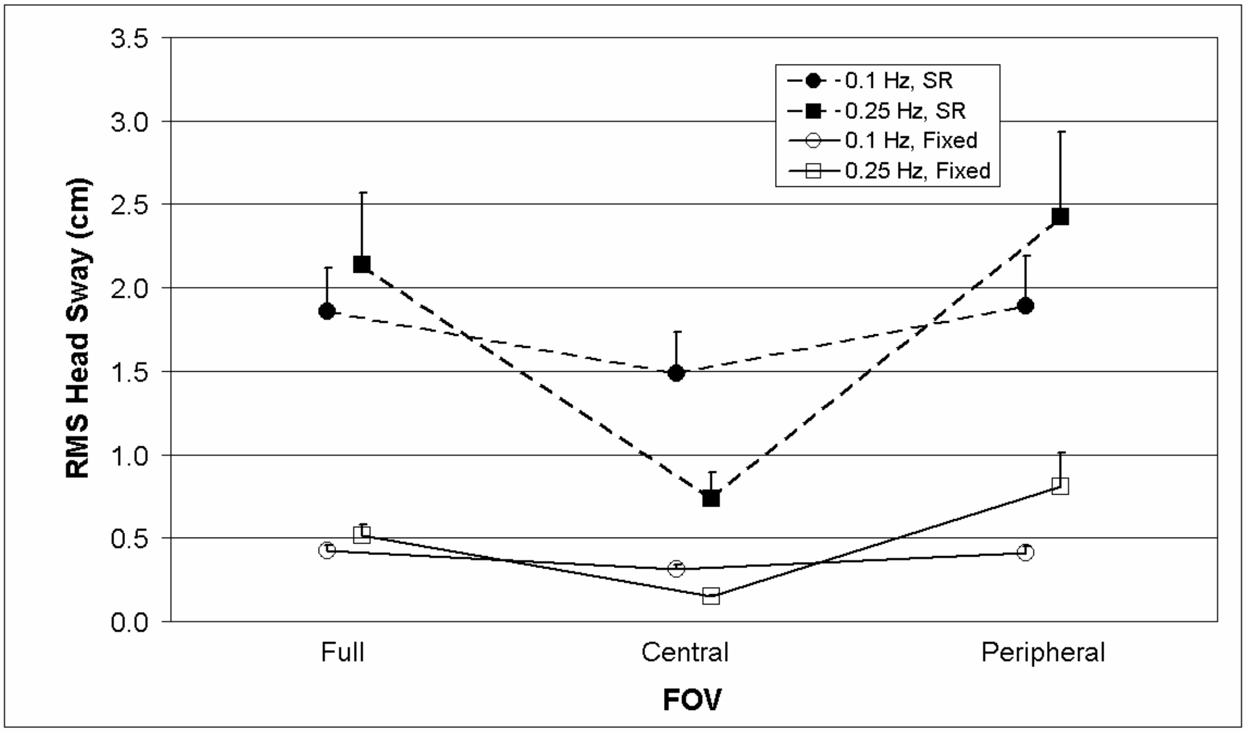


Figure 3.7. Averages of the consistent responders' RMS_{FILT} head sway during all visual/platform conditions (n = 10). Vertical bars indicate SEMs. Peak-to-peak stimulus amplitude was 16 cm. Data at 0.1 and 0.25 Hz are shifted horizontally from each other for clarity.

3.3.5 Quiet-Stance Sway Amplitudes

Figure 3.8 plots the mean $RMS_{QS,FILT}$ sway at both frequencies of interest, during the six stationary conditions. In each case there was significantly greater sway at 0.1 Hz than at 0.25 Hz ($p \leq 0.016$). Furthermore, when the platform was sway-referenced, there was significantly greater QS sway at both frequencies during the central FOV than during the full FOV ($p = 0.029$ for 0.1 Hz, and $p = 0.004$ for 0.25 Hz). However, no significant differences in QS sway were found between the central and peripheral FOVs. Since the RMS_{FILT} values include this QS component of sway, they do not reveal how much the subjects actually responded to the stimulus. Therefore, each of the subject's RMS_{FILT} values were normalized ($RMS_{FILT,NORM}$) by subtracting out the $RMS_{QS,FILT}$ component, and the results are plotted in Figure 3.9.

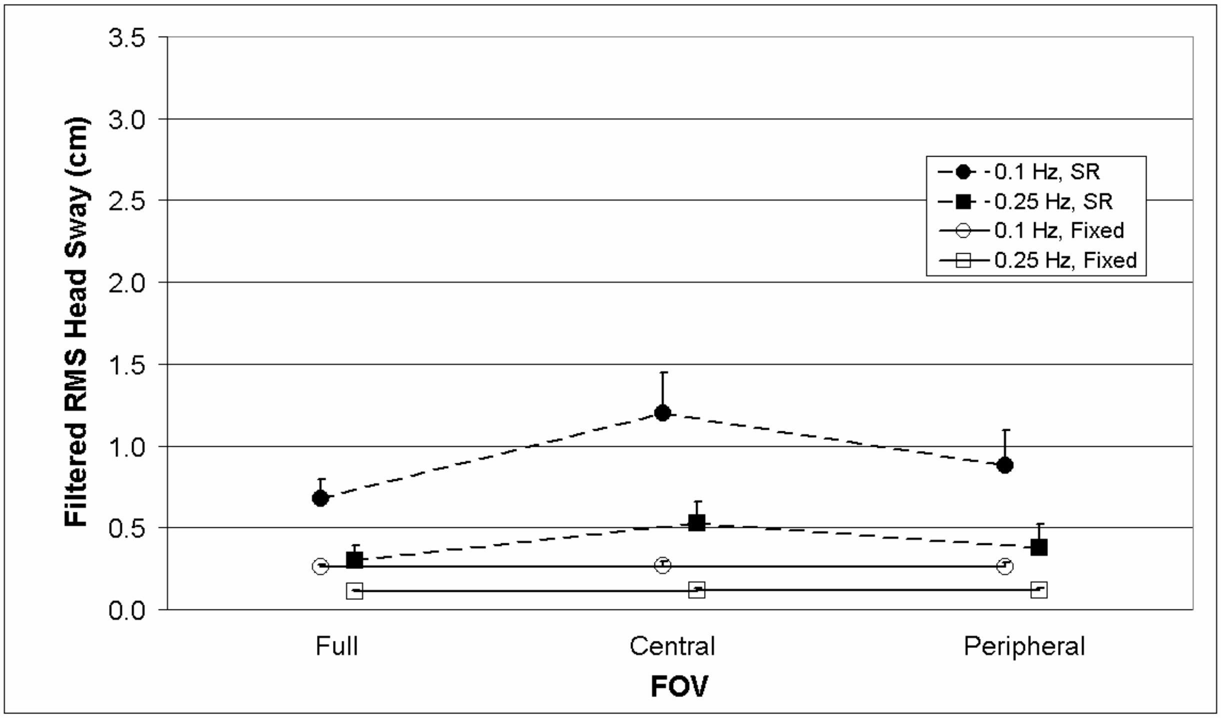


Figure 3.8. Averages of the consistent responders' $\text{RMS}_{\text{QS,FILT}}$ head sway at 0.1 and 0.25 Hz during all QS conditions (n = 10). Vertical bars indicate SEMs. Data at 0.1 and 0.25 Hz are shifted horizontally from each other for clarity.

3.3.6 Filtered-Normalized Sway Amplitudes

The FOV effect ($p = 0.001$) is clearly seen in the plot of the $RMS_{FILT,NORM}$ amplitudes (Figure 3.9). The central stimulus elicited very little response, regardless of the frequency of the stimulus or the platform condition. The normalized responses also varied with stimulus frequency ($p = 0.031$). In the full and peripheral FOVs – during both platforms - the 0.25 Hz stimuli caused a greater increase in sway than those moving at 0.1 Hz. This finding will be addressed further in the Discussion, but for now it should be mentioned that this Frequency effect does not necessarily indicate that the peripheral visual fields are more sensitive to 0.25 Hz. Lastly, there was also a significant FOV*Platform interaction ($p = 0.004$). When comparing the FOV effect between the two platform conditions, the difference in sway between the full/peripheral and central FOVs was greater during sway-referencing. The ANOVA results for Experiment 1 are summarized in Table 3.4.

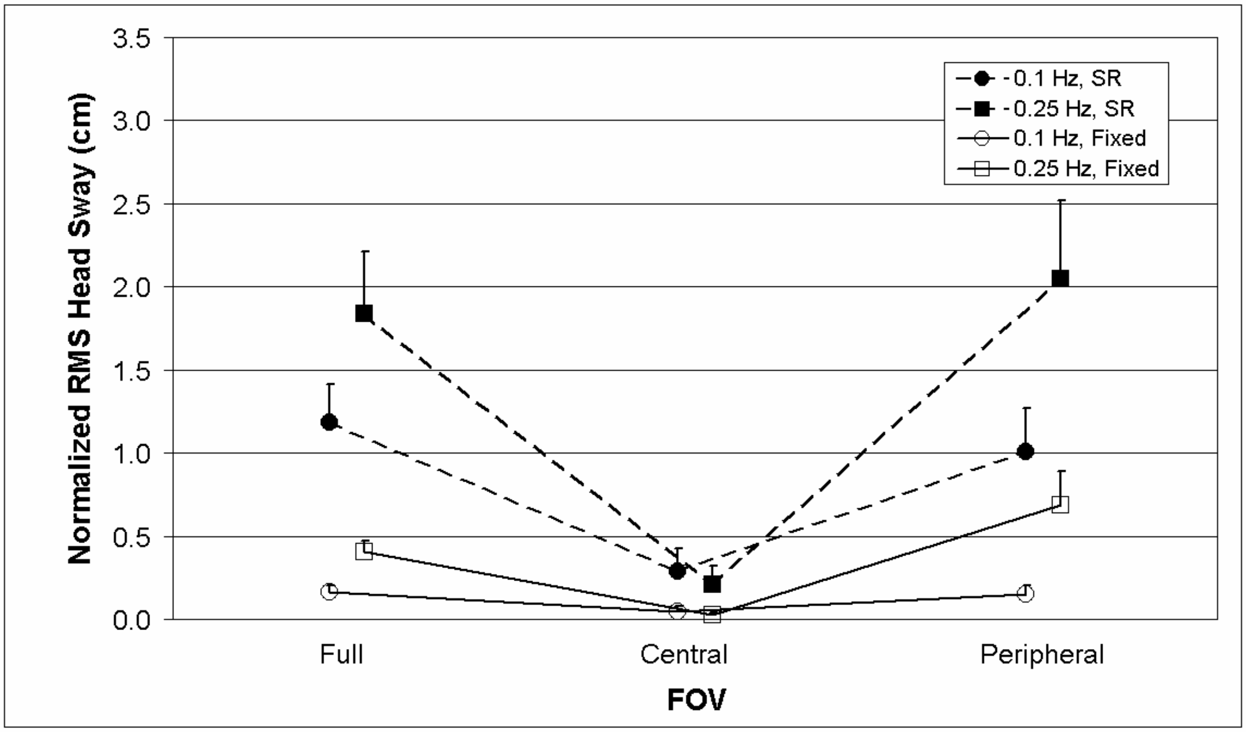


Figure 3.9. Averages of the consistent responders' $\mathrm{RMS}_{\mathrm{FILT,NORM}}$ head sway during all visual/platform conditions (n = 10). Vertical bars indicate SEMs. Peak-to-peak stimulus amplitude was 16 cm. Data at 0.1 and 0.25 Hz are shifted horizontally from each other for clarity.

Table 3.4. Summary of the ANOVA results for Experiment 1, testing for the effects of FOV, Frequency, Platform, and the interactions ($\alpha = 0.05$). Significant differences are indicated in **bold**.

	RMS_{RAW} (n = 20)	RMS_{FILT} (n = 10)	$\text{RMS}_{\text{FILT,NORM}}$ (n = 10)
	16 cm stimulus	16 cm stimulus	16 cm stimulus
FOV	**0.01**	**0.001**	**0.001**
Platform	**< 0.001**	**0.001**	**0.001**
Frequency	**0.02**	0.585	**0.031**
FOV*Plat	**0.026**	**0.019**	**0.004**
FOV*Freq	**0.033**	**0.014**	0.062
Plat*Freq	0.287	0.659	0.292
3-way Interaction	0.054	0.325	0.616

3.3.7 Phase Analysis

In general, the cycle-by-cycle phase differences of any given subject varied considerably during the course of a trial. In a few isolated instances, the phase values remained clustered within a range of ± 30 deg, but no clear trends were observed in the phase differences within or between subjects during the different visual/platform conditions. Table 3.5 shows the grand directional statistics of the responders during each visual/platform condition (note the varying group sizes). The large standard deviations indicate that there were no conditions in which the subjects' mean phase differences were tightly clustered around a given angle. In fact, there were only three conditions in which the subjects' mean directions differed significantly from uniform distributions (in **bold**).

Figure 3.10 displays the polar plots of the subjects' mean (± SD) phase differences during the three conditions for which the values were not uniformly distributed. Also included are the mean directional axes of the phase differences, since the values appear to form a roughly bimodal distribution, with two clusters positioned 180 degrees from each other. In Table 3.5 the mean phase listed for these conditions is the positive angle of the axis, and it is marked with an asterisk (*); the standard deviation is half of the unimodal value.

Table 3.5. Directional statistics for all visual/platform conditions. The three visual/platform conditions in which the subjects' mean phase values differed significantly from uniform distributions are indicated in **bold**. For these conditions, the phase values formed a roughly bimodal distribution, with two clusters positioned 180 degrees from each other. Directional axes were calculated for these cases, and the mean phase (marked by an asterisk) is the positive angle of the axis while the standard deviation is half of the unimodal value.

Platform	Frequency	FOV	Group Size	Mean Vector Length	Mean Phase (deg)	SD Phase (deg)	p-value Rao's Test
Fixed	0.1 Hz	Full	8	0.33	-7.47	66.54	0.18
		Central	4	0.59	-44.91	51.67	0.12
		Peripheral	12	0.13	-34.06	75.49	0.14
	0.25 Hz	Full	13	0.09	112.94	77.44	0.07
		Central	5	0.16	85.52	74.26	0.85
		Peripheral	**13**	**0.18**	**155.25***	**36.65**	**0.00**
Sway Referenced	0.1 Hz	Full	15	0.45	-7.43	60.11	0.42
		Central	9	0.41	-6.94	62.03	0.20
		Peripheral	11	0.24	-1.56	70.81	0.78
	0.25 Hz	Full	**16**	**0.13**	**137.77***	**37.70**	**0.01**
		Central	9	0.25	-3.48	70.39	0.50
		Peripheral	**17**	**0.15**	**134.40***	**37.38**	**0.02**

Peripheral FOV
0.25 Hz Stimulus
Fixed Platform
Group Size = 13

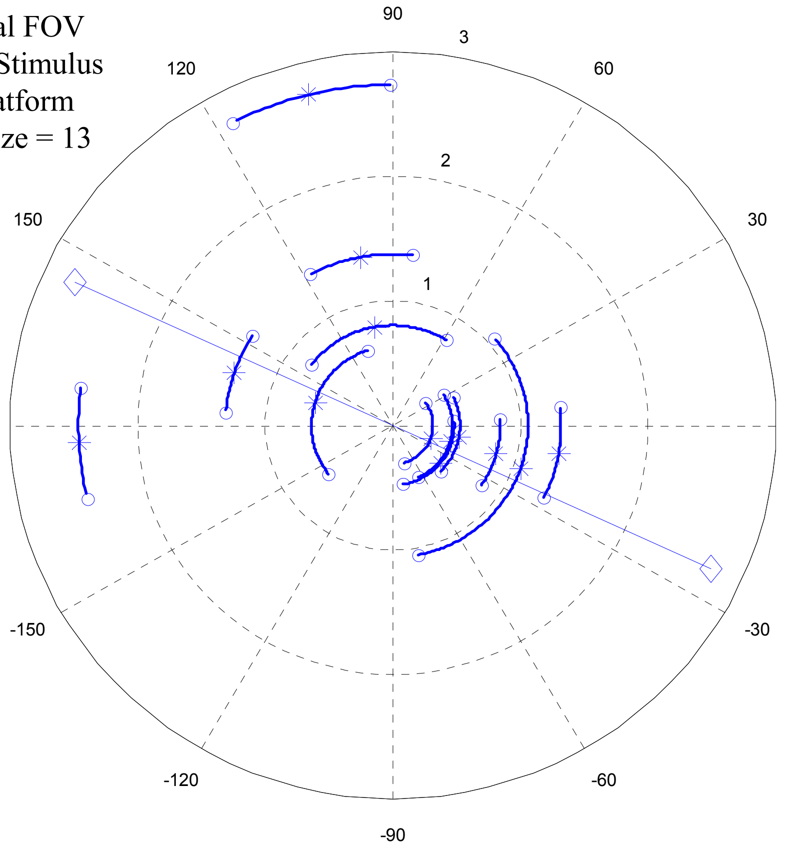


Figure 3.10 (continued on next page)

Full FOV
0.25 Hz Stimulus
Sway-Referenced Platform
Group Size = 16

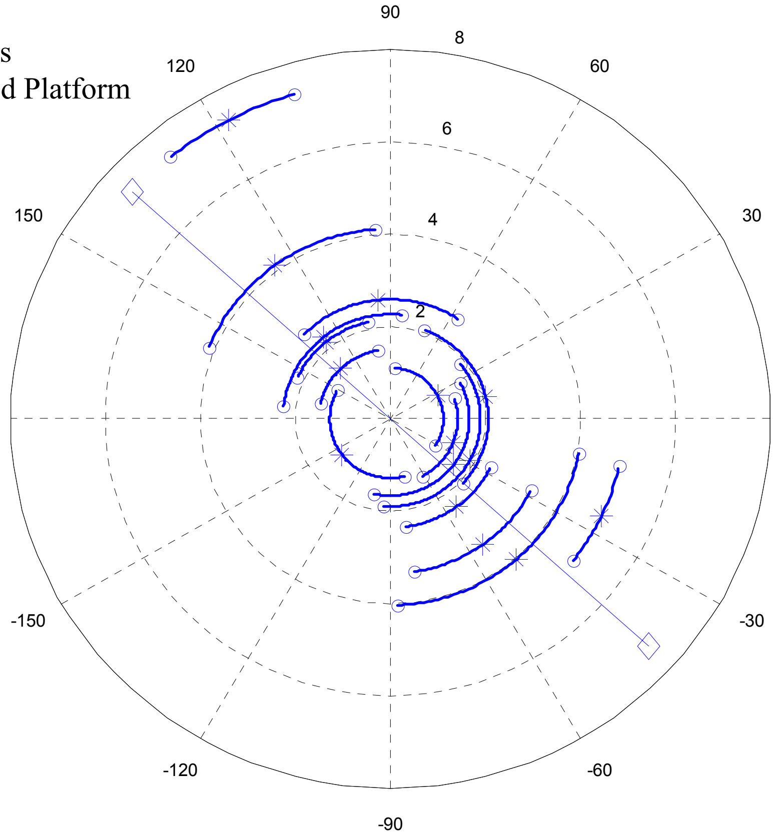


Figure 3.10 (continued on next page)

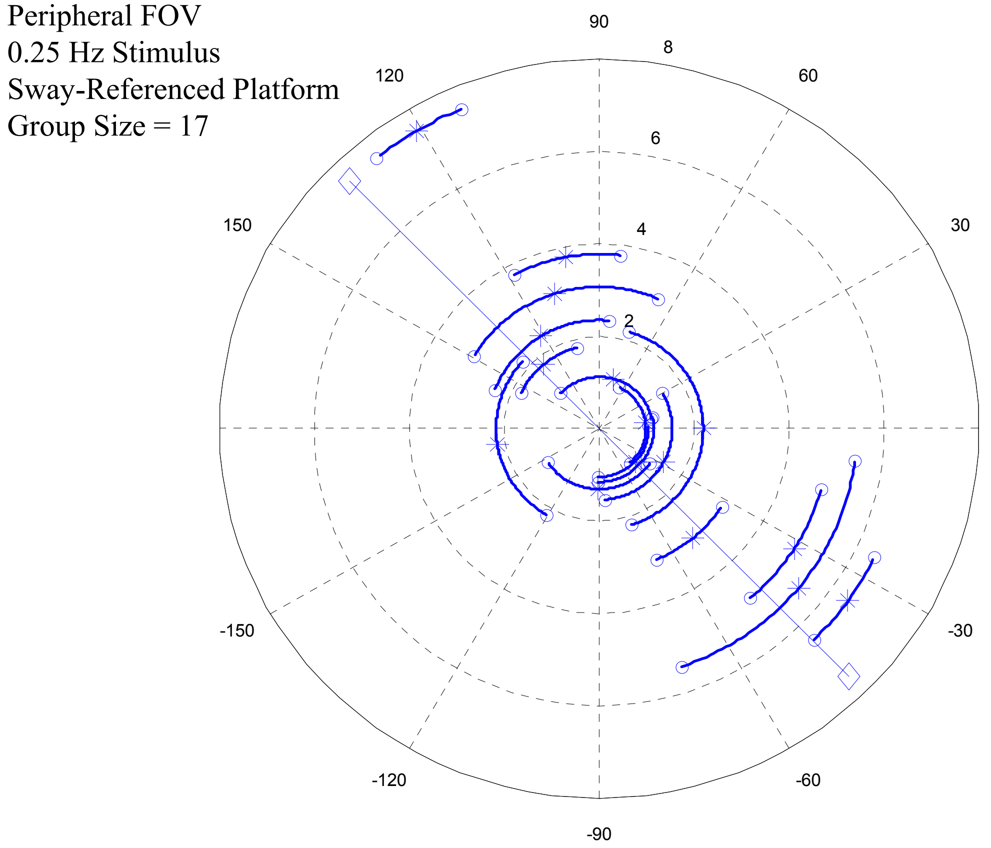


Figure 3.10. Phase-Amplitude plots for the conditions in which the subject-mean phase differences are not uniformly distributed. Within-subject phase values: mean (∗) ± SD (o). The scale located between 60 and 90 degrees indicates the mean amplitude of each subject's anterior-posterior sway. The mean directional axis is designated by a line running through the center of the plot, flanked by diamonds.

3.4 METHODS FOR EXPERIMENT 2

In Experiment 1 the peak-to-peak amplitude of the central and peripheral portions of the stimulus (16 cm) was measured using a linear world-reference frame. An alternative method of measuring the amplitude of the stimulus regions is to use spherical eye coordinates. If the 16 cm linear amplitudes of the two regions are converted into degrees of visual arc, it is found that the arc distance traversed by the checkered pattern is much greater than the arc distance traversed by the target. The results from Experiment 1 indicate that the checkered stimulus elicited greater RMS_{FILT} and $RMS_{FILT,NORM}$ sway than the central target at 16 cm, but it was not certain whether this was due to a greater sensitivity to the peripheral stimulus, or if it was merely a consequence of the disparate arc amplitudes.

The visual arc traveled by the peripheral stimulus was calculated with reference to an edge of a square located 90 degrees peripheral to the subject's line of sight. Since the linear peak-to-peak distance traveled by that edge during one cycle of the scene's oscillation was 16 cm, trigonometry was used to calculate the peak-to-peak visual arc amplitude of the peripheral stimulus: 7.6 degrees.

Calculating the peak-to-peak visual arc amplitude of the central target was more involved since the amplitude increases for each successive ring (moving from the center to the perimeter). The peak-to-peak radial expansion (in cm) of each of the six rings was measured, and trigonometric methods were employed to convert these values into peak-to-peak visual arcs. The arcs were then averaged across the rings to determine the mean peak-to-peak visual arc of the target's movement: 1.2 degrees. Since the difference in arc amplitudes was so drastic between the two stimulus regions, it seemed necessary to run an additional experiment in which the arc amplitudes of the peripheral and central stimulus regions were reversed. To determine the new linear amplitudes, the following ratio was calculated:

$$\frac{\text{[peak-to-peak visual arc amplitude of peripheral stimulus]}}{\text{[average peak-to-peak visual arc amplitude of central stimulus]}} = 6.58.$$

The ratio was then multiplied by 16 for the new central stimulus (7.6 deg or 105.3 cm), and divided by 16 for the new peripheral stimulus (1.2 deg or 2.4 cm).

Seven of the responsive subjects from Experiment 1 returned to participate in the second experiment. The new stimuli varied according to the same parameters: frequency (0.1 Hz and 0.25 Hz) and FOV (peripheral and central). The full FOV stimulus was not included since the central and peripheral regions would not be synchronized when moving at their adjusted amplitudes.

$\mathrm{RMS}_{\mathrm{FILT}}$ and $\mathrm{RMS}_{\mathrm{FILT,NORM}}$ amplitudes were again calculated by the same methods used in Experiment 1. For the statistical analysis, the data from both experiments were divided into the following two groups:

(1) The $\mathrm{RMS}_{\mathrm{FILT}}$ ($\mathrm{RMS}_{\mathrm{FILT,NORM}}$) responses to the 1.2 degree central stimulus (from Experiment 1) were combined with the $\mathrm{RMS}_{\mathrm{FILT}}$ ($\mathrm{RMS}_{\mathrm{FILT,NORM}}$) responses to the 1.2 degree peripheral stimulus (from Experiment 2). These data sets are hereafter referred to as the 1.2 degree data.

(2) The $\mathrm{RMS}_{\mathrm{FILT}}$ ($\mathrm{RMS}_{\mathrm{FILT,NORM}}$) responses to the 7.6 degree central stimulus (from Experiment 2) were combined with the $\mathrm{RMS}_{\mathrm{FILT}}$ ($\mathrm{RMS}_{\mathrm{FILT,NORM}}$) responses to the 7.6 degree peripheral stimulus (from Experiment 1). These data sets are hereafter referred to as the 7.6 degree data.

A 3-way repeated measures ANOVA was performed on each of the above data sets, to test for the main effects of Frequency, FOV, and Surface condition, as well as the 2-way and 3-way interactions ($\alpha = 0.05$).

3.5 RESULTS

3.5.1 Number of Significant Responses

Tables 3.6 and 3.7 show the results of the Tone Test for the 1.2-deg and 7.6-deg data, respectively. Increasing the amplitude of the central stimulus to 7.6-deg did not change the number of significant responses during the fixed platform, but it actually lessened the number of responses during sway-referencing. Therefore, the FOV effect observed in the 16-cm data also was observed in the 7.6-deg data ($\chi_1^2 = 26.09$, $p < 0.001$). Even after the peripheral optic flow was decreased to 1.2-deg, the subjects responded to it 1.5 times as often as they did to the central stimulus of the same visual arc, although the difference is not significant for the small sample size ($\chi_1^2 = 2.59$, $p = 0.108$). The number of responses did not vary significantly with frequency for either the 1.2-deg ($\chi_1^2 = 1.15$, $p = 0.284$) or 7.6-deg ($\chi_1^2 = 0.65$, $p = 0.420$) data, although they followed the same trend as seen in the 16-cm data (0.25 Hz > 0.1 Hz). Lastly, the number of responses to the 1.2-deg optic flow varied significantly with platform condition ($\chi_1^2 = 7.18$, $p = 0.007$), but surprisingly this effect was not observed for the larger amplitude ($\chi_1^2 = 0.07$, $p = 0.788$).

Table 3.6. Results of Tone Test for the 1.2-deg data (n = 7). Number of subjects who passed the Tone Test in each visual/platform condition, plus the totals for the fixed factors. Each of the Platform-Frequency Totals is out of a possible 14; FOV, Frequency, and Platform totals are out of 28. Grand total number of trials is 56.

	Fixed		Sway-Referenced		FOV Totals
	0.1 Hz	0.25 Hz	0.1 Hz	0.25 Hz	
Central: 1.2 deg.	1/7	1/7	5/7	5/7	12/28
Peripheral: 1.2 deg.	3/7	5/7	4/7	6/7	18/28
Platform-Frequency Totals	4/14	6/14	9/14	11/14	Grand Total: 30/56
Frequency Totals	0.1 Hz: 13/28		0.25 Hz: 17/28		
Platform Totals	Fixed: 10/28		Sway-Ref.: 20/28		

Table 3.7. Results of Tone Test for the 7.6-deg data (n = 7). Number of subjects who passed the Tone Test in each visual/platform condition, plus the totals for the fixed factors. Each of the Platform-Frequency Totals is out of a possible 14; FOV, Frequency, and Platform totals are out of 28. Grand total number of trials is 56.

	Fixed		Sway-Referenced		FOV Totals
	0.1 Hz	0.25 Hz	0.1 Hz	0.25 Hz	
Central: 7.6 deg.	1/7	2/7	1/7	2/7	6/28
Peripheral: 7.6 deg.	7/7	6/7	5/7	7/7	25/28
Platform-Frequency Totals	8/14	8/14	6/14	9/14	Grand Total: 31/56
Frequency Totals	0.1 Hz: 14/28		0.25 Hz: 17/28		
Platform Totals	Fixed: 16/28		Sway-Ref.: 15/28		

Table 3.8. Chi-Squared results for the 1.2-deg and 7.6-deg data, showing whether the number of responses to the stimuli was significantly influenced by the fixed factors ($\alpha = 0.05$). Significant effects are indicated in **bold**.

	1.2-degrees		7.6-degrees	
Factor	Chi-Squared Value	p-value	Chi-Squared Value	p-value
FOV	2.59	$p = 0.108$	**26.09**	**$p < 0.001$**
Frequency	1.15	$p = 0.284$	0.65	$p = 0.420$
Platform	**7.18**	**$p = 0.007$**	0.07	$p = 0.788$

3.5.2 Filtered-Absolute Sway Amplitudes

Figure 3.11 plots the mean RMS_{FILT} amplitudes of the 1.2 deg and 7.6 deg data. Note that the data at central-1.2 deg and peripheral-7.6 deg (from Experiment 1) include only the subjects who participated in Experiment 2. Interestingly, there were 1.5 times as many responses to the 1.2-deg peripheral stimulus (from Experiment 2) than there were to the 1.2-deg central stimulus (from Experiment 1): 18/28 vs. 12/28, respectively. However, the mean RMS_{FILT} amplitude in response to the peripheral optic flow was not significantly larger than the RMS_{FILT} amplitude to the central flow ($p = 0.54$). There is the expected Platform effect ($p = 0.013$), and the Frequency difference ($p = 0.002$) is due to the greater QS sway at 0.1 Hz. A Platform*Frequency interaction also exists ($p = 0.007$) because the difference in the amount of sway between the two frequencies is much larger during sway-referencing than when the platform is fixed. When the $RMS_{QS,FILT}$ sway is subtracted out in the normalized data (Figure 3.12), the frequencies do not cause different sway responses at such a small stimulus amplitude ($p = 0.938$).

In the 7.6 deg data the subjects showed significant responses to the central FOV in only 21% of the trials, but they responded to the peripheral FOV of the same arc amplitude 89% of the time. Consistent with these Tone-Test results, the peripheral checkers caused significantly more sway than the central target ($p = 0.027$). This FOV effect was much more prominent at 0.25 Hz than at 0.1 Hz, leading to a FOV*Frequency interaction ($p = 0.026$). During the 0.1 Hz-sway referenced condition, the response to the central stimulus was surprisingly somewhat greater than the response to the periphery, but this difference did not reach a significant level ($p = 0.52$). As was the case at 16 cm, the sway during the central stimulus was greater at 0.1 Hz than at 0.25 Hz (especially during sway-referencing), but this is simply due to greater QS sway at the lower frequency. The main Frequency effect was insignificant ($p = 0.708$), as were the FOV*Platform and Platform*Frequency interactions ($p = 0.185$ and $p = 0.223$, respectively). As expected, there was greater sway during sway-referencing ($p = 0.018$).

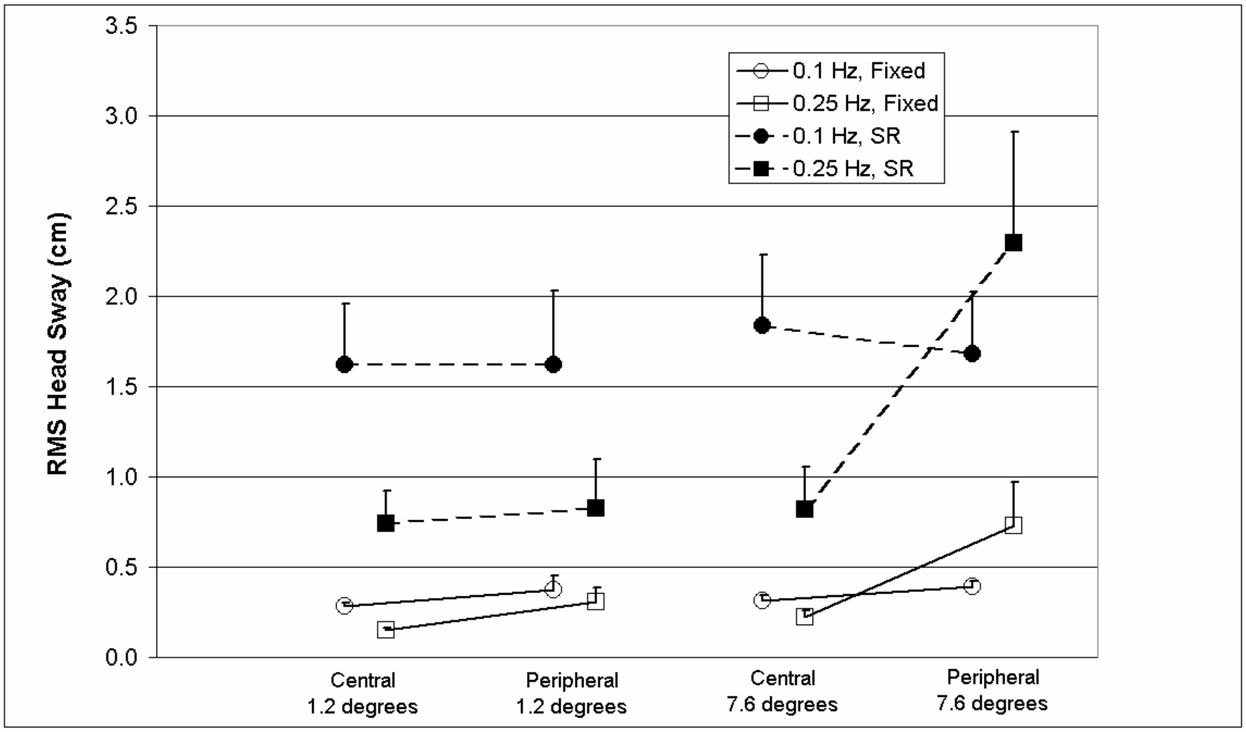


Figure 3.11. Average RMS_{FILT} head sway at 1.2-deg and 7.6-deg peak-to-peak stimulus amplitudes (n = 7). Vertical bars indicate SEMs. Data at 0.1 and 0.25 Hz are shifted horizontally from each other for clarity.

3.5.2 Filtered-Normalized Sway Amplitudes

When the 1.2 deg and 7.6 deg data were normalized, the Platform effect was observed in both ($p = 0.011$ and $p = 0.019$, respectively). However, the minimal sway caused by the smaller amplitude was not significantly influenced by any of the visual parameters ($0.369 \le p \le 0.979$). For the larger stimulus amplitude, the statistical trends of the normalized sway mirrored those of the absolute sway. There was a greater response during the peripheral FOV ($p = 0.005$), which was predominantly observed at 0.25 Hz (FOV*Freq: $p = 0.044$). The main Frequency effect ($p = 0.124$), and the FOV*Platform ($p = 0.466$) and Platform*Frequency ($p = 0.487$) interactions, did not reach a significant level. Note that with the smaller sample size ($n = 7$), the statistical test was more conservative. The ANOVA results for Experiment 2 are summarized in Table 3.9.

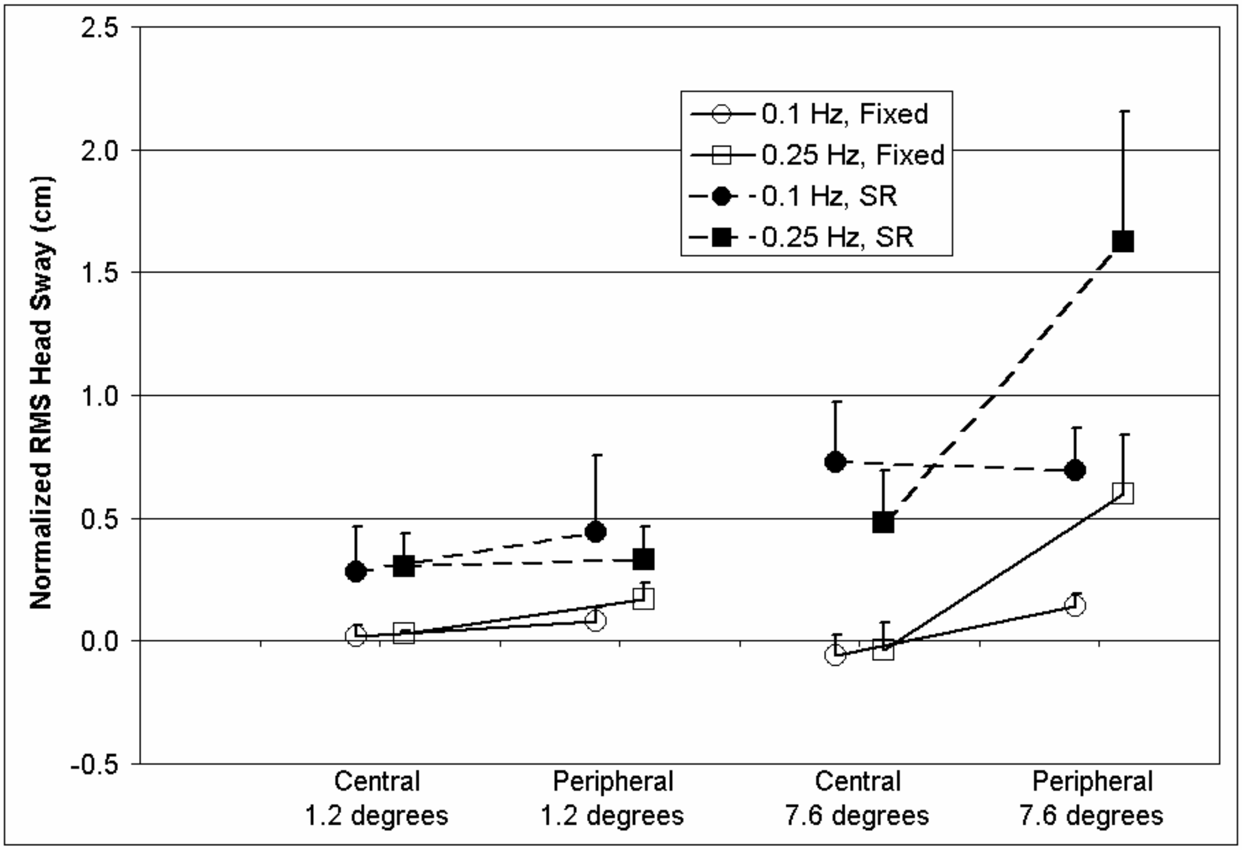


Figure 3.12. Average $\text{RMS}_{\text{FILT,NORM}}$ head sway at 1.2-deg and 7.6-deg peak-to-peak stimulus amplitudes (n = 7). Vertical bars indicate SEMs. Data at 0.1 and 0.25 Hz are shifted horizontally from each other for clarity.

Table 3.9. Summary of the ANOVA results for Experiment 2, testing for the effects of FOV, Frequency, Platform, and the interactions ($\alpha = 0.05$). Significant differences are indicated in **bold**.

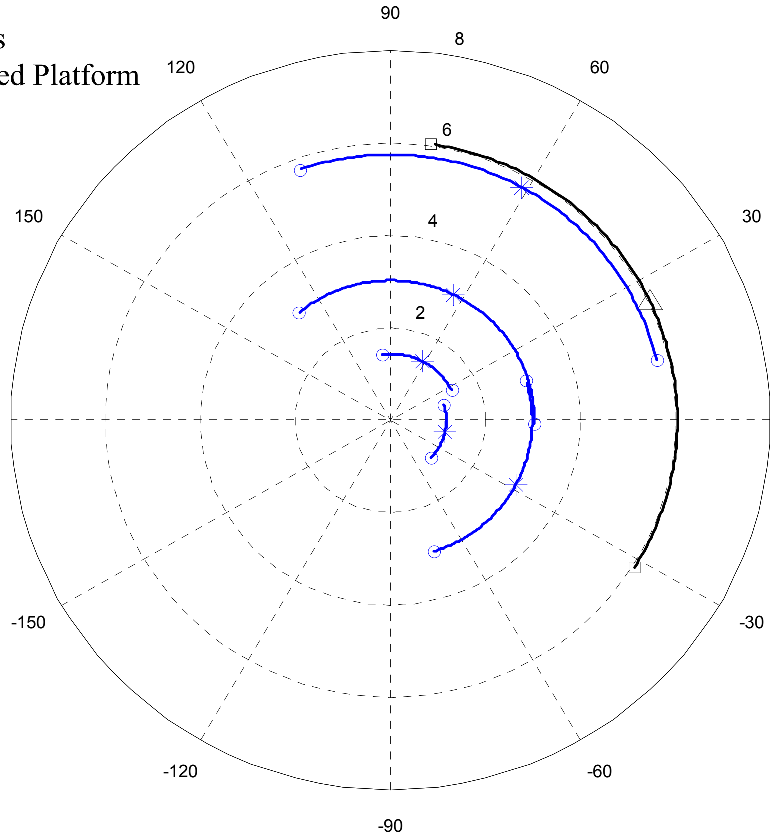
	RMS_{FILT} (n = 7)	$RMS_{FILT,NORM}$ (n = 7)	RMS_{FILT} (n = 7)	$RMS_{FILT,NORM}$ (n = 7)
	1.2 deg stimulus	1.2 deg stimulus	7.6 deg stimulus	7.6 deg stimulus
FOV	0.54	0.475	**0.027**	**0.005**
Platform	**0.013**	**0.011**	**0.011**	**0.019**
Frequency	**0.002**	0.938	0.708	0.124
FOV*Plat	0.648	0.979	0.185	0.466
FOV*Freq	0.415	0.915	**0.026**	**0.044**
Plat*Freq	**0.007**	0.369	0.223	0.487
3-way Interaction	0.92	0.71	0.111	0.195

3.5.3 Phase Analysis

Only a few subjects responded during the fixed platform conditions, and therefore no general conclusions can be made from the directional statistics in Table 3.10. During three of the sway-referencing conditions, the subjects' mean phase values differed significantly from uniform distributions (see rows in **bold**), but none of them formed bimodal distributions. Figure 3.13 displays the polar plots for these conditions.

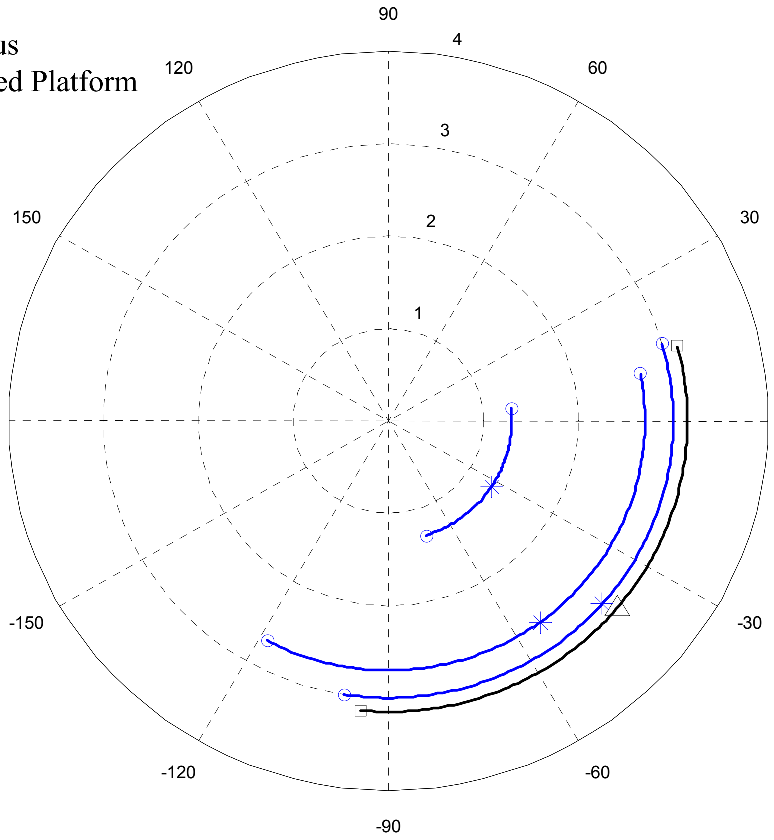
Table 3.10. Directional statistics for all adjusted-amplitude conditions.

Platform	Frequency	FOV	Group Size	Mean Vector Length	Mean Direction (deg)	SD Direction (deg)	p-value Rao's Test
Fixed	0.1 Hz	Central	1	0.73	167.40	42.18	0.93
		Peripheral	3	0.59	69.85	51.81	0.64
	0.25 Hz	Central	2	0.61	24.37	50.60	0.42
		Peripheral	5	0.27	34.37	69.45	0.42
Sway Referenced	0.1 Hz	Central	1	0.50	-144.39	57.30	0.93
		Peripheral	**5**	**0.51**	**25.02**	**56.84**	**0.05**
	0.25 Hz	Central	**3**	**0.54**	**-40.10**	**55.24**	**0.04**
		Peripheral	**6**	**0.49**	**-16.75**	**57.76**	**0.00**



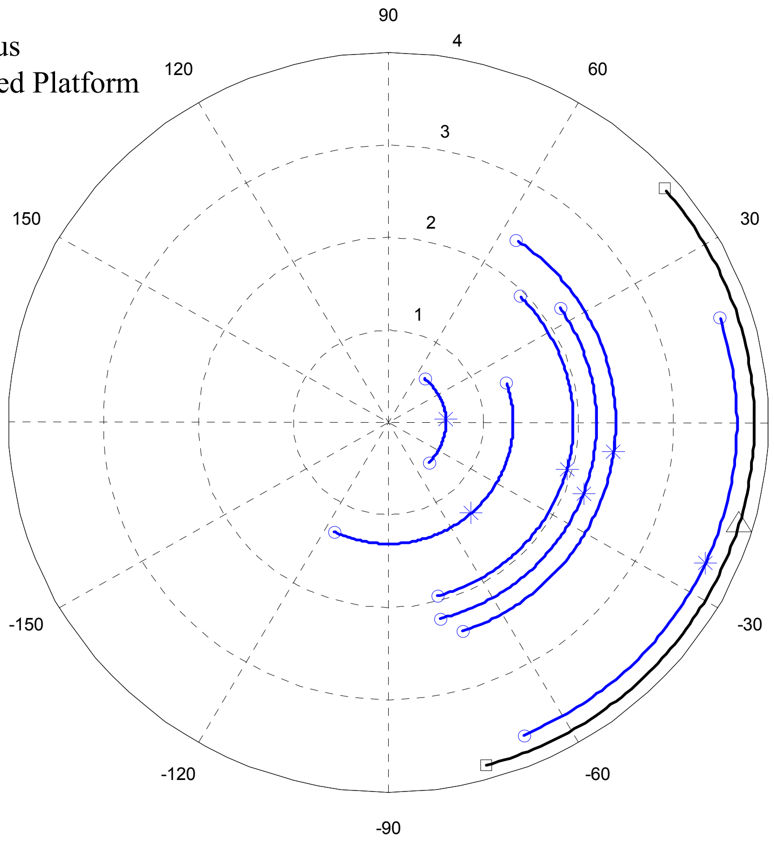
Peripheral FOV
0.1 Hz Stimulus
Sway-Referenced Platform
Group Size = 5

Figure 3.13 (continued on next page)



Central FOV
0.25 Hz Stimulus
Sway-Referenced Platform
Group Size = 3

Figure 3.13 (continued on next page)



Peripheral FOV
0.25 Hz Stimulus
Sway-Referenced Platform
Group Size = 6

Figure 3.13. Phase-Amplitude plots for the modified amplitude conditions in which the subject-mean phase differences are not uniformly distributed. Within-subject phase values: mean (∗) ± SD (o). Between-subject phase values: mean (Δ) ± SD (□). The scale located between 60 and 90 degrees indicates the mean amplitude of each subject's anterior-posterior sway.

3.6 DISCUSSION

In this discussion, we will first describe the wide variety of methodologies used in previous central-peripheral studies and then give a rationale for using our visual stimulus. Next, we will discuss the importance of normalizing the absolute sway amplitudes, and explain why the Frequency effect observed in the normalized data corroborates the Tone-Test results. Furthermore, we will discuss the valuable insights gleaned from performing Experiment 2, in which the amplitudes of the stimulus regions were equated in terms of visual arc. Our results will then be considered in light of the three theories concerning the functional sensitivities of central and peripheral vision in perceiving self-motion. Lastly, we will discuss the neuropysiological mechanisms responsible for the preferential sensitivity to visual motion in the peripheral fields.

3.6.1 The Dissimilar Methodologies of Central-Peripheral Experiments

Several studies have investigated the influence of central and peripheral vision in self-motion perception and postural control, but comparisons between results is difficult since they have used a wide variety of methodologies. There are several sources of variation. First, the structure of the visual environment has included checkered patterns (van Asten et al. 1988a), concentric rings (current study), and arrays of dots-and-dashes (Johansson 1977; Andersen and Braunstein 1985; Andersen and Dyre 1989; Warren and Kurtz 1992; Crowell and Banks 1993; Nakamura and Shimojo 1998; Bardy et al. 1999; Nakamura 2001). Second, the direction of the optic flow has included anterior-posterior (AP) (Andersen and Braunstein 1985; Stoffregen 1985, 1986; van Asten et al. 1988a; Andersen and Dyre 1989; Warren and Kurtz 1992; Crowell and Banks 1993; Bardy et al. 1999), medial-lateral (ML) (Stoffregen 1985, 1986; Andersen and Dyre 1989;

Nakamura and Shimojo 1998; Bardy et al. 1999; Nakamura 2001), vertical (Johansson 1977), rotational (Brandt et al. 1973), and intermediate (Bardy et al. 1999) varieties of several different speeds and amplitudes. Third, the velocity trajectories have been unidirectional (Brandt et al. 1973; Johansson 1977; Andersen and Braunstein 1985; Warren and Kurtz 1992; Crowell and Banks 1993; Nakamura and Shimojo 1998; Nakamura 2001) and sinusoidal (Stoffregen 1985, 1986; van Asten et al. 1988a; Andersen and Dyre 1989; Bardy et al. 1999).

Included in these variations of visual movements are the concepts of radial and lamellar flow. Radial flow is any visual motion that expands and contracts in relation to the observer and therefore has been presented mainly in the AP direction, although it has also been presented in the ML direction (Stoffregen 1985, 1986). Lamellar flow is any motion characterized by parallel lines or textures sweeping across the visual fields. In the case of an AP moving stimulus, lamellar flow would be present in the peripheral fields, while in vertical or ML motion, it can also exist in the central fields. While most central-peripheral studies have presented moving visual stimuli, others have examined postural stabilization while viewing a stationary scene of different FOVs (Amblard and Carblanc 1980; Straube et al. 1994).

A fourth source of variation in central-peripheral experiments is the outcome measure. Several studies required subjects to report whether or not they perceived themselves as moving (i.e., vection experiments), or to estimate the duration of their vection (Andersen and Braunstein 1985). Within the broader category of vection studies, some asked subjects to report the direction of their apparent motion (i.e., heading experiments) (Johansson 1977; Warren and Kurtz 1992; Crowell and Banks 1993). Still others measured the subjects' sway responses to motion presented in the central and/or peripheral visual fields (i.e., postural sway experiments)

(Amblard and Carblanc 1980; Stoffregen 1985, 1986; van Asten et al. 1988a; Andersen and Dyre 1989; Straube et al. 1994; Bardy et al. 1999).

Finally, there is a large disparity in the fields of view (FOVs) used in the various studies. Of the experiments cited in the central-peripheral literature, few have provided an immersive environment subtending 180 degrees of the horizontal FOV (Brandt et al. 1973; Amblard and Carblanc 1980; Stoffregen 1985; Howard and Heckmann 1989), and therefore little is known regarding the relative sensitivities of the retinal regions under these conditions. Of the studies not providing an immersive environment, few employed eccentricities as great as 90 degrees (Johansson 1977; van Asten et al. 1988a; Straube et al. 1994; Bardy et al. 1999), while others restricted their stimulation to much narrower regions (Andersen and Braunstein 1985; Andersen and Dyre 1989; Warren and Kurtz 1992; Crowell and Banks 1993; Nakamura and Shimojo 1998; Nakamura 2001). Furthermore, the size of a stimulus can be confounded with the eccentricity (or location) of the stimulus, since a larger central stimulus inevitably subtends more of the peripheral region of the observer's FOV, while a larger peripheral stimulus subtends more of the central FOV. Therefore, since there is a wide variety of protocols between the numerous central-peripheral experiments, it is difficult to directly compare results, and such comparisons should consider the above factors as thoroughly as possible.

3.6.2 Rationale for Using Our Stimulus

The stimulus used in this study was chosen for two main reasons. First, in a preliminary experiment conducted in our lab (see Appendix A.2), we observed little response to a 60-deg central stimulus consisting of an infinitely long tunnel. The stimulus offered limited optic flow since it did not display a distinct pattern near the subject's focal point. Thus, it was surmised that the small response was possibly due to inadequate optic motion, and that the concentric ring pattern may provide greater radial expansion/contraction. Second, the central-rings/peripheral-checkers environment used in this study was modeled after the environment used in two recent experiments (Peterka and Benolken 1995; Borger et al. 1999). Although these former studies did not specifically investigate the effects of central and peripheral vision (since they only used a Full FOV), they indicated that the environment was effective in eliciting notable sway responses.

3.6.3 Rationale for Normalizing RMS_{FILT} Sway

Since postural control mechanisms collectively act as a low-pass filter, there are prominent low-frequency components even in the absence of a moving stimulus. As shown in the spectral plots of Figure 3.6, the power of the quiet-stance (QS) sway decreased with increasing frequency. Thus, the power at 0.1 Hz was about 5 dB greater than it was at 0.25 Hz, during both platform conditions. The moving-stance (MS) data, which showed prominent peaks at the stimulus frequencies, followed this low-pass trend in which the spectral floor around 0.25 Hz was significantly lower than the floor around 0.1 Hz. Previous experiments using sinusoidal visual environments have shown a marked increase of sway in response to stimulus frequencies ranging between 0.1 and 0.5 Hz, and within this range the response amplitude attenuated with increasing frequency (van Asten et al. 1988a; van Asten et al. 1988b; Peterka and Benolken 1995). Although these studies also included plots of QS spectra, the MS sway amplitudes were not normalized, thus leading to an inaccurate conclusion that subjects were more responsive to lower frequencies.

Our absolute-filtered data at 16 cm did not reveal a main Frequency effect (across the three FOVs), but if our analysis were solely based on these values, we would have wrongly concluded that the central visual fields are more sensitive to motion at 0.1 Hz than at 0.25 Hz (Figure 3.7). After normalization, we realized that the greater absolute sway observed during the central-0.1 Hz condition was due to the greater QS sway at 0.1 Hz (Figure 3.8). In reality, the subjects' did not respond well to the central optic flow - regardless of platform or frequency condition – and their normalized responses to the peripheral optic flow were significantly greater at the higher frequency (Figure 3.9).

3.6.4 The Visual System Exhibits Greater Sensitivity to Higher-Frequency Optic Flow

Two of our outcome measures suggest that the visual system is more sensitive to higher-frequency stimuli. First, as already discussed, the filtered-normalized sway in response to the 0.25 Hz-peripheral stimuli exceeded the normalized-filtered sway responses to the 0.1 Hz-peripheral optic flow (Figure 3.9). Second, the consistent responders attended to the higher frequency more often than they attended to the 0.1 Hz stimuli. This was revealed by the Tone Test, which was able to detect the Frequency effect because the prewhitened spectra were not skewed by the greater QS sway at 0.1 Hz.

Before the Tone Test was performed, the frequency spectrum had to be flattened so that it resembled white noise, and this was done by using an auto-regressive filter on the spectrum. In order to avoid bias in the model fit due to a large component at the stimulus frequency, the component at the stimulus frequency was replaced by a linear interpolation of the power at neighboring frequency bins (see Chapter 2 for a detailed description of the method). Since the MS data at 0.1 and 0.25 Hz were both whitened (or normalized) by this method, any difference in the QS component between the two frequencies was eliminated. Consequently, the Tone Test shows that the subjects swayed at the higher stimulus frequency more often.

In summary, our only outcome measure that failed to reveal a greater sensitivity to 0.25 Hz was the filtered-absolute amplitudes. When the QS components were accounted for, the higher frequency was shown to be more influential in modulating the subjects' posture.

3.6.5 Central-Peripheral Effects Observed in the Current Study

The results of this study indicate that peripheral optic flow has a dominant influence on upright postural sway within our immersive environment. In all three sets of data (16 cm, 1.2-deg, and 7.6-deg), there was a greater number of significant responses to the stimulus frequency when the optic flow was presented in the periphery than when it was presented in the central FOV, indicating that the subjects were more sensitive to the peripheral motion. Furthermore, when the peak-to-peak stimulus amplitude was either 16 cm or 7.6 deg, the absolute and normalized RMS sway amplitudes in response to the full/peripheral optic flow were significantly greater than the responses to the central optic flow. This FOV effect was observed within each of the four platform/frequency conditions, and it was accentuated in the normalized data. The 16-cm data also exhibited a significant FOV*Platform interaction. When comparing the FOV effect between the two platform conditions, one can see that the difference in sway between the full/peripheral and central FOVs is greater during sway-referencing. Therefore, not only does peripheral vision appear to be more sensitive to the given stimulus conditions, but when somatosensory inputs are unreliable, the increase in visual sensitivity is greater in the peripheral fields than it is centrally.

It was very informative to conduct the second experiment in which the amplitudes of the stimulus regions were equated in terms of visual arc. Based on the results of Experiment 1, it was uncertain whether the FOV effect was due to a differential sensitivity of the central and peripheral fields, or if it was merely a result of too little stimulation in the central region. The RMS amplitudes at 1.2 degrees showed that such a small stimulus amplitude does not elicit much of a response regardless of the FOV. Although the number of significant responses to the peripheral optic flow exceeded the responses to the central flow, the sway amplitudes were not significantly greater in the peripheral condition. Increasing the central stimulus to 7.6 deg had virtually no effect on the subjects' sway amplitudes, and in fact it decreased the number of responses during sway-referencing. Note that the linear amplitude of the 7.6-deg central optic flow was 105.3 cm, while the linear amplitude of the 1.2-deg peripheral optic flow was 2.4 cm; nonetheless, there were three times the number of significant responses to the latter stimulus as there were to the former.

It is possible that the 7.6-degree central stimulus was so large that it no longer provided useful information to the postural control system. If stimulus motions are subtle but large enough to result in a perception of self-motion, they lead to compensatory postural responses. However, if stimulus motions are too extreme, observers realize that only the environment is moving, in which case their postural adjustments are minimal. Stoffregen (1986) observed this effect when he examined the role of optic velocity in the control of stance. Subjects generally swayed more in response to a moving room with an RMS velocity of 0.233 cm/sec than they did to the same room moving at an RMS velocity of 0.933 cm/sec. At the higher velocity all of his subjects reported that they noticed the room motion, whereas at the lower velocity, no subject reported awareness of any motion (Stoffregen 1986).

The dimensions of Stoffregen's moving room were similar to the dimensions of our immersive environment, but since his stimulus (a marble textured pattern) was very different than ours, one cannot compare the optic flow characteristics between his and our stimuli by simply comparing the stimulus velocity. That being said, our RMS velocities at 16 cm were an order of magnitude larger than his: 3.55 cm/sec for 0.1 Hz and 8.88 cm/sec for 0.25 Hz. The RMS velocities of our adjusted central stimulus were two orders of magnitude larger: 23.36 cm/sec for 0.1 Hz and 58.43 cm/sec for 0.25 Hz. Our 16 cm (7.6 degree) peripheral stimulus caused a significant response and therefore was not too large to elicit a perception of self-motion, but the motion of the 7.6-degree central stimulus may have been too rapid to effect compensatory sway. Unfortunately, we did not ask the subjects to report whether they perceived self-motion or motion of the environment after each trial. However, a comparison of the Tone-Test results between the two central-stimulus amplitudes reveals that the seven subjects responded to the 1.2-degree stimulus twice as often as they responded to the 7.6-degree stimulus: 12/28 trials (42.8%) vs. 6/28 trials (21.4%), respectively. If the central visual field is preferentially sensitive to certain stimulus velocities, perhaps the range is intermediate to the ones presented in this study.

3.6.6 Comparisons to Previous Central-Peripheral Studies

The peripheral dominance hypothesis is probably the earliest of the three paradigms used to characterize the relative sensitivities of central and peripheral vision in motion perception and postural control (Brandt et al. 1973; Johansson 1977; Amblard and Carblanc 1980). For example, Amblard and Carblanc (1980) measured the postural sway of subjects viewing a stationary scene while standing on a compliant foam surface. The FOVs were full (180 degrees horizontally), foveal (central 1.2 degrees), and peripheral (area excluding the foveal area). They observed that balance was significantly impaired with foveal vision compared to full or peripheral vision, and thus concluded that foveal vision plays only a supplementary role in the maintenance of postural equilibrium. Considering that the foveal area was so small, it is possible that the greater postural stability observed during the full and peripheral conditions resulted merely from a greater amount of retinal stimulation, regardless of the specific regions of stimulation (Amblard and Carblanc 1980). However, our central FOV was much larger (60 degrees), and when the platform was sway-referenced, we also observed greater QS sway during this condition than during the full FOV. Therefore, it appears that peripheral vision is significantly involved in the stabilization of posture during quiet stance.

Other studies offered support for the peripheral dominance hypothesis by investigating people's conscious perception of self-motion. For example, Brandt et al (1973) conducted an experiment in which subjects sat inside a vertically striped cylinder that rotated about its long axis at various constant speeds. It was found that with the periphery blocked, exposures up to 60 degrees of visual angle to the central retina produced little or no perceived self-motion. In the periphery (with the center blocked out), much smaller exposures yielded strong sensations of rotation (Brandt et al. 1973). In addition, Johansson observed central-peripheral differences when seated subjects viewed a vertically moving random pattern of black dots on a white background. In one experiment subjects viewed a flow of vertical motion presented to limited areas of their peripheral retina (45-90 degrees) while their central visual field viewed a stationary wall. Most subjects perceived themselves as sitting in an elevator moving upward or downward. When the moving stimulus was presented to the central part of the retina, the subjects perceived object motion but did not feel like they were moving. Thus, Johansson concluded that peripheral motion stimulation over a few percent of the retina determines movement perception (Johansson 1977). A limitation of these vection studies is that they did not measure postural responses but instead relied on the subjects' conscious perception and verbal report of their apparent motion. Although a perception of self-motion often leads to a postural response, it should not be assumed that detection thresholds for the two phenomena are the same. In fact, studies examining both postural adjustments and self-motion perception have shown that subjects increase their sway in response to stimuli they do not consciously perceive (Lee and Lishman 1975; Kapteyn et al. 1979; Stoffregen 1986; Gielen and van Asten 1990); therefore, postural sway is a more sensitive indicator of a moving scene's influence.

Although our current results conflict with the retinal invariance hypothesis, they are not irreconcilable with the findings used to support it. The divergence in conclusions between studies can be attributed to the dissimilarities in experimental protocol. For example, Crowell and Banks (1993) examined the ability to use optic flow to judge heading at different retinal eccentricities (i.e., the angle between the fovea and the center of the stimulus), and at different head directions (i.e., the angle between the specified heading and the center of the stimulus). The stimuli subtended 10 degrees in diameter and simulated translation (straight-line motion) through a cloud of random dots. Verbal reports of heading direction were much more accurate with radial flow fields (small heading eccentricities) than with lamellar fields (large heading eccentricities), regardless of the region of the retina being stimulated (Crowell and Banks 1993). However, the accuracy of heading judgments may have varied between eccentricities if the FOV of the stimulus was not so restrictive. Furthermore, since postural sway was not measured, it is uncertain whether the subjects responded differently to the stimuli at different eccentricities.

Nakamura (1998) also concluded that central and peripheral presentations of a moving visual pattern produce similar perceptions of self-motion. The visual stimuli were random patterns of dots moving linearly in the ML direction. The radius of the central stimulus varied between 10–45 degrees on a screen subtending 90 x 60 degrees (vert. x horiz.). Subjects held a button in each hand, and were instructed to press the one corresponding to the direction of perceived self-motion. It was concluded that vection strength is determined by the stimulus size and speed but not by its eccentricity. However, Nakamura acknowledged that stimulus eccentricity could be confounded with stimulus size, since a larger stimulus inevitably stimulates more of the peripheral region of the observer's visual field (Nakamura and Shimojo 1998). In addition, the limitations cited in the Crowell and Banks (1993) study also apply here.

Bardy et al. (1999) supported the retinal invariance hypothesis when he found that subjects responded with large amplitudes of postural sway that were similar across various flow patterns and retinal eccentricities of sinusoidal stimuli. Differences between his protocol and ours include the following: First, the subjects walked on a treadmill, but in this study they merely stood on a platform. Second, the visual stimulus was presented on one screen (22 degrees in diameter), whereas the current study offered an immersive environment. Third, the amplitude of the stimulus (10.7 cm peak-to-peak) was smaller than any of our amplitudes. Fourth, during Bardy's central conditions the subjects viewed the screen binocularly, but in the peripheral conditions they viewed the screen monocularly with the right eye. It is possible that the peripheral condition would have elicited more sway than the central condition if the former were also viewed binocularly. Fifth, their stimuli were comprised of densely spaced arrows oriented in either a radial, intermediate, or lamellar flow pattern; such an environment may have been more conducive to stimulating the central retina than our target pattern, leading to a smaller differential in the amounts of sway caused by the two FOVs. Finally, although Bardy observed similar postural responses at the different retinal eccentricities presented in his study, it does not exclude the possibility that even greater responses would be observed at eccentricities extending beyond 22 degrees.

In summary, the retinal invariance hypothesis cannot be proven on the basis of experiments that did not include an immersive environment. Our results do not oppose the findings that central visual motion elicits significant postural responses (Stoffregen 1985; Delorme and Martin 1986; Stoffregen 1986; Andersen and Dyre 1989; Paulus et al. 1989) as well as vection sensations (Andersen and Braunstein 1985; Howard and Heckmann 1989; Nakamura and Shimojo 1998; Nakamura 2001). Our moving stimuli presented in the central FOV also caused significantly more sway than what was observed during the stationary central FOV. Nevertheless, the response to the peripheral FOV (which spanned a visual arc of 30 – 90 degrees in each hemifield), far exceeded the response to the central FOV (spanning a 60 degree diameter).

The last of the three central-peripheral paradigms is the functional sensitivity hypothesis, which states that the peripheral fields are most sensitive to lamellar flow while the central fields are most sensitive to radial flow (Lishman and Lee 1973; Stoffregen 1985; van Asten et al. 1988a; Warren and Kurtz 1992). Even though our central stimulus elicited little normalized sway, our results do not contradict this hypothesis. Several of the studies supporting functional sensitivity used central stimuli comprised of radially expanding lines and dots, and such a stimulus may be more provocative than our concentric rings if it provides more texture and contrast. However, our results do contradict the notion that the sensitivity of central vision to radial flow is equivalent or even comparable to the sensitivity of peripheral vision to lamellar flow.

The authors are unaware of any central-peripheral experiment other than Stoffregen's (1985) that used an AP optic flow stimulus encompassing the subjects' entire horizontal FOV. In that experiment subjects were inside a moving room textured with a marble pattern of various

FOVs. They were presented with radial flow in the central field and lamellar flow in both peripheral fields while they faced straight ahead. This resulted in a greater response to the periphery, which corroborates our findings. Furthermore, the results of Warren and Kurtz (1992) have also been cited in support of the functional sensitivity hypothesis. In this heading experiment, they found that central vision accurately extracts radial, rotary, and lamellar flow, whereas peripheral vision extracts lamellar flow but is less sensitive to radial and rotary flow. These results are not at odds with our experiment but are limited because they relied on the subjects' conscious awareness of motion, and because their full FOV only subtended 40 degrees (Warren and Kurtz 1992).

Lastly, van Asten et al. (1988) compared subjects' postural responses to a radially checkered stimulus with their responses to a lamellar tunnel stimulus; both scenes moved sinusoidally in the AP direction and were viewed monocularly with a FOV 80 degrees in diameter. It was found that the central masking of a moving tunnel with a large peripheral shear component had only a minimal effect. This corroborates the results of our first pilot study, in which we used a tunnel stimulus in both the central and peripheral regions (see Appendix A.2). However, van Asten also observed that masking the central portion (15 horiz. x 30 vert. degrees) of a scene that contained a large central radial expansion almost eliminated the postural responses, whereas in our study the elimination of the central rings had minimal effect (i.e., going from full to peripheral FOV). The conflicting results may be attributed to the different stimuli since the center of van Asten's radially checkered scene provided several distinct edges, while the center of our target did not (van Asten et al. 1988a).

In a separate condition within the same experiment, van Asten et al. also presented their subjects with concentric rings, and they found that this stimulus caused 50 percent as much sway than their radially checkered scene. They noted that this difference was surprising since "most theories describing how optic flow information may be used to control posture or 'self-motion' assume that the divergence of the optic flow field (i.e. the expansion/contraction component) determines the forward/backward movements of a subject" (p. 381). However, the concentric rings and the radially checkered scene had the same divergence. The only difference between the two scenes is that that the radially checkered pattern provided more contrast lines, which probably caused optic flow components to be detected more effectively than in the concentric rings. A future area of research would be to compare sway responses to the concentric rings and a radially checkered stimulus in our visual environment.

3.6.7 The Cortical Magnification Factor

It has been shown that visual fields of the same size but different retinal locations differ quantitatively, because representation of the visual fields within the primary striate cortex (area V1) decreases with increasing eccentricity (Cowey and Rolls 1974). Thus, a peripheral field has a much smaller cortical representation in area V1 than does a central field. This relationship has been quantified by the cortical magnification factor (CMF), which reflects the linear extent of the primary visual cortex to which each point on the retina projects. In other words, the CMF quantifies the exponential decrease of cortical representation within the primary visual cortex as retinal eccentricity increases (Cowey and Rolls 1974). The human CMF was estimated (Rovamo and Virsu 1979) using the areal cortical magnification factor (M^2), and M^2 is directly proportional to ganglion cell density in the retina (Tusa et al. 1978).

The CMF is relevant to postural studies examining central-peripheral effects, because a confounding factor in these studies is the relationship between the area of retinal stimulation and the eccentricity of that stimulation. Since the central stimulus is centered at zero eccentricity, its area inevitably increases with its eccentricity. Therefore, it has been postulated that greater self-motion perception and postural stability have been observed in the peripheral FOVs simply because they stimulated a greater retinal area. However, the authors could only find one peripheral dominance study to which this argument applies (Amblard and Carblanc 1980). The other studies observed greater perceptions of self-motion in response to peripheral stimuli when these stimuli were no larger than the central FOVs (Brandt et al. 1973; Johansson 1977; Dichgans and Brandt 1978).

Interestingly, some studies measuring postural stability during stationary scenes have observed that the reduction of postural sway is greater when viewing central FOVs than when viewing peripheral FOVs of comparable area (Paulus et al. 1984; Brandt et al. 1986). However, our QS results – and those of other studies (Amblard and Carblanc 1980) - disagree with these findings. When comparing the unfiltered and filtered QS sway between the different FOVs in the current study, the only significant differences were observed during sway-referencing, in which the QS_{FILT} sway during the central FOV was significantly greater than the QS sway during the full FOV. These diverging results raise the question of whether central and peripheral vision have differential effects on the stabilization of posture during quiet stance.

Straube et al. (1994) applied the CMF to a study in which subjects monocularly viewed a stationary scene at eccentricities of 0, 10, 20, and 30 degrees while balancing on a foamrubber support. This compliant support surface was probably similar to our sway-referenced platform. The visual field increased with increased eccentricity in accordance with the CMF; however, according to our calculations, the visual fields were about 15% smaller than the values required by the CMF equation provided in their paper. This lack of precision was probably due to constraints in their setup. Nonetheless, the postural sway was virtually constant across the experimental conditions. There was a slight (but not statistically significant) increase in sway with increased eccentricity, but perhaps the sway would have been less if the visual fields were slightly larger. Their conclusion was that visual control of balance is roughly homogeneous across the visual field once the stimulation areas are adjusted to equal areas of cortical representation (Straube et al. 1994).

Again, there are several dissimilarities between our stationary conditions and Straube's. First, we used an immersive environment while his FOVs were quite small. Second, his subject's viewed the scene monoculary while ours viewed it binocularly. Third, his most eccentric condition was 30 degrees while ours extended to 90 degrees in each hemifield. Fourth, the structure of our peripheral stimulus was different than our central stimulus, while he used the same stimulus at each eccentricity. Those differences notwithstanding, our QS results during the fixed platform condition are similar to theirs because we also did not observe a FOV effect for the unfiltered QS sway, or for the QS sway filtered at 0.1 Hz or 0.25 Hz. However, since they used a compliant, foamrubber support, it is more appropriate to compare their results to our QS results during sway-referencing. What we found was that the unfiltered QS sway, as well as the QS sway filtered at 0.1 and 0.25 Hz, was significantly greater during the central FOV than during the full FOV; no differences were observed between the central and peripheral FOVs. According to the CMF, the area of primary visual cortex stimulated by the central FOV would be much greater than the area stimulated by the peripheral checkers, and therefore the central FOV would have the predominant effect in visual stabilization. However, our results indicate that the addition of the peripheral stimulus significantly decreased the subjects' sway while on the sway-referenced platform. This implies that the mechanisms involved in maintaining stable posture cannot be accounted for simply by adjusting for the CMF. It is necessary to also consider the functions of higher visual cortical areas, including the ventral and dorsal cortical streams.

A rough approximation could be made of how large each peripheral FOV would have to be in order to equal the cortical stimulation provided by the central target. Our central FOV subtended a diameter of 60 degrees from the subject's line of sight, which means that it subtended 30 degrees in each hemifield ($C_{hemi} = 30$ degrees). Each hemifield of our peripheral FOV subtended 60 degrees, starting 30 degrees from center to 90 degrees perpendicular to the subjects' line of sight ($P_{hemi} = 90 - 30 = 60$ degrees). The peripheral eccentricity in each hemifield would be the midpoint of the visual arc subtended by one side of the peripheral stimulus, which would be 60 degrees ($P_{hemi}/2 + C_{hemi} = 60$ degrees). When these numbers are put into the CMF equation, it is found that even the largest possible peripheral FOV (i.e., 90 degrees in each hemifield) would not be sufficient to equal the cortical stimulation provided the central FOV. The point of making this comparison is to emphasize that according to the CMF, our central FOV stimulated a disproportionately larger area of striate cortex than did our peripheral FOV. Nonetheless, our stationary central FOV did not stabilize the subjects' posture more than our stationary peripheral FOV during either of our platform conditions. In fact, during sway-referencing the full FOV resulted in greater stability compared to the central FOV, suggesting that the peripheral FOV had a significant effect even though it stimulated a lesser area of striate cortex.

3.6.8 Neurophysiological Correlate to the Peripheral Dominance of Motion Perception

Electrophysiological and behavioral studies in macaque monkeys, as well as neuroimaging studies in humans, have indicated that visual information is divided into two different cortical streams. The ventral stream located in the inferior temporal cortex is mainly responsible for the identification of an object's shape and color, while the dorsal stream in the posterior parietal cortex modulates spatial and motion vision (Ungerleider and Mishkin 1982; Van Essen and Maunsell 1983). The information coming from the two major types of retinal ganglion cells is processed differently. Parvocellular (small-diameter) ganglion cells are more prevalent near the fovea, while magnocellular (larger-diameter) ganglion cells are more prevalent in the periphery (Wright and Ikeda 1974). These different cell-types project to different parts of the lateral geniculate nucleus (LGN) (Wiesel and Hubel 1966; Schiller and Malpeli 1978; Leventhal et al. 1981; Perry et al. 1984).

Parvocellular cells generally relay information to the ventral stream visual areas, including the striate cortex (V1), the extrastriate cortex (V2), the inferior occipito-temporal cortex, and the ventral anterior striate region (V4) (Livingstone and Hubel 1987). From V4, shape recognition is conveyed to the inferior temporal cortex (Perrett et al. 1979; Hasselmo et al. 1989; Perrett et al. 1991). In contrast, magnocellular cells transfer information to the dorsal stream visual areas, including V1, V2, the medial temporal region (MT), the medial superior temporal area (MST), the ventral intraparietal area (VIP), and higher regions of the partietal cortex (Livingstone and Hubel 1987). These areas appear to be most dominant in optic-flow processing.

The vast majority of cells in area MT (or V5) are tuned for the direction and speed of a moving visual stimulus (Albright 1984; Mikami et al. 1986a, b; Lagae et al. 1993). Cells with similar preferred directions are clustered in columns (Albright 1984), and the directions are uniformly distributed (Albright 1989). Information in area MT is sent to the medial superior temporal (MST) and ventral intraparietal (VIP) areas. Electrophysiological studies indicate that the MST region responds selectively to visual stimuli simulating forward (expansion) or backward (contraction) motion, translational movements, as well as rotational and spiral stimuli (Saito et al. 1986; Tanaka et al. 1986; Tanaka et al. 1989; Tanaka and Saito 1989; Duffy and Wurtz 1991b, a; Graziano et al. 1994; Lagae et al. 1994; Duffy and Wurtz 1995; Lappe et al. 1996; Bremmer et al. 1999). Neurons in area VIP are also involved in the processing of self-motion information (Bremmer et al. 1995; Schaafsma and Duysens 1996; Bremmer et al. 1997; Schaafsma et al. 1997), showing specific responses for the direction and speed of moving stimuli (Duhamel et al. 1991; Colby et al. 1993).

The motion-sensitive part of the dorsal visual stream continues beyond areas MST and VIP in the macaque visual cortical system, as both areas send feed-forward connections to area 7a. Some neurons in 7a exhibit the classical tuning for the direction of optic flow (e.g., they prefer expansion over contraction stimuli), while others are tuned for classes of optic flow [e.g., they prefer radial optic flow (expansion and contraction) over rotational optic flow (clockwise and counterclockwise)] (Bremmer et al. 1994; Read and Siegel 1997; Siegel and Read 1997). Although visual information is largely segregated between the ventral and the dorsal pathways, the anterior part of the macaque superior temporal polysensory area (STPa) is a region where signals from both cortical streams converge. STPa receives input from the inferotemporal area (TEO) in the ventral stream and from areas MST and 7a in the dorsal stream (Boussaoud et al. 1990), and it has been reported that most STPa neurons respond only to visual motion originating from movements of external objects rather than to retinal stimulus motion caused by a movement of the animal (Hietanen and Perrett 1996a, b). This response feature may represent a functional link between the object-recognition of the ventral stream and the motion processing of the dorsal stream (Bremmer et al. 1999).

In the human visual cortex, neuroimaging techniques have revealed that different stimulus features are processed in the ventral and dorsal streams (Haxby et al. 1991; Zeki et al. 1991; Tootell et al. 1996). Several studies (Probst et al. 1993), (Zeki et al. 1991; Watson et al. 1993; Dupont et al. 1994; Tootell et al. 1995; Anderson et al. 1996) have shown significant activation of the occipitotemporal and/or temporoparietooccipital junction (TPO) while subjects viewed optic flow stimuli. These cortical regions are considered to be human homologues of areas V5/V5a; however, they do not appear to be selectively active during the presentation of optic flow stimuli (de Jong et al. 1994). Instead, three other regions may form a specific optic flow processing network in the higher parietal areas of humans: the right area V3/V3a (Reppas et al. 1997; Tootell et al. 1997), a region in the right superior parietal lobule (de Jong et al. 1994; Cheng et al. 1995), and the bilateral occipitotemporo ventral surface (also known as the kinetic occipital cortex) (Dupont et al. 1994).

As the above findings indicate, the dorsal cortical stream plays a significant role in the optic-flow processing of primates. Furthermore, there is evidence that this dorsal stream activity can be correlated to a peripheral dominance in motion perception. Ungerleider and colleagues have emphasized the connection of central and peripheral retinal stimulation to the activation of the ventral and dorsal streams, respectively (Ungerleider and Desimone 1986b; Desimone and Ungerleider 1989; Boussaoud et al. 1990; Baizer et al. 1991; Boussaoud et al. 1991). This suggests that the cortical stream most responsible for the perception of self-motion is also most activated by stimuli in the peripheral visual fields. This hypothesis has recently been supported in a human neuroimaging study (Stephen et al. 2002). The study found that two dorsal stream areas - the superior lateral occipital gyrus (putative MT) and the intraparietal sulcus – were activated faster than ventral areas, in response to the initial onset of the peripheral visual stimulus. Moreover, there was a larger prevalence of dorsal stream areas active during peripheral stimulation than during central stimulation. These results provide a strong neurophysiological correlate for peripheral dominance in self-motion perception and postural sway.

3.6.9 Interpretation of Phase Results

The phase differences between the stimulus motion and the subjects' responses were generally quite variable, but such variability was also observed in previous studies (van Asten et al. 1988a; van Asten et al. 1988b; Dijkstra et al. 1994a; Dijkstra et al. 1994b). Between the two experiments, the mean phase values differed significantly from uniform distributions during only six visual/platform conditions, and in five of these cases the FOV included the peripheral stimulus, the frequency was 0.25 Hz., and the platform was sway-referenced. For the 16 cm data, the non-uniform distributions were roughly bimodal, but this was not observed during the adjusted stimulus amplitudes. In the one instance where there was a non-uniform phase distribution during the 0.1 Hz stimulus (1.2-deg/peripheral FOV/sway-referencing), the response led the stimulus motion by 25 deg. Conversely, all of the non-uniform responses to the 0.25 Hz stimulus had prominent phase-lag components. The shift from a phase lead at 0.1 Hz to a phase lag at 0.25 Hz is consistent with a linear second-order lowpass system with a 0.5 Hz cutoff (Lestienne et al. 1977; van Asten et al. 1988a; Dijkstra et al. 1994a; Dijkstra et al. 1994b; Dijkstra 2000; Peterka 2002). However, the disparity in phase responses has demonstrated the need to also consider nonlinear dynamic analyses (Dijkstra et al. 1994a; Dijkstra et al. 1994b; Dijkstra 2000; Loughlin and Redfern 2001).

3.6.10 Future Studies

A next step in testing the peripheral dominance hypothesis would be to test whether it applies to medial-lateral (ML) optic flow as well as it applies to anterior-posterior (AP) flow. In other words, would the peripheral fields still dominate postural control in an immersive environment that provides lamellar flow in the central FOV and radial flow in the periphery? Stoffregen (1985) examined this using a textured environment of various FOVs; the visual motion was in the AP direction with respect to the subjects' trunk, and in order to provide radial flow to their peripheral vision, they stood with their head turned 90 degrees with respect to their trunk. He found that radial flow presented to the periphery induced no compensatory sway, while medial-lateral lamellar flow presented in the central FOV produced some sway. He later performed this same experiment again using different stimulus velocities, and he obtained the same result. One potential reason for the lack of response to the radial flow in the periphery is that the radial flow was only presented in one peripheral hemifield. In addition, turning the head with respect to the trunk may introduce other postural mechanisms that affect the response characteristics. Radial flow presented to the peripheral fields may have a greater influence on postural sway if the head is straight with respect to the trunk.

The visual environment used in the current study could be modified in order to provide radial flow to both peripheral fields. For example, two patterns of concentric rings could be presented in the periphery and a checkered pattern presented in the center. The two targets would remain a certain distance apart, separated by the checkered wall, and the direction of the environment's motion would be parallel to the front screen. ML sway could be measured if the subjects faced the front screen, and AP sway could be measured if the subjects turned their body to face one side and then turned their head to face the front screen.

It would also be informative to present an array of dots and/or dashes in our immersive environment since this was one of the most common types of optic flow used in the central-peripheral studies cited in this paper. Such a stimulus may be more provocative than ours, especially in the central FOV. Most of the previous experiments presented an array of dots only within a limited central FOV, but it in order to adequately evaluate central-peripheral differences, it would be necessary to determine how this stimulus influences posture at wider eccentricities.

3.7 SUMMARY

The results of this study suggest that the postural system is more sensitive to anterior-posterior optic flow in the peripheral FOV, regardless of stimulus frequency. When the stimulus amplitude was either 16 cm or 7.6 deg, the significant postural responses to the peripheral optic flow greatly outnumbered the responses to the central optic flow. The absolute and normalized sway amplitudes in response to the full/peripheral optic flow were significantly greater than the responses to the central optic flow. Furthermore, the number and size of the postural responses to the peripheral optic flow were greater when the stimuli moved at 0.25 Hz than when they moved at 0.1 Hz. This challenges the idea that people are more sensitive to optic flow of lower frequencies.

These findings have implications for the use of virtual environments, showing that head-mounted displays with a limited central FOV do not provide the visual information most important for postural control. Furthermore, the results suggest that rehabilitation therapists should incorporate peripheral movement cues in treatment to enhance balance retraining.

4.0 THE ROLE OF CENTRAL AND PERIPHERAL OPTIC FLOW IN THE CONTROL OF UPRIGHT POSTURE WITHIN MIXED-FREQUENCY VISUAL ENVIRONMENTS

4.1 INTRODUCTION

The purpose of the following study was the same as in the Single-Frequency experiment: to examine the influence of central and peripheral optic flow on upright posture. While the Single-Frequency experiment examined this issue by varying the field-of-view (FOV) of an oscillatory visual environment, the current study utilized only a full FOV condition in which the central and peripheral regions moved simultaneously but at different frequencies. By using this novel visual environment, we sought to determine whether a subject's postural response was predominantly characterized by the frequency of either of the stimulus regions. This may give us further insight into what central-peripheral theory is best reflected by the data. (For a more detailed discussion of these theories, see section 3.1).

There have only been a few studies previous to this that have examined central-peripheral effects by using conflicting visual motion in the different FOVs. For example, in two separate experiments, subjects were asked to report their circularvection as they sat in a vertical cylinder rotating about its long axis. They viewed a stimulus in which the central region moved in a direction opposite the periphery, and it was found that their vection was generally determined by the peripheral motion (Brandt et al. 1973; Howard and Heckmann 1989). Another study challenged this conclusion, arguing that vection strength is determined by the stimulus size and speed but not by its eccentricity (Nakamura 2001).

In contrast to these vection experiments, the present study measured the subjects' sway responses within the mixed visual environments. Although the perception of self-motion should lead to postural adjustments, it should not be assumed that detection thresholds for the two are the same. In fact, studies examining both postural sway and self-motion perception have reported a dissociation of the two phenomena, showing that subjects increase their sway in response to stimuli they do not consciously perceive (Lee and Lishman 1975; Kapteyn et al. 1979; Stoffregen 1986; Gielen and van Asten 1990). Therefore, the measurement of postural adjustments is necessary in order to better understand the influence of central and peripheral optic flow when they offer conflicting visual cues.

4.2 METHODS

4.2.1 Subjects

The same twenty subjects who were used in the single-frequency study participated in this experiment after providing informed consent.

4.2.2 Equipment

Postural sway data of the subject's head and pelvis were acquired in the anterior-posterior (AP) direction using the Polhemus Fastrak™ system. The head transducer was attached to the crown of an adjustable head strap, and the pelvis transducer was attached to an adjustable velcro belt and positioned at the height of the subject's iliac crest. The data from the Polhemus transducers were digitized at a rate of 20 Hz and stored in a Pentium III computer using the software LabView™ (National Instruments). Center-of-pressure (COP) data were also recorded in the AP direction at 100 Hz from a moveable NeuroTest™ force platform, which could rotate about an axis collinear with the subject's ankles.

During each trial, the subjects were surrounded by a contiguous front screen and two side screens, encompassing 180 degrees horizontal and 70 degrees vertical field of view (FOV) (see Figure 3.1 in previous chapter). The images were projected onto the screens using three VREX Stereoscopic projectors (model VR-2210), with a resolution of 1024 (vert.) x 768 (horiz.). Each of the projectors was interfaced to a Pentium III computer, and the three processors were synchronized to a central computer responsible for generating the visual stimulus. The subjects were asked to stand comfortably and look straight ahead with their arms crossed in front of their chest. A harness system was used to prevent injury from falling during testing, but it did not impede the subjects' movement. The examiner stood directly behind the subjects to stop an impending fall, and if they became unstable and did not regain their balance within a few seconds, the trial was stopped and repeated after a momentary rest.

4.2.3 Visual Stimulus

The central portion of the stimulus was a black-and-white target pattern comprised of a black center circle (5° in radius) and five alternating rings (each 5° wide), giving the entire target a diameter of 60°. The height of the target was adjusted so that its center was aligned with the subjects' eye height. The periphery of the stimulus was a black-and-white checkered pattern comprised of squares that were modeled to be $(0.15 \text{ m})^2$. See Figure 4.1.

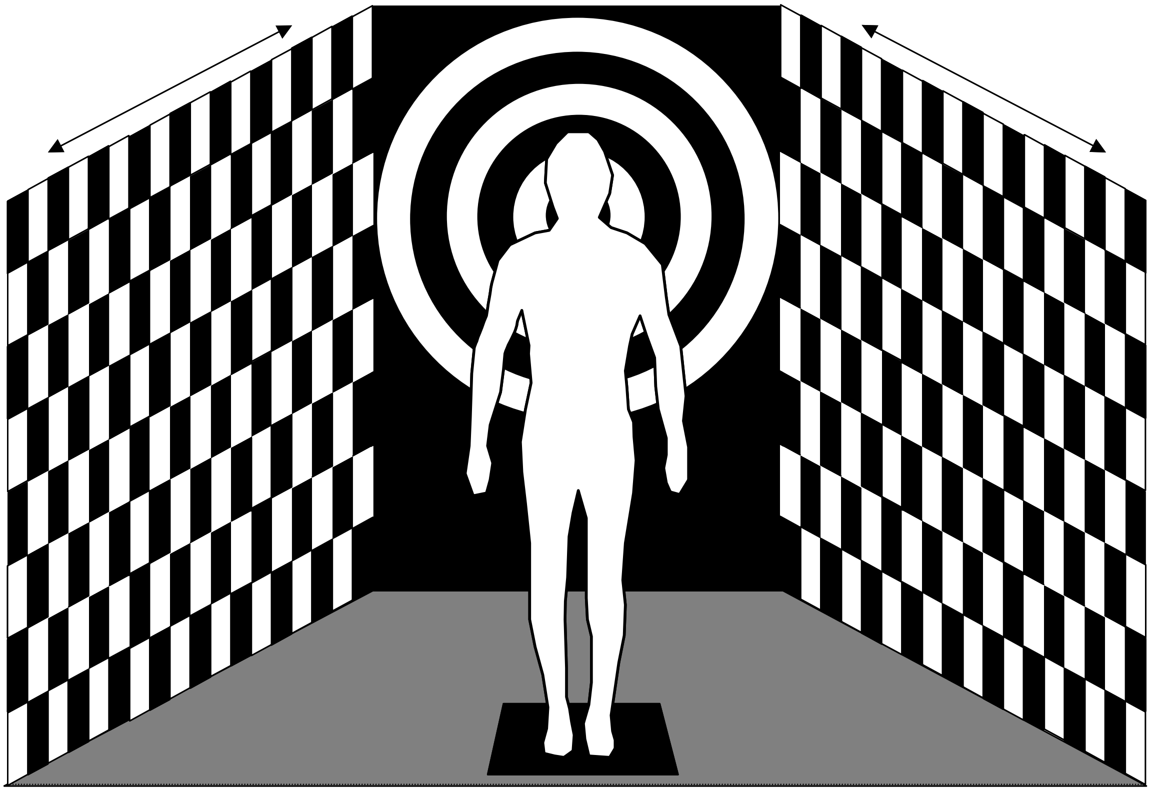


Figure 4.1. Schematic of a subject in the visual environment. The arrows on the top of the figure indicate the anterior-posterior direction of the oscillatory optic flow. The checkered patterns provided lamellar flow to the subjects' periphery while the concentric rings radially expanded and contracted in the subjects' central field of view.

4.2.4 Experiment 1

The stimulus frequencies were 0.1 and 0.25 Hz, and movement was exclusively in the AP direction. The two visual combinations are listed in Table 4.1, and each was viewed during fixed and sway-referenced platform conditions. Sway-referencing was performed to reduce the subjects' ability to use information from somatosensation to maintain upright posture. AP movements of the hip were referenced to a mean displacement that was calculated during a 30-second quiet-stance (QS) trial in which the subjects stood in the dark. The movements were converted to angular displacements and sent to the platform's rotation motor at a rate of 20 Hz. The signal was not filtered and had a lag of 0.05 seconds.

The trajectories of the two stimuli are plotted in Figure 4.2. Both regions of the stimulus had a peak-to-peak amplitude of 16 cm. They began their trajectories by moving 8 cm away from the subject, and continued for the entire 90-second duration of each trial. A QS trial was also performed during each support-surface condition, in which the subjects viewed a stationary target and checkers.

Table 4.1. Mixed-Frequency Stimuli.

Stimulus Region	Stimulus 1	Stimulus 2
Central Target	0.1 Hz 16 cm peak-to-peak	0.25 Hz 16 cm peak-to-peak
Peripheral Checkers	0.25 Hz 16 cm peak-to-peak	0.1 Hz 16 cm peak-to-peak

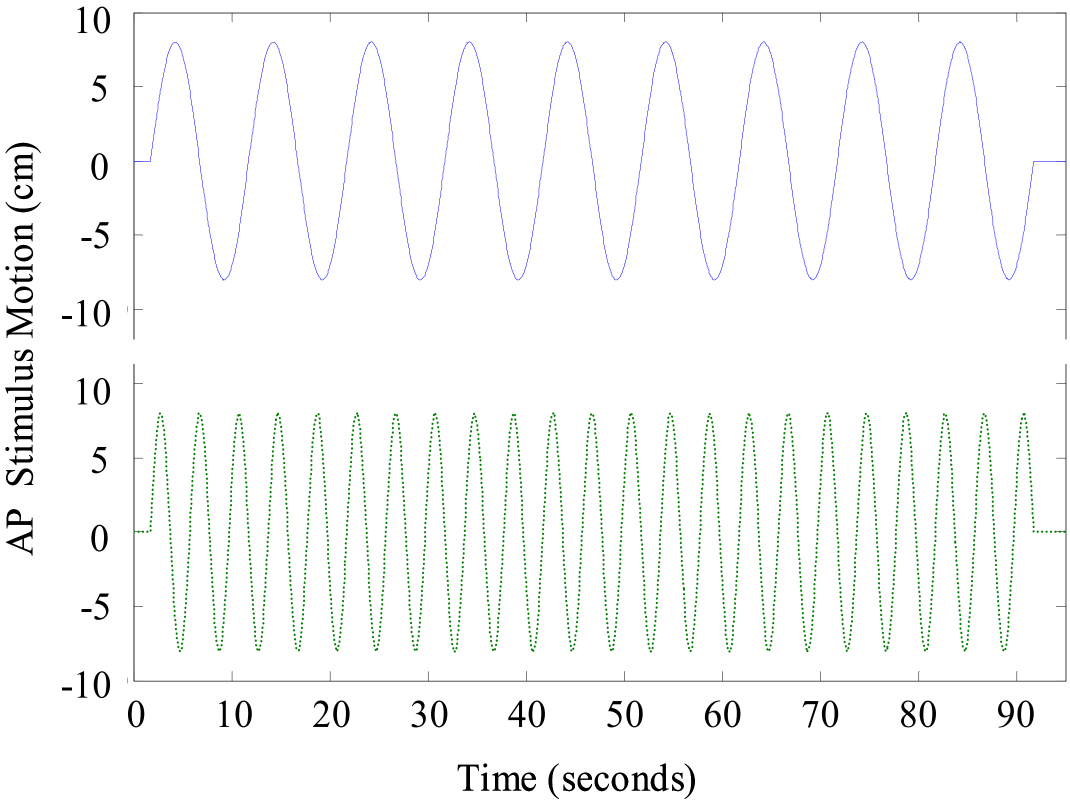


Figure 4.2. The trajectories of the 0.1 Hz (top) and 0.25 Hz (bottom) stimuli. During any given trial, the central rings moved at one frequency while the peripheral checkers moved at the other.

4.2.5 Data Analysis

All data analysis was performed using MATLAB (The MathWorks, Inc.). The original time series of the unfiltered head, pelvis, and COP data were highly correlated with each other; therefore, the inverted pendulum model was assumed, and analysis was restricted to the subject's head AP movement. The time series was zero-meaned, and at each stimulus frequency it was filtered forward and backward with a 2^{nd}-order Butterworth bandpass filter (±0.05 Hz). The attenuation at the cutoff frequencies was 3 dB, but this was doubled since the filter was implemented in both directions. The magnitude responses of the filter centered at 0.1 and 0.25 Hz are plotted in Figure 4.3. Root-Mean-Square (RMS_{FILT}) amplitudes were calculated from the filtered data strings.

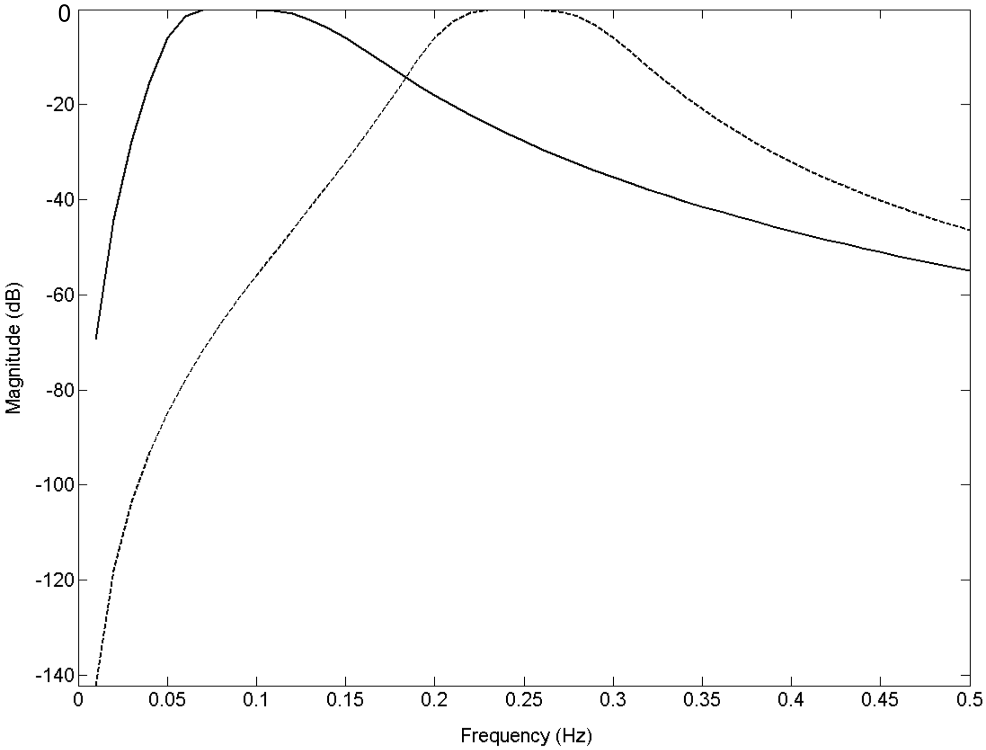


Figure 4.3. The magnitude response of the 2^{nd}-order Butterworth bandpass filter centered at 0.1 Hz (solid) and 0.25 Hz (dashed).

4.2.6 Evaluation of the Subjects' Responses to the Stimulus Frequencies

Previous studies have shown that visual stimulation typically elicits postural responses in only one-half to two-thirds of participants (Dijkstra 1994; Warren et al. 1996). Therfore, as was done in the Single-Frequency Experiment (Chapter 4), "consistent responders" were distinguished from " inconsistent responders" based on the results of the Tone Test (described in Chapter 3). The algorithm was implemented twice on each time series to test for the presence of each stimulus frequency separately. Subjects who responded to at least one of the stimulus frequencies in 3 of their 4 visual/platform conditions were considered "consistent responders." Within each visual/platform condition, tabulations were made of how many subjects responded to 0.1 Hz only, 0.25 Hz only, both frequencies, and neither frequency; this was done for all 20 subjects and for the consistent responders only. In addition, χ^2 statistics were used to compare the number of significant responses to the central stimulus with the number of significant responses to the peripheral stimulus within each visual/platform condition (for all subjects and for consistent responders only). The inconsistent responders' data were excluded from the analysis of the RMS_{FILT} sway amplitudes.

Furthermore, each subject's RMS_{FILT} values were referenced to his/her QS sway. From the stationary trials, the RMS of the subjects' QS sway (RMS_{QS}) at the two stimulus frequencies was calculated. These two values were then subtracted from the corresponding RMS values during the motion trials to attain the normalized sway ($RMS_{FILT,NORM}$) at each frequency: $RMS_{FILT,NORM} = RMS_{FILT} - RMS_{QS}$. For the statistical analysis, several paired t-tests were performed on both the RMS_{FILT} and $RMS_{FILT,NORM}$ amplitudes ($\alpha = 0.05$). These comparisons are listed in Table 4.2.

Table 4.2. Paired t-tests performed on $\mathrm{RMS}_{\mathrm{FILT}}$ and $\mathrm{RMS}_{\mathrm{FILT,NORM}}$ amplitudes.

Comparison of the sway at the two stimulus frequencies, within one visual/platform condition
1. Fixed Platform: Central-0.1 Hz vs. Peripheral-0.25 Hz
2. Fixed Platform: Central-0.25 Hz vs. Peripheral-0.1 Hz
3. Sway-Referenced Platform: Central-0.1 Hz vs. Peripheral-0.25 Hz
4. Sway-Referenced Platform: Central-0.25 Hz vs. Peripheral-0.1 Hz
Comparison of the sway at one stimulus frequency, between two visual/platform conditions
5. Fixed Platform: Central-0.1 Hz vs. Peripheral-0.1 Hz
6. Fixed Platform: Central-0.25 Hz vs. Peripheral-0.25 Hz
7. Sway-Referenced Platform: Central-0.1 Hz vs. Peripheral-0.1 Hz
8. Sway-Referenced Platform: Central-0.25 Hz vs. Peripheral-0.25 Hz

4.3 RESULTS

4.3.1 Examples of Single and Double Responses to the Mixed-Frequency Environment

Figure 4.4 plots the anterior-posterior (AP) head position and prewhitened power spectra of two subjects' responses during the Fixed Platform, Central-0.25 Hz/Peripheral-0.1 Hz condition. Subplots a and b are the head motion and power spectrum, respectively, of a subject who responded significantly to both stimulus frequencies (0.1 and 0.25 Hz), while subplots c and d are the same plots for a subject who only responded significantly to the Peripheral-0.1 Hz stimulus.

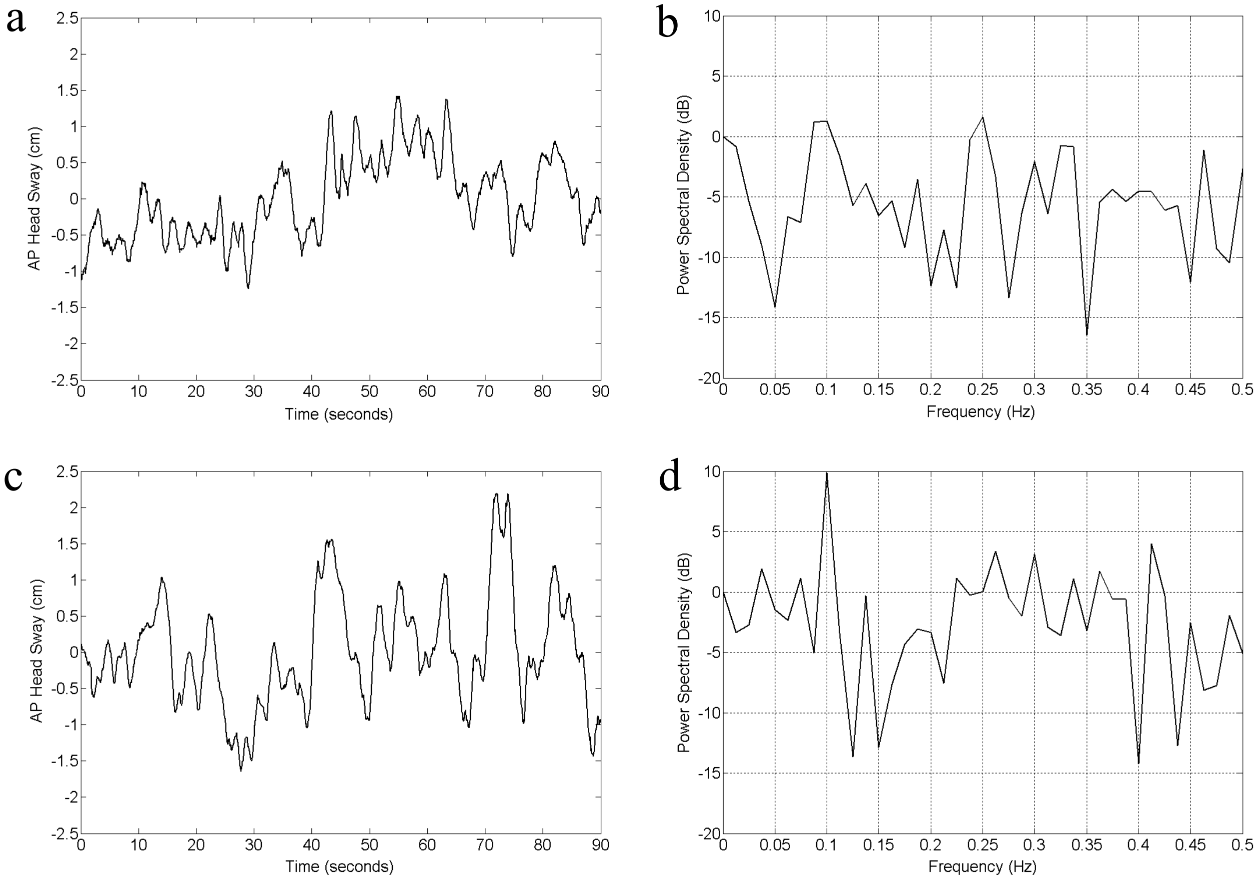


Figure 4.4. Time series and prewhitened power spectra of single and double responses during the Fixed Platform, Central-0.25 Hz/Peripheral-0.1 Hz condition. Subplots a and b are the anterior-posterior (AP) head motion and power spectrum, respectively, of a subject who responded significantly to both stimulus frequencies (0.1 and 0.25 Hz). Subplots c and d are the head motion and prewhitened power spectrum of a subject who only responded significantly to the Peripheral-0.1 Hz stimulus.

4.3.2 Number of Significant Responses

Table 4.3 shows the number of significant responses to the stimulus frequencies during each visual/platform condition. Each of the four rows corresponds to one of the conditions, and the sum of the numbers across each row equals the number of subjects (n = 20). During the fixed platform, the number of responses to the peripheral stimulus was significantly greater than the number of responses to the central stimulus for both frequency combinations: Central-0.1 Hz/Peripheral-0.25 Hz ($\chi_1^2 = 21.54$, $p < 0.001$) and Central-0.25 Hz/Peripheral-0.1 Hz ($\chi_1^2 = 16.94$, $p < 0.001$). During sway-referencing, the number of responses to the periphery was significantly greater for the Center-0.1 Hz/Periphery-0.25 Hz condition ($\chi_1^2 = 8.29$, $p = 0.004$), but not for the reverse combination ($\chi_1^2 = 3.64$, $p = 0.057$). Thirteen of the subjects responded to at least one of the stimulus frequencies in 3 of their 4 trials and were therefore designated as consistent responders; the other subjects' data were excluded from the subsequent analysis. Table 4.4 shows the consistent responders' Tone-Test results, which followed the same trends as in Table 4.3. Note that only in two instances (out of the 52 trials from this subgroup) was there not a significant response to either stimulus frequency. For this subgroup, the number of responses to the periphery was significantly greater than the number of responses to the center during all visual/platform conditions ($\chi_1^2 > 4.25$, $p \le 0.039$). The χ^2 results for all 20 subjects and for the 13 consistent responders are summarized in Tables 5.5 and 5.6, respectively.

Table 4.3. Number of significant responses to the stimulus frequencies, including all subjects.

Platform	Amplitude	Frequency Combination	0.1 Hz only	0.25 Hz only	Both	Neither
Fixed	Cent = 16 cm Peri = 16 cm	Cent = 0.1 Hz, Peri = 0.25 Hz	0	14	0	6
		Cent = 0.25 Hz, Peri = 0.1 Hz	13	0	3	4
Sway	Cent = 16 cm Peri = 16 cm	Cent = 0.1 Hz, Peri = 0.25 Hz	1	10	6	3
		Cent = 0.25 Hz, Peri = 0.1 Hz	8	2	4	6

Table 4.4. Number of significant responses to the stimulus frequencies, including only the 13 subjects who were consistent responders.

Platform	Amplitude	Frequency	0.1 Hz only	0.25 Hz only	Both	Neither
Fixed	Cent = 16 cm Peri = 16 cm	Cent = 0.1 Hz, Peri = 0.25 Hz	0	12	0	1
		Cent = 0.25 Hz, Peri = 0.1 Hz	9	0	3	1
Sway	Cent = 16 cm Peri = 16 cm	Cent = 0.1 Hz, Peri = 0.25 Hz	0	8	5	0
		Cent = 0.25 Hz, Peri = 0.1 Hz	7	2	4	0

Table 4.5. Number of responses to the central and peripheral stimulus frequency during each of the visual/platform conditions, as well as χ^2 statistics, including all 20 subjects. If responses were observed at both stimulus frequencies in one trial, a response was tabulated for each stimulus region.

Platform	Amplitude	Frequency	Central	Peripheral	Chi-Squared Value	p-value
Fixed	Cent = 16 cm Peri = 16 cm	Cent = 0.1 Hz, Peri = 0.25 Hz	0	14	21.54	$p < 0.001$
		Cent = 0.25 Hz, Peri = 0.1 Hz	3	16	16.94	$p < 0.001$
Sway	Cent = 16 cm Peri = 16 cm	Cent = 0.1 Hz, Peri = 0.25 Hz	7	16	8.29	$p = 0.004$
		Cent = 0.25 Hz, Peri = 0.1 Hz	6	12	3.64	$p = 0.057$

Table 4.6. Number of responses to the central and peripheral stimulus frequencies during each of the visual/platform conditions, as well as χ^2 statistics. Data only includes the 13 subjects who were consistent responders. If responses were observed at both stimulus frequencies in one trial, a response was tabulated for each stimulus region.

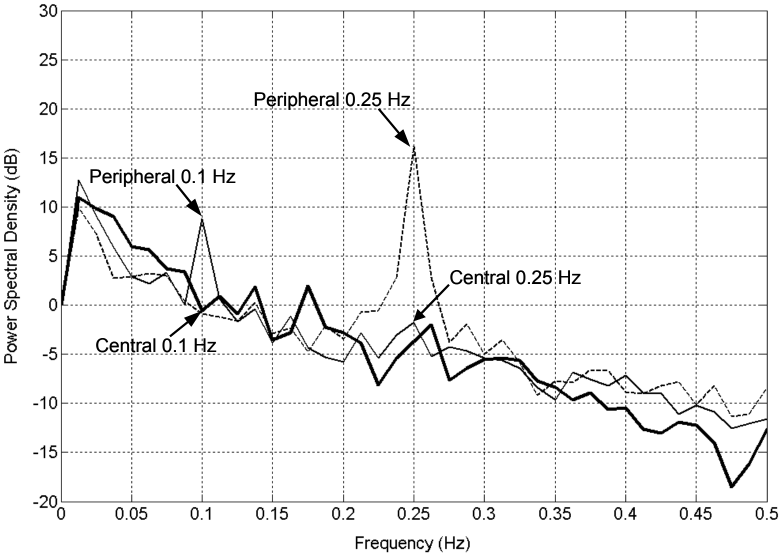
Platform	Amplitude	Frequency	Central	Peripheral	Chi-Squared Value	p-value
Fixed	Cent = 16 cm Peri = 16 cm	Cent = 0.1 Hz, Peri = 0.25 Hz	0	12	22.29	$p < 0.001$
		Cent = 0.25 Hz, Peri = 0.1 Hz	3	12	12.76	$p < 0.001$
Sway	Cent = 16 cm Peri = 16 cm	Cent = 0.1 Hz, Peri = 0.25 Hz	5	13	11.56	$p = 0.001$
		Cent = 0.25 Hz, Peri = 0.1 Hz	6	11	4.25	$p = 0.039$

4.3.3 Power Spectral Densities of the Consistent Responders' Sway

Figure 4.5 plots the averages of the consistent responders' power spectral densities during the fixed (top) and sway-referenced (bottom) platform conditions. Each graph contains the average spectra from the following visual conditions: quiet stance (QS), Central-0.1 Hz/Peripheral-0.25 Hz, and Central-0.25 Hz/Peripheral-0.1 Hz. Postural sway data routinely exhibit a low-pass spectrum in which the signal attenuates with increasing frequency. This is observed in the quiet-stance spectra of both platform conditions (thick line), and in the spectral floors of the moving scene averages, which show roughly a 20-25 dB rolloff in signal power from 0 to 0.5 Hz. Note that during the fixed platform (Figure 4.5a), the Central-0.1/Peripheral-0.25 data exhibit virtually no power at the central stimulus frequency (beyond what exists during QS), and this agrees with the zero significant responses given by the Tone Test. The opposite frequency combination during the fixed surface exhibits a small peak at the central frequency, corresponding to only 3/13 responses reported by the Tone Test. However, both frequency combinations show significant peaks at the peripheral stimuli, with the peak at 0.25 Hz exceeding that at 0.1 Hz. This occurs despite the fact that the spectral floor neighboring the peak at 0.1 Hz is about 5 dB greater than the floor neighboring the 0.25 Hz peak.

During sway-referencing (Figure 4.5b) modest peaks are observed at the central frequencies during both visual combinations, since 5 of the consistent responders attended to the Central-0.1 Hz stimulus and 6 attended to the Central-0.25 Hz stimulus. The peaks at the peripheral frequencies are nevertheless much greater, and the power at 0.25 Hz is slightly greater than the power at 0.1 Hz. Again, note the large differential in QS sway between the two frequencies of interest (~ 10 dB).

a)



b)

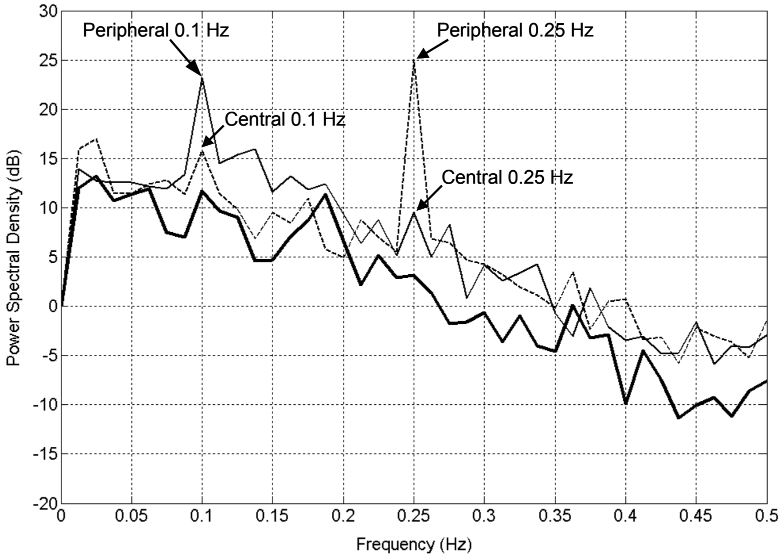


Figure 4.5. Averages of the consistent responders' power spectral densities during the fixed (top) and sway-referenced (bottom) support-surface conditions. Each graph contains the average spectra from the following visual conditions: quiet stance (thick solid line), Central-0.1 Hz/Peripheral-0.25 Hz (thin dashed line), and Central-0.25 Hz/Peripheral-0.1 Hz (thin solid line). Note that the power of the quiet-stance spectra decreases with increasing frequency, and that the spectral floors of the moving-stance averages follow this trend.

4.3.4 Comparison of the Absolute Sway at the Two Stimulus Frequencies Within Each Visual/Platform Condition

Figure 4.6 plots the means of the RMS_{FILT} amplitudes at both frequencies during all of the visual/platform conditions. Within each of the four conditions, the bar on the right designates the response to the peripheral stimulus. The solid bars refer to 0.1 Hz, and the textured bars, to 0.25 Hz. When comparing the RMS_{FILT} amplitudes within each condition, the amount of sway at the peripheral frequency appears to be greater than the sway at the central frequency, but the difference only reached a significant level when the peripheral frequency was 0.1 Hz (pairs 2 and 4; $p < 0.001$ for both).

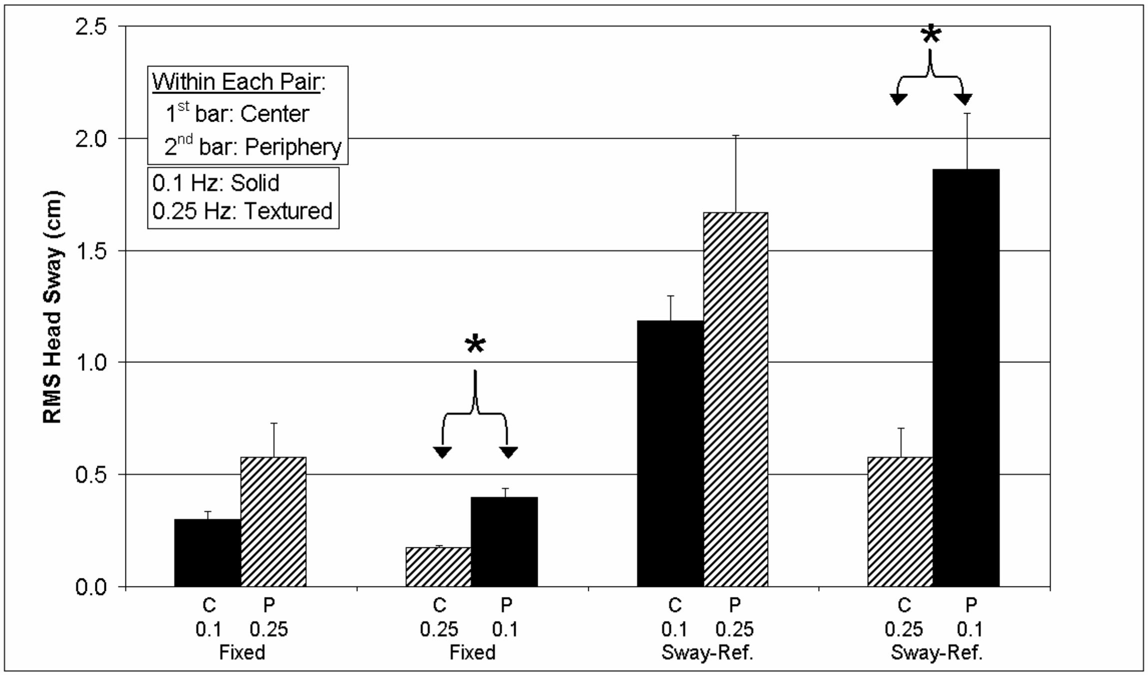


Figure 4.6. Comparison of the responders' $\mathrm{RMS}_{\mathrm{FILT}}$ sway at the two stimulus frequencies within each visual/platform condition. The four pairings correspond to the four conditions. Within each pairing, the bar on the left represents the average (± SEM) $\mathrm{RMS}_{\mathrm{FILT}}$ sway at the central stimulus frequency, while the bar on the right represents the average (± SEM) $\mathrm{RMS}_{\mathrm{FILT}}$ sway at the peripheral stimulus frequency. The solid bars refer to 0.1 Hz, and the textured bars, to 0.25 Hz. Significant differences were observed in the bracketed pairs marked with asterisks (*).

4.3.5 Comparison of the Normalized Sway at the Two Stimulus Frequencies Within Each Visual/Platform Condition

Figure 4.7 shows that during the full-scene stationary stimulus, the subjects' mean RMS_{QS} sway was significantly greater at 0.1 Hz than at 0.25 Hz, for both platforms ($p < 0.001$). In order to compare the subjects' actual responses to the scene's movement, the QS component of the subjects' sway was subtracted. The normalized RMS responses ($RMS_{FILT,NORM}$) are displayed in Figure 4.8. Within 3 of the 4 visual/platform conditions, the $RMS_{FILT,NORM}$ sway at the peripheral frequency was significantly greater than the normalized sway at the central frequency ($p \leq 0.012$). The one condition in which a significant difference was not observed was Central-0.25 Hz/Peripheral-0.1 Hz, Fixed Surface ($p = 0.386$).

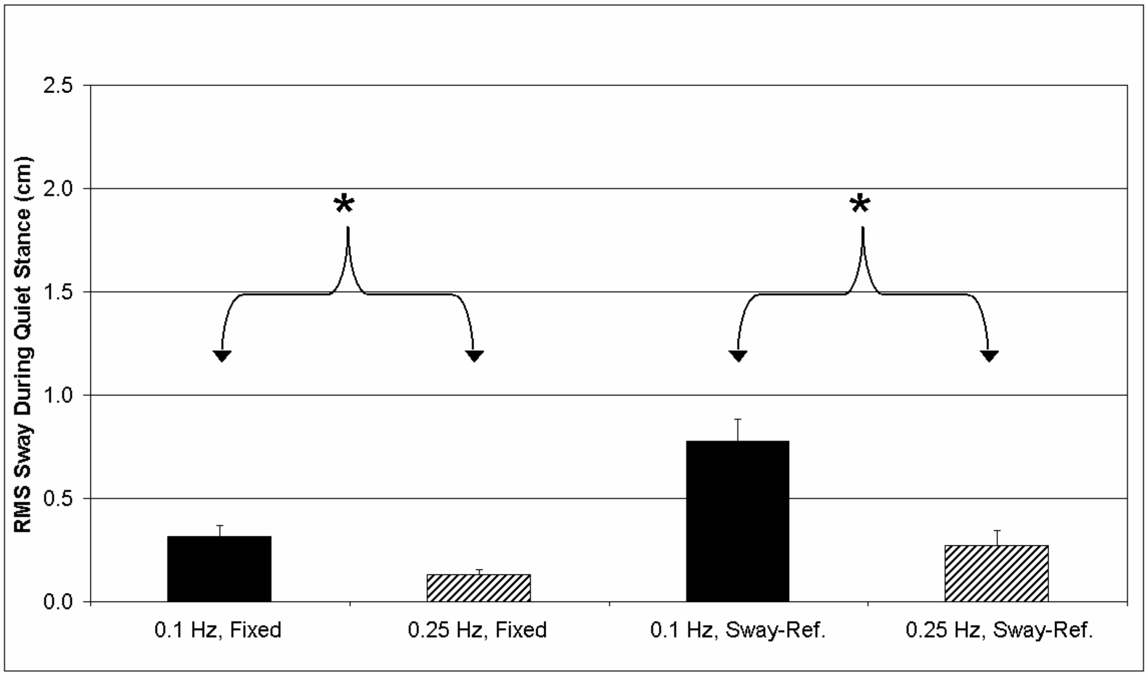


Figure 4.7. Averages (± SEM) of the consistent responders' $\mathrm{RMS}_{\mathrm{QS,FILT}}$ sway at 0.1 Hz and 0.25 Hz during the Full FOV stationary condition (for both support-surfaces). The QS sway at 0.1 Hz was significantly greater than the QS sway at 0.25, indicated by the bracketed pairs marked with asterisks (*).

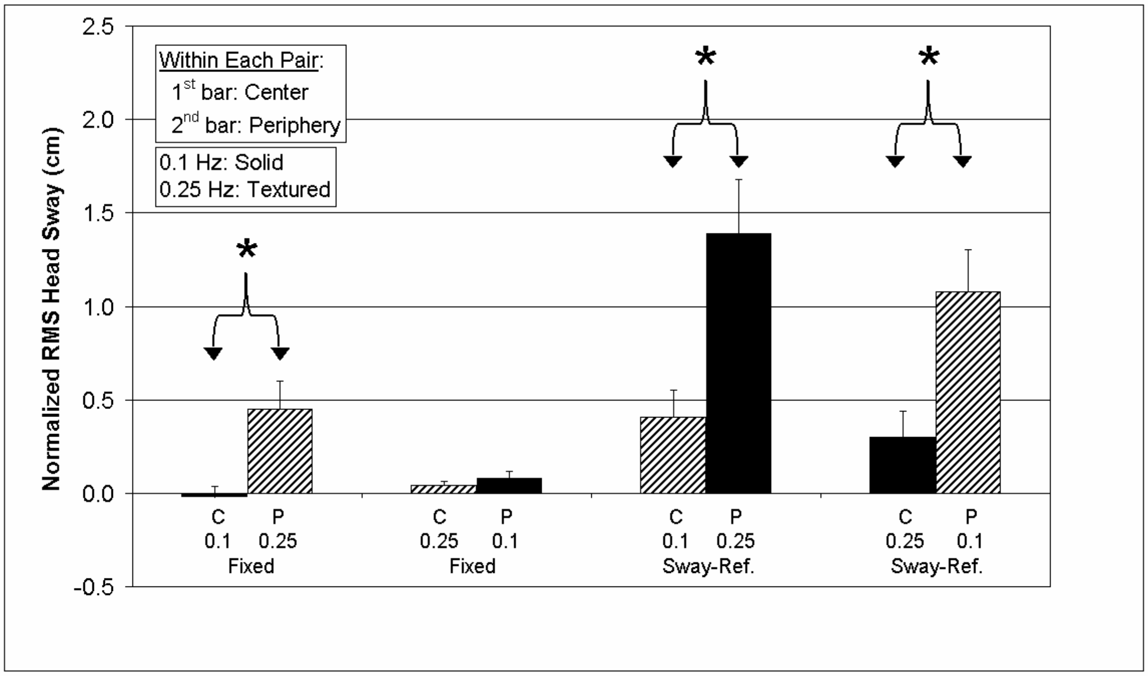


Figure 4.8. Comparison of the consistent responders' $\mathrm{RMS}_{\mathrm{FILT,NORM}}$ sway at the two stimulus frequencies within each visual/platform condition. The four pairings correspond to the four conditions. Within each pairing, the bar on the left represents the average (± SEM) $\mathrm{RMS}_{\mathrm{FILT,NORM}}$ sway at the central stimulus frequency, while the bar on the right represents the average (± SEM) $\mathrm{RMS}_{\mathrm{FILT,NORM}}$ sway at the peripheral stimulus frequency. The solid bars refer to 0.1 Hz, and the textured bars, to 0.25 Hz. Significant differences were observed in the bracketed pairs marked with asterisks (*).

4.3.6 Comparison of the Sway at One Stimulus Frequency Between the Two Visual Conditions

The RMS_{FILT} sway at a given frequency was also compared between the two frequency combinations (e.g., Center-0.1 Hz vs. Periphery-0.1 Hz), and in all four cases, the response to the frequency presented in the peripheral stimulus was significantly greater than when the same frequency was presented in the center (Figure 4.9, $p \leq 0.039$). The normalized data (Figure 4.10) gave exactly the same p-values, which would be expected in a paired t-test model. (Normalization - i.e., subtracting out the QS sway at the stimulus frequency - does not change the variance between the two groups since the value being subtracted out for each subject is the same regardless of the stimulus region oscillating at that frequency.)

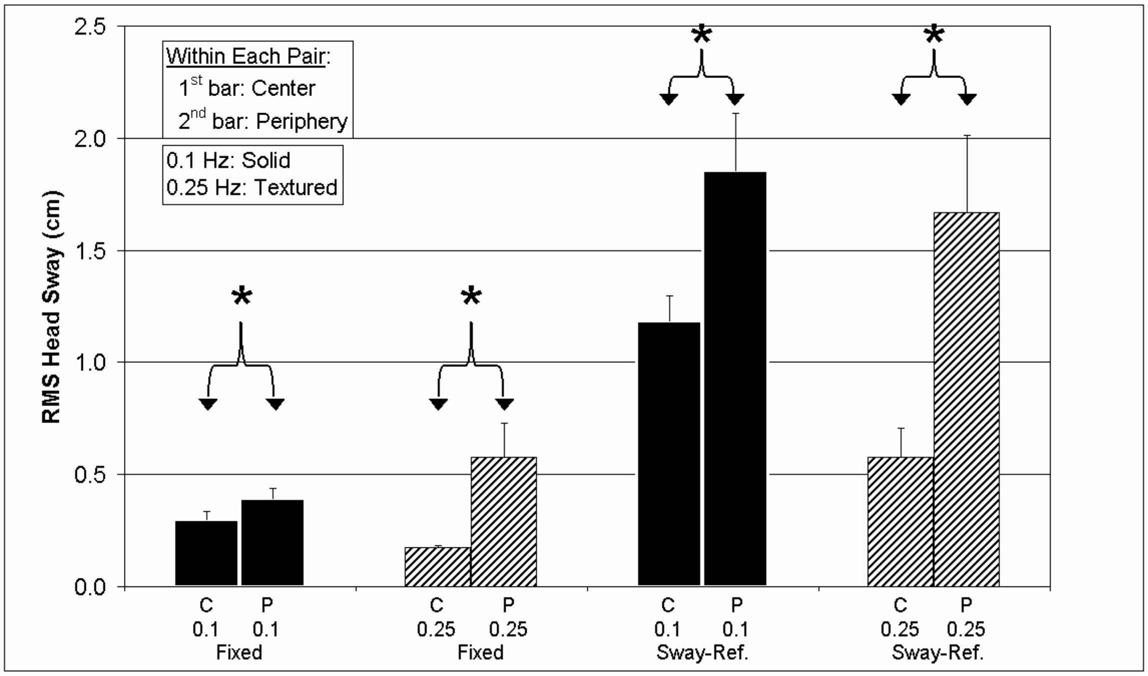


Figure 4.9. Comparison of the consistent responders' RMS_{FILT} sway at one stimulus frequency between the two visual conditions (for each support surface). The four pairings correspond to the four conditions. Within each pair the bar on the left represents the average (± SEM) RMS_{FILT} sway at the stimulus frequency when presented to the central FOV, while the bar on the right represents the average (± SEM) RMS_{FILT} sway at the same frequency presented to the peripheral FOV. The solid bars refer to 0.1 Hz, and the textured bars, to 0.25 Hz. Significant differences were observed in all pairs, bracketed with asterisks (*).

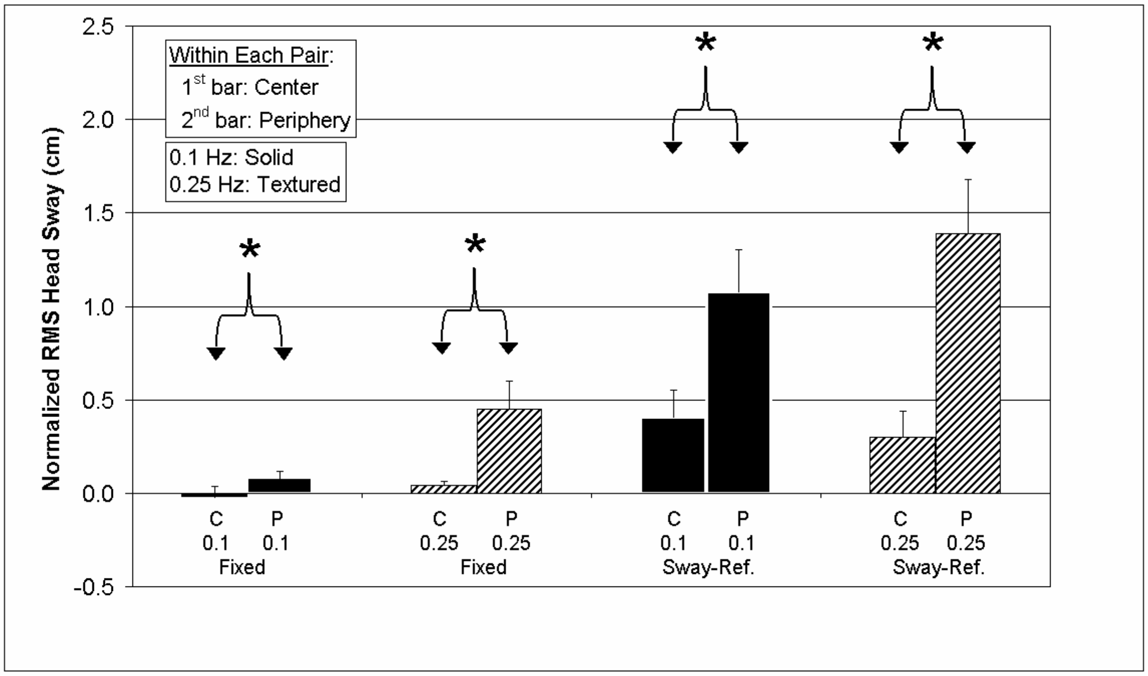


Figure 4.10. Comparison of the consistent responders' $RMS_{FILT,NORM}$ sway at one stimulus frequency between the two visual conditions (for each support surface). The four pairings correspond to the four conditions. Within each pair the bar on the left represents the average (± SEM) $RMS_{FILT,NORM}$ sway at the stimulus frequency when presented to the central FOV, while the bar on the right represents the average (± SEM) $RMS_{FILT,NORM}$ sway at the same frequency presented to the peripheral FOV. The solid bars refer to 0.1 Hz, and the textured bars, to 0.25 Hz. Significant differences were observed in all pairs, bracketed with asterisks (*).

4.4 METHODS FOR EXPERIMENT 2

In Experiment 1 the peak-to-peak amplitude of the central and peripheral portions of the stimulus (16 cm) was measured using a linear world-reference frame. An alternative method of measuring the amplitude of the stimulus regions is to use spherical eye coordinates. If the 16 cm linear amplitudes of the two regions are converted into degrees of visual arc, it is found that the arc distance traversed by the checkered pattern is much greater than the arc distance traversed by the target. The results from Experiment 1 indicate that the checkered stimulus elicited greater RMS_{FILT} and $RMS_{FILT,NORM}$ sway than the central target at 16 cm, but it was not certain whether this was due to a greater sensitivity to the peripheral stimulus, or if it was merely a consequence of the disparate arc amplitudes. In the Single-Frequency study, the amplitude of the central stimulus was increased to 7.6 deg p-p visual arc, which is the arc amplitude of the periphery at 16 cm. Refer to section 4.4 for an explanation of how the amplitude was converted from linear to spherical units. For the second phase of this study, the modified amplitude of the central stimulus was used so that the central and peripheral regions moved at different frequencies but the same arc amplitude (7.6 deg p-p). The same frequency combinations shown in Table 4.1 were repeated for both support-surface conditions, and the QS trials were also repeated. Data were collected from the same 7 subjects who participated in Experiment 2 of the Single-Frequency study. In Experiment 1 of the current (Mixed-Frequency) study, all 7 of these subjects met the criterion for being a responder during the mixed-frequency trials. The Tone-Test results were again analyzed using the same χ^2 analysis as performed in Experiment 1. Furthermore, the same 8 paired t-test comparisons listed in Table 4.2 were performed on the RMS_{FILT} and $RMS_{FILT,NORM}$ amplitudes.

4.5 RESULTS FOR EXPERIMENT 2

4.5.1 Number of Significant Responses

Despite the increase in amplitude of the central stimulus, few subjects responded to it (see Table 4.7). Within each surface condition, the number of responses to the peripheral stimulus significantly outnumbered the responses to the central stimulus when the periphery moved at 0.25 Hz (fixed: $\chi_1^2 = 14.00$, $p < 0.001$; sway-referenced: $\chi_1^2 = 10.50$, $p = 0.001$), but not when the periphery moved at 0.1 Hz (fixed: $\chi_1^2 = 1.17$, $p = 0.280$; sway-referenced: $\chi_1^2 = 0.31$, $p = 0.577$). The difference in each of the latter cases was not significant because two subjects responded well to both frequencies in the same trial. There was only 1 trial out of the 28 in which no significant response was observed at either frequency. The χ^2 results for Experiment 2 are summarized in Table 4.8.

Table 4.7. Number of significant responses to stimulus frequencies. Amplitude of each stimulus region is 7.6 degrees (n = 7).

Platform	Amplitude	Frequency	0.1 Hz only	0.25 Hz only	Both	Neither
Fixed	Cent = 7.6 deg Peri = 7.6 deg	Cent = 0.1 Hz, Peri = 0.25 Hz	0	7	0	0
		Cent = 0.25 Hz, Peri = 0.1 Hz	3	1	2	1
Sway	Cent = 7.6 deg Peri = 7.6 deg	Cent = 0.1 Hz, Peri = 0.25 Hz	0	6	1	0
		Cent = 0.25 Hz, Peri = 0.1 Hz	3	2	2	0

Table 4.8. Number of responses to the central and peripheral stimulus frequencies during each of the visual/platform conditions in Experiment 2, as well as Chi-Squared statistics ($n = 7$). If responses were observed at both stimulus frequencies in one trial, a response was tabulated for each stimulus region.

Platform	Amplitude	Frequency	Central	Peripheral	Chi-Squared Value	p-value
Fixed	Cent = 7.6 deg Peri = 7.6 deg	Cent = 0.1 Hz, Peri = 0.25 Hz	0	7	14.00	$p < 0.001$
		Cent = 0.25 Hz, Peri = 0.1 Hz	3	5	1.17	$p = 0.280$
Sway	Cent = 7.6 deg Peri = 7.6 deg	Cent = 0.1 Hz, Peri = 0.25 Hz	1	7	10.50	$p = 0.001$
		Cent = 0.25 Hz, Peri = 0.1 Hz	4	5	0.31	$p = 0.577$

4.5.2 Comparison of the Sway at the Two Stimulus Frequencies Within Each Visual/Platform Condition

Figure 4.11 combines the RMS_{FILT} data of both mixed-frequency experiments. Within each visual/platform condition, the first two bars show exactly the same values as shown in the plots of the first experiment (n = 13); the last two bars in each condition show the corresponding data for the second experiment (n = 7). Within each condition, comparisons between the amounts of sway at the peripheral and central stimuli at 7.6 deg mirrored what was seen at 16 cm. The amount of sway at the peripheral frequency was significantly greater than the sway at the central frequency only when the periphery moved at 0.1 Hz (fixed: $p = 0.013$; sway-ref.: $p = 0.003$). Not surprisingly, the $RMS_{QS,FILT}$ sway was again significantly greater at 0.1 Hz than at 0.25 Hz, during the fixed ($p = 0.035$) and sway-referenced ($p = 0.049$) support-surface conditions (see Figure 4.12). When the QS component of sway was subtracted, the $RMS_{FILT,NORM}$ responses (Figure 4.13) failed to show any significant central/peripheral effects within any of the visual/platform conditions ($0.06 \leq p \leq 0.987$). According to the plots, the sway at the peripheral frequency appears to be greater than the sway at the central frequency during the Central-0.1 Hz/Peripheral-0.25 Hz condition for both platforms. However, the statistical test was conservative due to the smaller sample size (n =7).

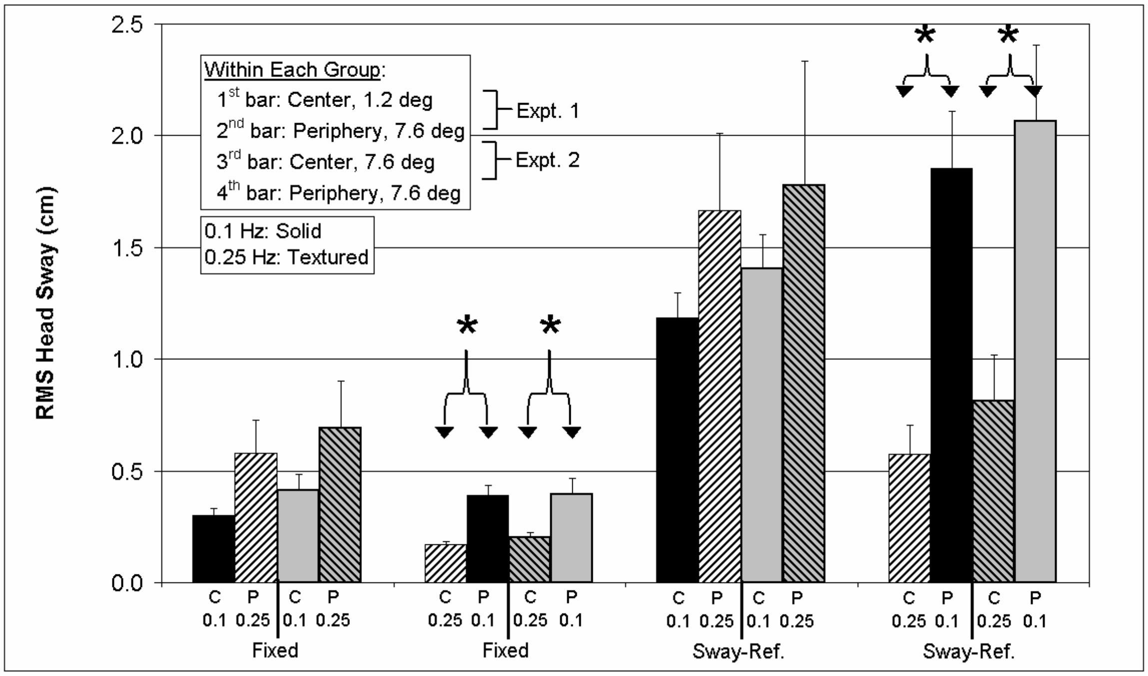


Figure 4.11. Comparison of the $\mathrm{RMS}_{\mathrm{FILT}}$ sway at the two stimulus frequencies within each visual/platform condition. The four groups correspond to the four conditions. Within each group, the first two bars are from Experiment 1 (n = 13, shown previously in Figure 4.6), and the second two are the corresponding data from Experiment 2 (n = 7). Within each pair the bar on the left represents the average (± SEM) $\mathrm{RMS}_{\mathrm{FILT}}$ sway at the central stimulus frequency, while the bar on the right represents the average (± SEM) $\mathrm{RMS}_{\mathrm{FILT}}$ sway at the peripheral stimulus frequency. The solid bars refer to 0.1 Hz, and the textured bars, to 0.25 Hz. Significant differences were observed in the bracketed pairs marked with asterisks (*).

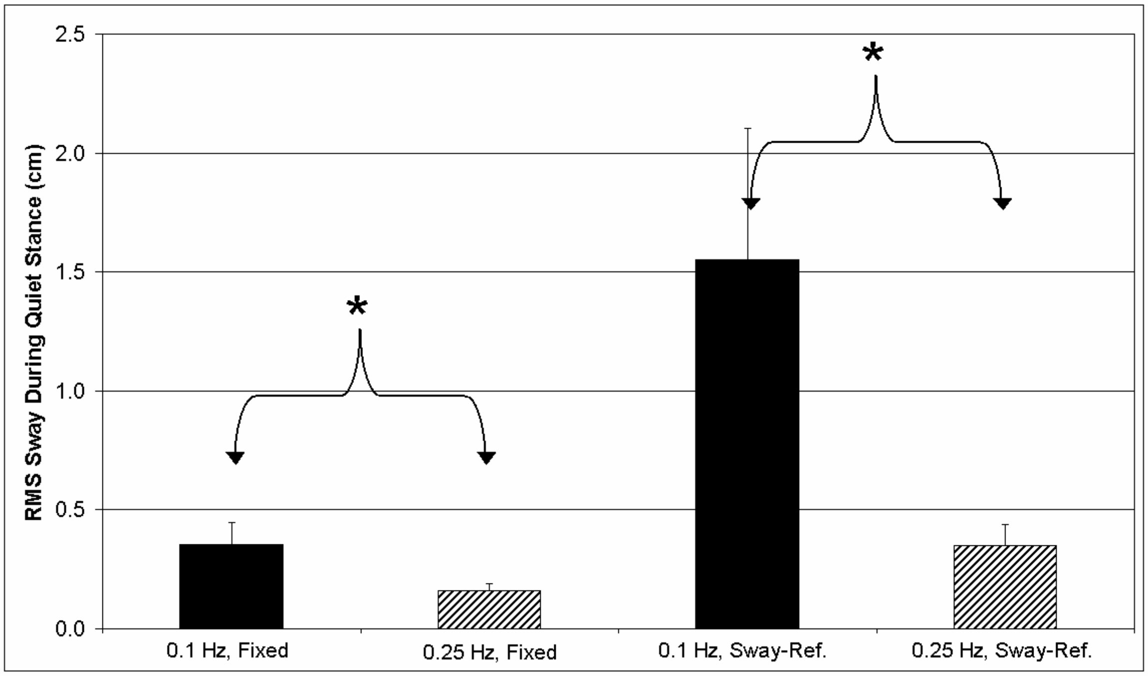


Figure 4.12. Averages (± SEM) of the consistent responders' $\mathrm{RMS}_{\mathrm{QS,FILT}}$ sway at 0.1 Hz and 0.25 Hz during the Full FOV stationary condition of Experiment 2. The QS sway at 0.1 Hz was significantly greater than the QS sway at 0.25 Hz during both support-surface conditions.

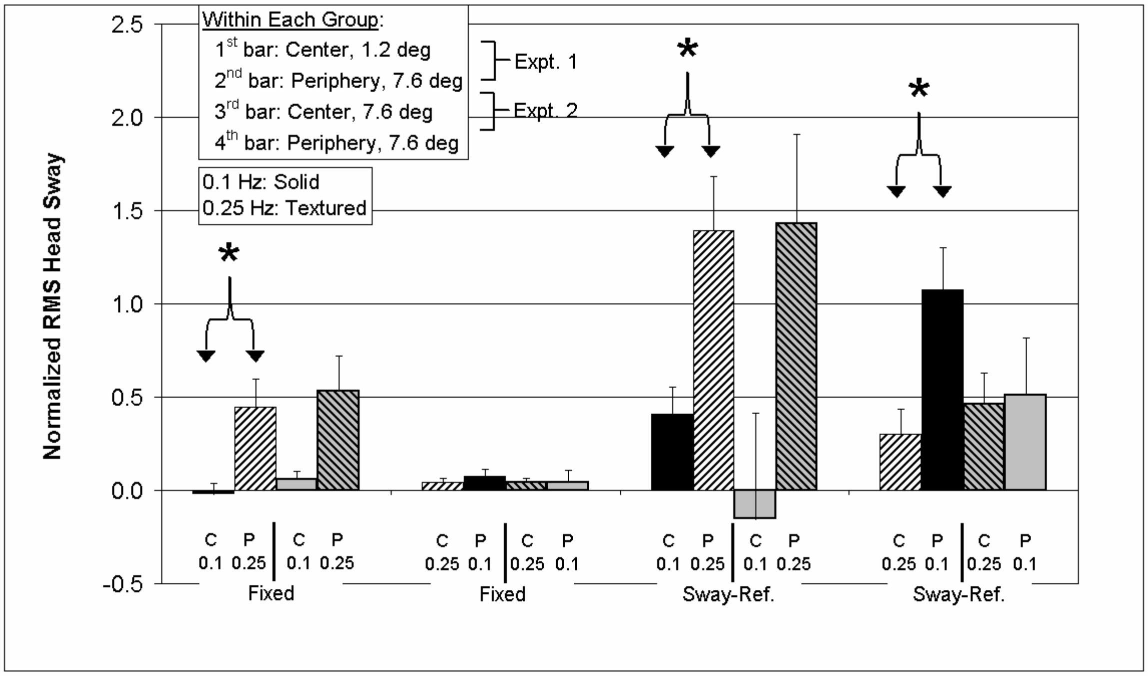


Figure 4.13. Comparison of the $\mathrm{RMS}_{\mathrm{FILT,NORM}}$ sway at the two stimulus frequencies within each visual/platform condition. The four groups correspond to the four conditions. Within each group, the first two bars are from Experiment 1 (n = 13, shown previously in Figure 4.8), and the second two are the corresponding data from Experiment 2 (n = 7). Within each pair the bar on the left represents the average (± SEM) $\mathrm{RMS}_{\mathrm{FILT,NORM}}$ sway at the central stimulus frequency, while the bar on the right represents the average (± SEM) $\mathrm{RMS}_{\mathrm{FILT,NORM}}$ sway at the peripheral stimulus frequency. The solid bars refer to 0.1 Hz, and the textured bars, to 0.25 Hz. Significant differences were observed in the bracketed pairs marked with asterisks (*).

4.5.3 Comparison of the Sway at One Stimulus Frequency Between the Two Visual Conditions

Lastly, the RMS sway at a given stimulus frequency was also compared between the two frequency combinations. Figures 5.14 and 5.15 display the absolute and normalized values, respectively. None of the pairs showed a significant central/peripheral effect ($0.053 \leq p \leq 0.801$). The results of the paired t-tests of Experiments 1 and 2 are summarized in Tables 5.9 and 5.10.

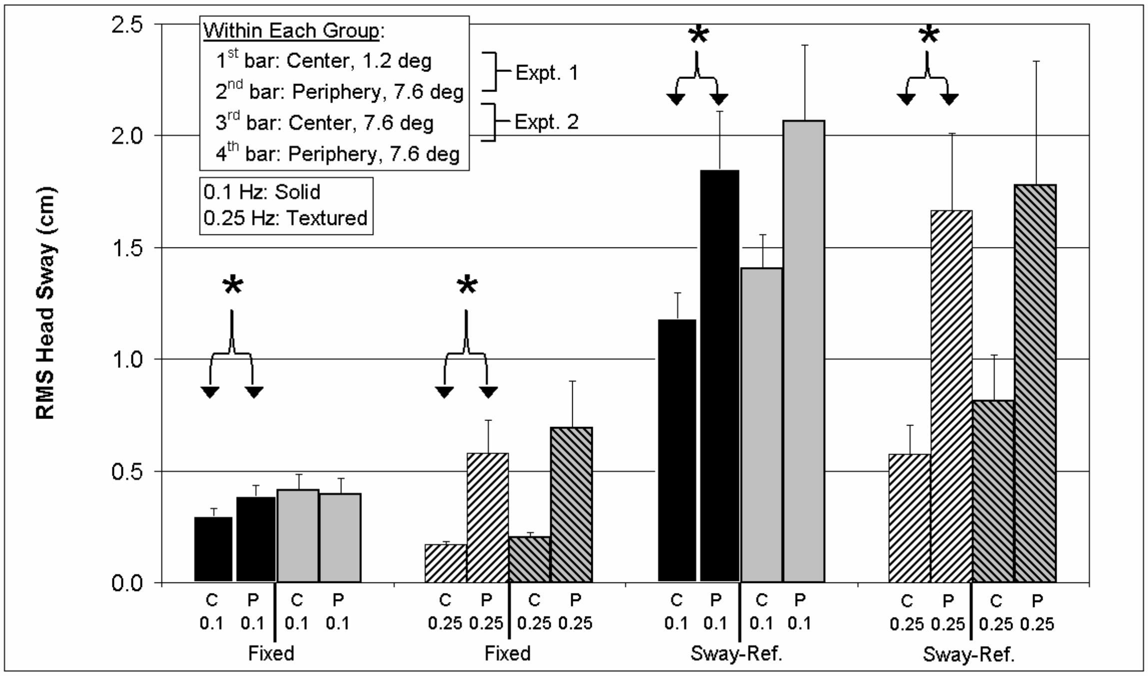


Figure 4.14. Comparison of the consistent responders' $\mathrm{RMS}_{\mathrm{FILT}}$ sway at one stimulus frequency between the two visual conditions (for each support surface). The four groups correspond to the four conditions. Within each group, the first two bars are from Experiment 1 (n = 13, shown previously in Figure 4.9), and the second two are the corresponding data from Experiment 2 (n = 7). Within each pair the bar on the left represents the average (± SEM) $\mathrm{RMS}_{\mathrm{FILT}}$ sway at the stimulus frequency when presented to the central FOV, while the bar on the right represents the average (± SEM) $\mathrm{RMS}_{\mathrm{FILT}}$ sway at the same frequency presented to the peripheral FOV. The solid bars refer to 0.1 Hz, and the textured bars, to 0.25 Hz. Significant differences were observed in the bracketed pairs marked with asterisks (*).

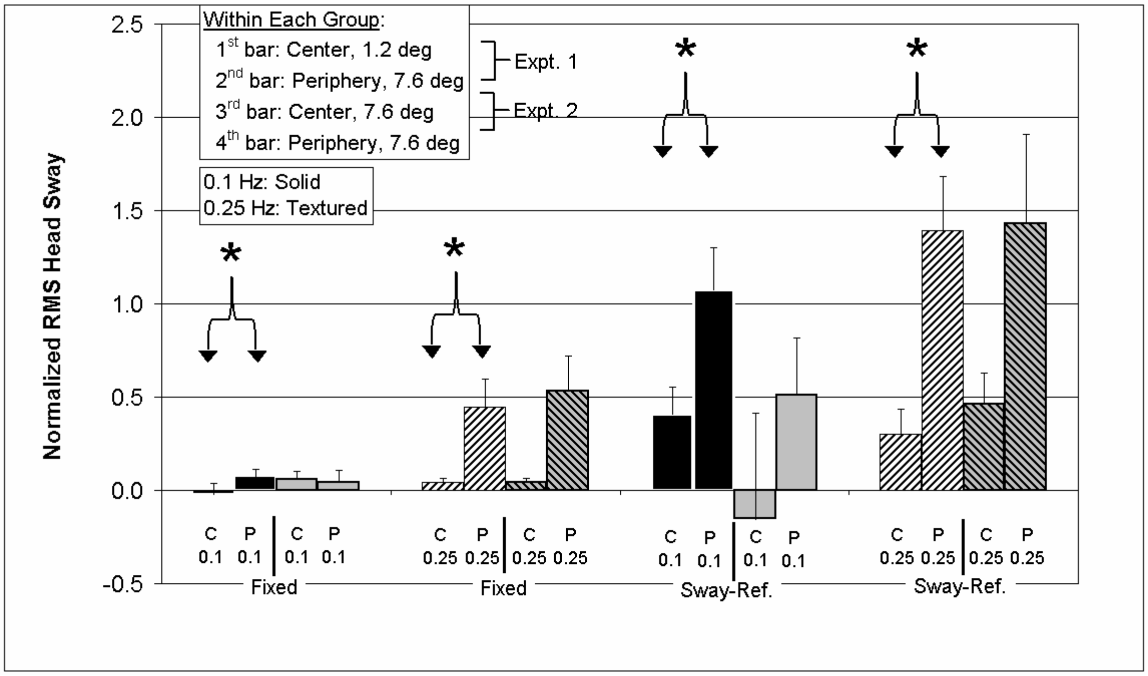


Figure 4.15. Comparison of the consistent responders' $\mathrm{RMS}_{\mathrm{FILT,NORM}}$ sway at one stimulus frequency between the two visual conditions (for each support surface). The four groups correspond to the four conditions. Within each group, the first two bars are from Experiment 1 (n = 13, shown previously in Figure 4.10), and the second two are the corresponding data from Experiment 2 (n = 7). Within each pair the bar on the left represents the average (± SEM) $\mathrm{RMS}_{\mathrm{FILT,NOMR}}$ sway at the stimulus frequency when presented to the central FOV, while the bar on the right represents the average (± SEM) $\mathrm{RMS}_{\mathrm{FILT,NORM}}$ sway at the same frequency presented to the peripheral FOV. The solid bars refer to 0.1 Hz, and the textured bars, to 0.25 Hz. Significant differences were observed in the bracketed pairs marked with asterisks (*).

Table 4.9. Paired t-test results for the comparisons of sway at the two stimulus frequencies within each visual/platform condition ($\alpha = 0.05$). The significant results are in **bold**, and for each of these cases, the sway at the peripheral frequency was greater than the sway at the central frequency.

Platform	Frequency Combination	Absolute RMS		Normalized RMS	
		16 cm	7.6 deg	16 cm	7.6 deg
Fixed	Cent = 0.1 Hz, Peri = 0.25 Hz	0.051	0.115	**0.003**	0.06
	Cent = 0.25 Hz, Peri = 0.1 Hz	**< 0.001**	**0.013**	0.386	0.987
Sway-Referenced	Cent = 0.1 Hz, Peri = 0.25 Hz	0.18	0.516	**0.012**	0.169
	Cent = 0.25 Hz, Peri = 0.1 Hz	**< 0.001**	**0.003**	**0.001**	0.863

Table 4.10. Paired t-test results for the comparisons of sway at one stimulus frequency between two visual conditions (for each support surface, $\alpha = 0.05$). The significant results are in **bold**, and for each of these cases, the sway at a given stimulus frequency was greater when it was presented in the periphery than when it was presented in the center.

Platform	Frequency Combination	Absolute RMS		Normalized RMS	
		16 cm	7.6 deg	16 cm	7.6 deg
Fixed	Cent = 0.1 Hz, Peri = 0.1 Hz	**0.039**	0.801	**0.039**	0.801
	Cent = 0.25 Hz, Peri = 0.25 Hz	**0.016**	0.053	**0.016**	0.053
Sway-Referenced	Cent = 0.1 Hz, Peri = 0.1 Hz	**0.01**	0.09	**0.01**	0.09
	Cent = 0.25 Hz, Peri = 0.25 Hz	**0.003**	0.093	**0.003**	0.093

4.6 DISCUSSION

In this discussion we will not only interpret the results of the Mixed-Frequency study, but we will also compare them to the Single-Frequency results of Chapter 4 to emphasize how the findings of the two studies corroborate each other.

4.6.1 Tone-Test Results

The Tone-Test results of the Single- and Mixed-Frequency studies were highly correlated when the central and peripheral stimuli had the same linear amplitude of 16 cm. In both visual environments, the subjects almost exclusively responded to the periphery while the platform was fixed. During sway-referencing, there was again a significantly greater number of responses to the peripheral optic flow, but almost half of the consistent responders also entrained to the central stimulus. In the mixed-frequency environment, during the fixed platform condition, 3/26 responded to the central optic flow while 11/26 responded to it during sway-referencing; 24/26 responded to the periphery during both platform conditions. A similar result was observed in the Single-Frequency study, in which the consistent responders (n = 10) more than doubled their responses to the 16-cm central stimulus during sway referencing (12/20), compared to the fixed-platform condition (5/20). Thus, in both environments, the consistent responders almost always attended to the peripheral optic flow, regardless of platform condition, but their sensitivity to the central stimulus increased when they were less able to use information from somatosensation to maintain their posture.

When the amplitude of the central stimulus was increased to 7.6 degrees in the Mixed-Frequency study, the number of significant responses was greatly influenced by its frequency of oscillation. During the central-0.1 Hz/peripheral-0.25 Hz condition, there was only one significant response to the central optic flow (during sway-referencing), while all seven subjects responded to the peripheral stimulus (for both platforms). However, during the opposite visual combination, there were nearly as many responses to the central stimulus (3/7 for fixed platform; 4/7 for sway-referencing) as there were to the peripheral stimulus (5/7 for both platforms). It was surprising that the adjusted central amplitude had this frequency effect in the mixed environment because it was not observed in the Single-Frequency study. When the central FOV was presented alone, only one subject responded to its movement at 0.1 Hz while only two responded to the 0.25 Hz stimulus (during each platform). It is difficult to interpret these results, except to say that central vision may prefer the higher frequency in certain mixed-environment conditions.

4.6.2 Absolute and Normalized Sway Responses to Central and Peripheral Stimuli of Equal Linear Amplitude

The spectral plots of Figure 4.5 emphasize two main factors which need to be considered when analyzing the RMS_{FILT} amplitudes: (1) there is greater quiet-stance (QS) sway at lower frequencies; (2) there is a greater moving-stance (MS) sway at the peripheral frequency. First, for both the fixed and sway-referenced platform conditions, the magnitude of the QS spectra attenuates with increasing frequency, meaning that even in the absence of a moving visual environment, there is greater natural sway at 0.1 Hz than at 0.25 Hz. This low-pass trend is also observed at the non-stimulus frequencies of the MS spectra, and therefore the peaks at 0.25 Hz begin from a lower spectral floor than the peaks at 0.1 Hz. It is important to note that the sway at the peripheral frequency changed little between visual combinations (fixed platform: $p = 0.245$; sway-referenced platform: $p = 0.349$). The main change between the visual combinations was the sway at the central stimulus. There was greater sway at the central frequency when it moved at 0.1 Hz than when it moved at 0.25 Hz (both platforms: $p \leq 0.001$) precisely because there was greater QS sway at the lower frequency. A second factor emphasized by the spectral plots is that the MS sway at the peripheral frequency is much greater than the power of the central frequency, regardless of the frequency combination of the moving environment. The sway characteristics observed in the first phase of the Mixed-Frequency study can be understood in light of these two factors.

There was greater RMS_{FILT} sway in response to the peripheral stimulus within all four visual/platform conditions, but the difference only reached a significant level during the Central-0.25 Hz/Peripheral-0.1 Hz condition. In this frequency combination, the frequency at which there was greater QS sway was also the peripheral frequency; therefore, two factors converged, resulting in a significant central/peripheral effect. During the other frequency combination, there was greater QS sway at the frequency for which there was a lesser response to the scene's motion (i.e., 0.1 Hz-Central). Consequently, the absolute RMS sway at the 0.25 Hz-peripheral stimulus was not large enough to cause a significant central/peripheral effect (fixed: $p = 0.051$; sway-ref.: $p = 0.180$). After the subjects' responses were normalized to their QS sway, it was shown that they were more sensitive to the peripheral optic flow in 3 of the 4 visual/platform conditions.

Not only was there greater sway at the peripheral frequency during both frequency combinations, but the subjects also swayed more at each frequency when it was presented in the periphery than when it was presented in the center. These combined results show that the peripheral dominance observed in the subjects' responses not only exists within a certain frequency combination but also is observed between frequency combinations. Furthermore, after normalization, the sway amplitudes in response to the peripheral-0.25 Hz optic flow were greater than the sway response to the peripheral-0.1 Hz, but this difference was only significant when the platform was fixed (p =0.025); during sway-referencing, p = 0.109. These results corroborate those of the Single-Frequency study, which also indicated a greater sensitivity to the higher frequency (see section 3.6.3).

4.6.3 Absolute and Normalized Sway Responses to Central and Peripheral Stimuli of Equal Arc Amplitude

When the amplitude of the central stimulus was adjusted so that it equaled the arc amplitude of the peripheral stimulus, the central-peripheral differences in the normalized sway responses were no longer significant. The peripheral optic flow generally caused more sway than the central flow, but given the small sample size, the results are inconclusive. Although the filtered-absolute sway at the peripheral frequency was significantly greater than the absolute sway at the central frequency during the Central-0.25 Hz/Peripheral-0.1 Hz condition (for both platforms), this effect was mainly due to the greater QS sway at 0.1 Hz. It is possible that the following comparisons would have reached a significant level with a larger sample since the p-values were fairly low: Central-0.1 Hz vs. Peripheral-0.25 Hz, Fixed (p = 0.06); Central-0.25 Hz vs. Peripheral-0.25 Hz, Fixed (p = 0.053); Central-0.1 Hz vs. Peripheral-0.1 Hz, Sway-Referenced (p = 0.09); and Central-0.25 Hz vs. Peripheral-0.25 Hz, Sway-Referenced (p = 0.093).

It was somewhat surprising that the central-peripheral differences did not maintain a significant level after the central amplitude was increased, considering that the field-of-view (FOV) effect was preserved in the Single-Frequency study after the same adjustment. One reason for these diverging results is that the subjects had more significant responses to the central-0.25 Hz stimulus in the mixed environment than they did in the Single-Frequency environment (as discussed above). However, even though the central-peripheral differences were lessened within the adjusted Mixed-Frequency environment, the responses to the original (equilinear) amplitudes seem to be more relevant to real-world surroundings. This is because the vast majority of visual motion stimulates the central and peripheral visual fields with equal linear amplitudes. Whether an observer is moving within an environment, or part of the environment is moving in relation to a stationary observer, the resultant optic flow often has same linear amplitude across different retinal eccentricities since the central and peripheral portions of the stimulus are spatially connected.

4.6.4 Previous Studies Using Mixed Visual Environments

The authors are unaware of any previous central-peripheral studies examining postural sway responses to mixed visual environments. However, a few vection experiments have presented conflicting visual cues in the central and peripheral FOVs in order to determine their relative influence in self-motion perception. For example, Brandt et al. (1973) conducted an experiment in which subjects sat in the center of a closed vertical cylinder that rotated about its long axis at various constant speeds ranging from 10-360 degrees/sec. The visual stimulus was comprised of vertical black and white stripes subtending 7 degrees of visual angle. The central 30 degrees of the stimulus moved in a direction opposite the periphery, and the area of the peripheral display was at least eight times the central area. The subjects were asked to report the direction, duration, and velocity of their perceived self-motion. It was found that they perceived themselves as moving in the direction opposite the peripheral stimulus. The motion of the central stimulus was perceived only as object motion but did not cause a sensation of self-motion in the opposite direction. When the diameter of the central stimulus was increased up to a diameter of 100 degrees, self-rotation was suppressed and replaced by an exclusive object-motion perception of both the central and peripheral stimuli. When the central stimulus was further enlarged, self-motion perception resumed. Therefore, Brandt et al. concluded that self-motion is dominated by peripheral optic flow (Brandt et al. 1973).

Howard and Heckman (1989) also examined how displays in the central and peripheral FOVs contribute to circular vection. In their first experiment, they used a central display of luminous dots, subtending up to 54 deg x 44 deg (horiz. x vert.), and a peripheral display of dots subtending 180 deg x 135 deg (horiz. x vert.). The displays rotated about the long axis of the cylinder in which the subjects were seated. A variable unique to this mixed-motion study was the relative distance between the central and peripheral stimuli: The central display was placed either 15 cm in front of, or 15 cm behind the peripheral display. The subjects reported sensations of self-motion by positioning a lever-potentiometer in the direction of their perceived motion and maintaining the position for the duration of the vection. It was found that the effect of a display, whether center or surround, was stronger when it was the more distant display than when it was the nearer one. When the surround was moving, the direction of vection was always consistent with its motion (i.e., the subjects felt like they were moving in the direction opposite the stimulus' motion). However, vection was reduced in strength by a central display moving in the opposite direction, which was also reported by Brandt et al. (1973). In their second experiment, Howard and Heckman equated the two areas of the central and peripheral displays by reducing the size of the peripheral region. A moving center seen behind a moving surround of equal area reduced surround-consistent vection almost to zero; a moving center seen in front of a moving surround enhanced surround-consistent vection, probably because the central motion made the peripheral stimulus appear to be moving faster. Several other conditions were presented that are not as relevant to the current study, but the general conclusion was that one cannot assume peripheral vision dominates self-motion perception without considering the relative distances and sizes of the displays and the motion contrast between them (Howard and Heckmann 1989).

Nakamura (2001) also conducted a vection experiment using a mixed-motion environment, and he concluded that the effects of central and peripheral optic flow on self-motion perception are equivalent. His visual stimuli were two random patterns of dots (presented in the central and peripheral FOVs), which moved at the same linear speed but in opposite medial-lateral directions. The radius of the central stimulus varied between 10–45 degrees on a screen subtending 90 x 60 degrees (vert. x horiz.). In addition, the speed of visual motion varied between the FOVs in one of the experiments. The subjects held a button in each hand, and were instructed to press the one corresponding to the direction of perceived self-motion. It was concluded that vection strength is determined by the stimulus size and speed but not by its eccentricity. However, Nakamura acknowledged that stimulus eccentricity could be confounded with stimulus size, since a larger stimulus inevitably stimulates more of the peripheral region of the observer's visual field (Nakamura 2001).

It is difficult to compare the results of the vection experiments with the postural responses of our study since the protocols are quite different. None of the previous mixed-motion experiments provided optic flow in the AP direction; furthermore, since postural responses can occur in the absence of vection (Lee and Lishman 1975; Kapteyn et al. 1979; Stoffregen 1986; Gielen and van Asten 1990), the two outcome measures are not always linked. Nonetheless, two of the studies cited above (Brandt et al. 1973; Howard and Heckmann 1989) reported that peripheral optic flow is more influential than central flow in the perception of self-motion under most stimulus conditions. Our findings that peripheral vision is more influential in postural control corroborate their results, given the assumption that motion-perception and postural sway are correlated. Our visual environment, as well as those of Brandt et al. (1973) and Howard and Heckman (1989), provided a full 180-degree horizontal FOV, and such an environment is necessary to properly test the central-peripheral hypotheses. The experiment that challenged the peripheral dominance theory (Nakamura 2001) only provided a 90-degree horizontal FOV, which is not sufficient to accurately test the question at hand.

4.7 SUMMARY

The results of this study, like the results of the Single-Frequency experiment, suggest that the postural system is more sensitive to anterior-posterior optic flow in the peripheral FOV, regardless of stimulus frequency. When the central and peripheral regions both moved with an amplitude of 16 cm, there were 3.5 times as many significant postural responses to the peripheral optic flow stimulus as there were to the central optic flow. In 3 of the 4 visual/platform conditions, the normalized RMS sway at the peripheral frequency was significantly greater than the normalized sway at the central frequency. When the central stimulus was increased to equal the arc amplitude of the peripheral optic flow (7.6 deg), the normalized sway was generally greater at the peripheral frequency, but none of the differences reached a significant level. However, the responses to the original amplitude condition seem to be more relevant, since in most real-world surroundings, the central and peripheral amplitudes of a stimulus move at the same linear amplitude.

APPENDIX A. PRELIMINARY STUDIES

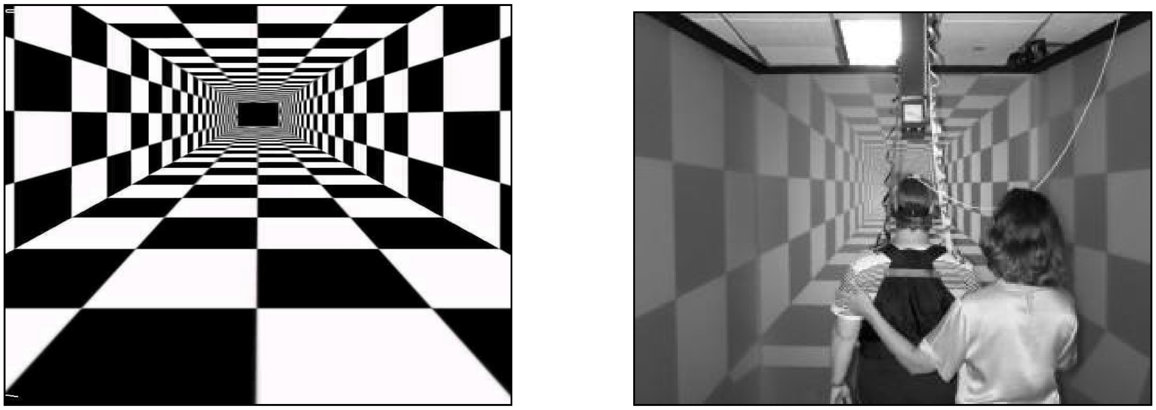
A.1 INTRODUCTION

The experiments discussed in Chapters 3 and 4 were developed based on the results of two pilot studies. Both studies investigated the influence of movement in the central and peripheral fields of view (FOVs) on upright posture at different stimulus frequencies. The first experiment used a sinusoidal stimulus of alternating black and white squares in both the central and peripheral regions. The second experiment used a pattern of black-and-white concentric rings in the central FOV, and a black-and-white checkered pattern in the periphery.

A.2 FIRST PILOT STUDY: THE INFLUENCE OF CENTRAL AND PERIPHERAL VISION ON UPRIGHT POSTURE DURING THE ANTERIOR-POSTERIOR MOVEMENT OF A CHECKERED TUNNEL

A.2.1 Methods

The postural responses of 11 subjects were measured as they viewed computer-generated oscillatory stimuli. They faced three contiguous screens that encompassed 180 x 70 deg (horizontal x vertical) of their field of view (FOV), while standing on a force platform that measured their center-of-pressure (COP). The images were displayed using three VREX stereoscopic projectors (model VR-2210), each of which were controlled by a Pentium III computer, and the computers were time-synchronized by a central computer responsible for generating the movement. The visual stimulus was a black-and-white checkered tunnel whose center was aligned to the subject's eye height. The opening of the tunnel was modeled to be $(2.4\ \text{m})^2$, and the dimensions of each checkerboard block were modeled at $(0.6\ \text{m})^2$, making each wall four blocks high. Figure A.1a shows the virtual tunnel generated by the central computer, and Figure A.1b shows the same scene projected on the screens in front of a subject.



a

b

Figure A.1. a) The computer-generated scene observed during the full field-of-view condition. b) The visual environment projected onto three contiguous screens surrounding the subject's filed of view.

During each trial, the subject observed a visual scene with two independent parameters. The first parameter was the tunnel's frequency of oscillation, and the second was the FOV of the stimulus. The two frequencies were: (1) 0.1 Hz and (2) 0.25 Hz, both of which followed the form of a sine function moving at a Root-Mean-Square (RMS) velocity of 1.2 m/s. Since the RMS velocity was constant, the amplitude of the tunnel's oscillations was larger for the lower frequency. The three FOVs were: (1) full, encompassing 180 degrees horizontal and 70 degrees vertical FOV; (2) peripheral (~60° of the central FOV were masked by a black disc); and (3) central (the other 120° were masked). Thus, there were a total of six stimulus conditions observed by each subject:

$$\begin{bmatrix} 0.1Hz \\ 0.25Hz \end{bmatrix} * \begin{bmatrix} Full\,FOV & Peripheral\ FOV & Central\,FOV \end{bmatrix}$$

Each trial lasted 80 seconds, and their order was randomized. For the ten-second segments at the beginning and end of the trial, the tunnel was stationary; during the minute in between, the tunnel oscillated at one of the specified frequencies. After each trial, the subjects sat and rested momentarily, but the position of their feet on the force plate was constant between trials.

A.2.2 Data Measurement and Analysis

In addition to the COP data, postural sway of the head, the thorax, and the pelvis were recorded in the anterior-to-posterior (AP) direction using the Polhemus Fastrak™. All data were subsequently analyzed using MATLAB (The MathWorks, Inc.). The original time series of the unfiltered head, pelvis, and COP data were highly correlated with each other; therefore, the inverted pendulum model was assumed, and analysis was restricted to the subjects' head AP movement. RMS amplitudes of the zero-meaned time series were calculated after they were filtered with a 4^{th}-order Butterworth bandpass filter centered at the stimulus frequency (±0.05

Hz). For the statistical analysis, a 2-way repeated measures ANOVA was performed to test for the effects of Frequency and FOV ($\alpha = 0.05$).

A.2.3 Results

The ANOVA model showed significant effects due to Frequency ($p < 0.001$) and FOV ($p < 0.001$) but no interaction effect ($p = 0.596$). The results are summarized in Figure A.2. The RMS sway at 0.1 Hz was greater than the sway at 0.25 Hz, and this result is consistent with previous studies that showed greater sway at lower frequencies. For the FOVs there was no significant difference in sway between the full and peripheral stimuli, but both the full and peripheral conditions elicited significantly more sway than the central stimulus. However, it should be noted that there was very little optic flow during the central condition, since the tunnel – which extended into infinity - did not display a distinct pattern at the subject’s focal point. In fact, a central gray square was used to mask any aliasing effects that occurred near the point of convergence. Therefore, even if the central and peripheral fields are differentially sensitive to optic flow, the results of this study do not conclusively show this, since the lesser sway caused by the central FOV may be merely due to the lesser optic flow provided by this stimulus. In the second pilot study the stimulus was modeled after the environment used in two recent experiments (Peterka and Benolken 1995; Borger et al. 1999). Although these former studies did not specifically investigate the effects of central and peripheral vision (since they only used a full FOV), their results indicated that the environment was effective in eliciting notable sway responses.

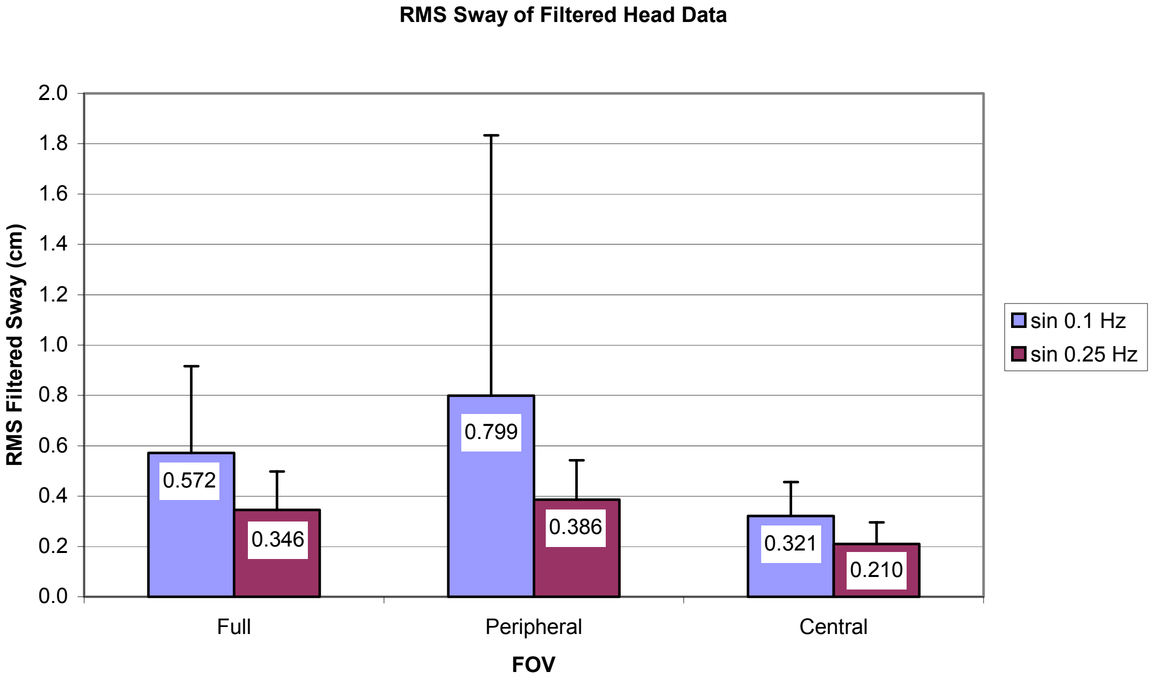


Figure A.2. Root-mean-square (RMS) sway of filtered AP head data during each frequency/FOV combination, averaged over 11 subjects.

A.3 SECOND PILOT STUDY: THE INFLUENCE OF CENTRAL AND PERIPHERAL VISION ON UPRIGHT POSTURE DURING THE ANTERIOR-POSTERIOR MOVEMENT OF CENTRAL RINGS AND PERIPHERAL CHECKERS

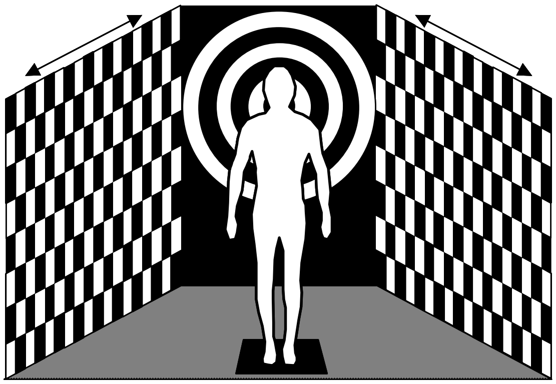
A.3.1 Methods

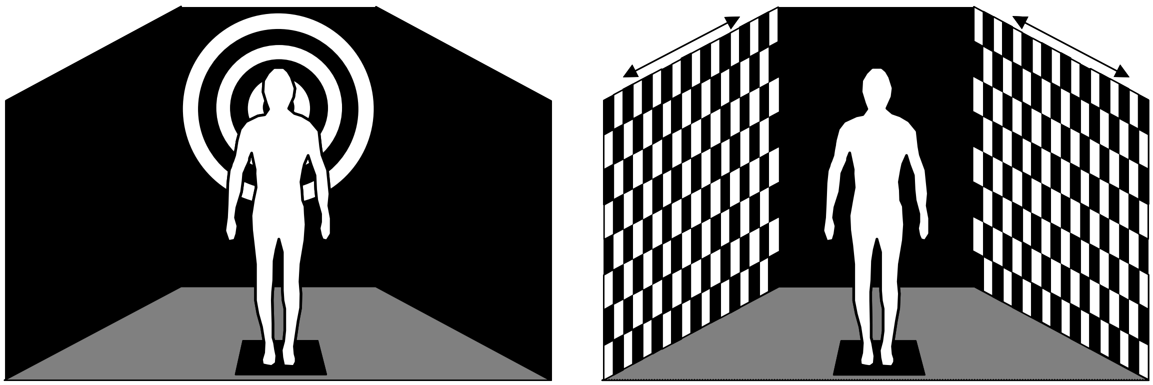
After completing the above pilot study, we conducted a small experiment in which three subjects viewed a visual environment that provided greater optic flow in both the peripheral and central FOVs. The central portion of the stimulus was a black-and-white target pattern comprised of a black center circle (5° in radius) and five alternating rings (each 5° wide), giving the entire target a radius of 30°. The height of the target was adjusted so that its center was aligned with the subject's eye height. The periphery of the stimulus was a black-and-white checkered pattern comprised of squares that were modeled to be $(0.15 \text{ m})^2$.

This study included single-frequency trials in which the central and peripheral portions of the stimulus oscillated at the same frequency, as well as mixed-frequency trials in which the periphery of the scene moved at a different frequency than the center. As in the previous study, the single-frequency trials varied according to two independent visual parameters: (1) the frequency at which the stimulus oscillated in the AP direction: 0.1 Hz and 0.25 Hz; and (2) the FOV of the stimulus: full, peripheral, and central. For the full FOV condition, both the central and the peripheral objects were present; for the peripheral FOV condition, only the checkered pattern was present; and for the central FOV, only the target was seen (Figure A.3).

For the mixed-frequency trials, the full FOV was always present, but there were two visual conditions: one in which the center moved at 0.1 Hz and the periphery moved at 0.25 Hz, and the other in which the frequencies were reversed. For both the single- and mixed-frequency trials, the peak-to-peak amplitude of the stimuli was 16 cm, and the scene began its trajectory by moving 8 cm away from the subject. Finally, each of the visual conditions was observed when the platform was fixed and sway-referenced, resulting in a total of ten trials, each of which lasted 90 seconds.

a) Full FOV





b) Central FOV

c) Peripheral FOV

Figure A.3. Schematics of a subject in the visual environment during the a) Full, b) Central, and c) Peripheral field-of-view (FOV) conditions. The arrows on the top of subplots a) and c) indicate the anterior-posterior direction of the oscillatory optic flow. The checkered patterns provided lamellar flow to the subjects' periphery while the concentric rings radially expanded and contracted in the subjects' central FOV.

A.3.2 Data Measurement and Analysis

The same methods of data collection were used as in the first pilot study. For the single-frequency data, RMS amplitudes of the AP head sway were calculated after the data were filtered with a 4th-order Butterworth bandpass filter centered at the stimulus frequency (±0.05 Hz). For the mixed-frequency data, power spectral density (PSD) estimates were calculated at the stimulus frequencies, with a frequency resolution of 0.025 Hz.

A.3.3 Results

As seen in Figure A.4, the results of the single-frequency conditions mirrored those of the first pilot study. There was again greater sway at 0.1 Hz than at 0.25 Hz, and the full and peripheral stimuli produced similar amounts of sway, both of which were greater than the sway caused by the central condition. Even though the optic flow of the central and peripheral stimuli was increased, it does not appear that this caused a notable increase in sway. These preliminary results seem to support the peripheral dominance hypothesis, but more data need to be collected in order for the results to be statistically verified. As would be expected, the sway-referenced platform condition elicited greater sway across all visual stimuli, due to an attenuation of somatosensory inputs.

For the mixed-frequency trials, the power spectra of the subjects' responses show that in the trials where the central stimulus moved at 0.25 Hz and the side checkers move at 0.1 Hz, the sway was predominantly characterized by the frequency of the peripheral stimulus (see Figure A.5, Trials 2 and 4). However, in the trials where the frequencies are reversed (the central target moves at 0.1 Hz and the side checkers move at 0.25 Hz), there is not a noticeable difference in power between the two stimulus frequencies (excluding the outlier point in trial 3).

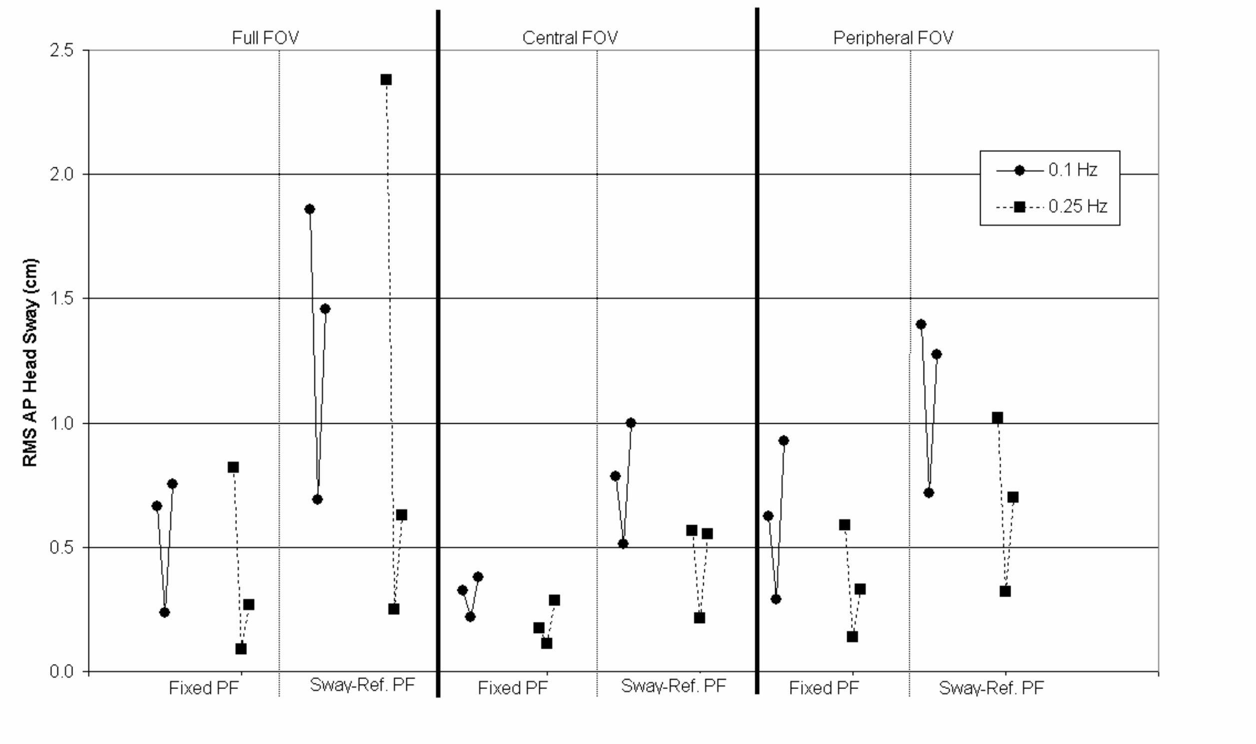


Figure A.4. RMS of the filtered AP head sway during the single-frequency conditions. Each field-of-view condition is subdivided into the two platform conditions (fixed and sway-referenced). Within each of these subdivisions, the left group of connected points (dark diamonds) shows the data from the 0.1 Hz oscillation, and the right set of points (light squares) shows the data for the 0.25 Hz movement. The first, second, and third point of each set is the RMS value of the first, second, and third subject, respectively.

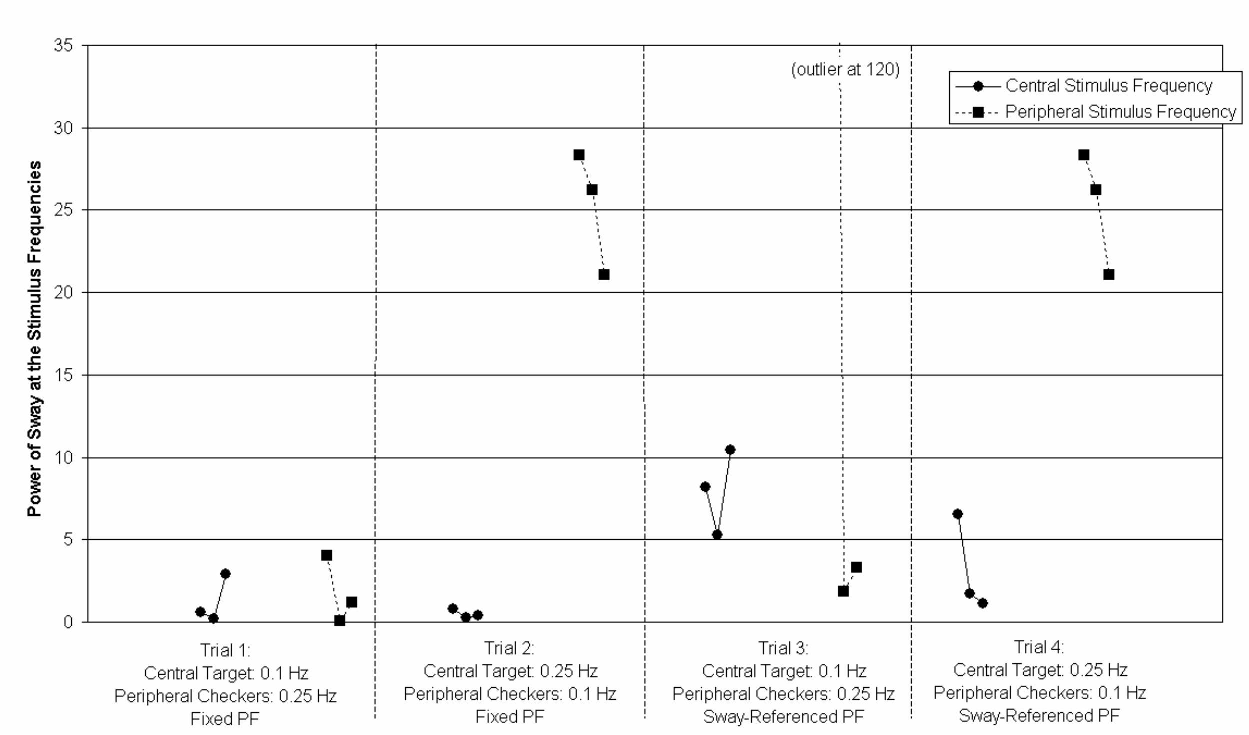


Figure A.5. Power Spectral Density (PSD) estimates of the unfiltered AP head sway data during the mixed-frequency trials. The dashed lines divide the data according to the four mixed-frequency trials. The frequencies of oscillation of the central and peripheral regions of the stimulus, as well as the platform (PF) condition, are indicated under each trial number. Within each trial, the left group of connected points (dark diamonds) show the power of sway at the central stimulus frequency, and the right set of points (light squares) show the power of sway at the peripheral stimulus frequency (± 0.05 Hz). Note: The outlying point located off the scale in Trial 3 has a value of 97.7.

APPENDIX B. PREWHITENING FILTER USED IN TONE TEST

The pre-whitening filter was constructed by fitting an 8th order autoregressive model to the optic flow data. In the frequency domain:

$$X(f) \sim AR_p = \frac{1}{a_0 + \sum_{q=1}^{p} a_q e^{-i2\pi f q \Delta t}} \quad (7)$$

Note that in order to avoid bias in the model fit due to a large component at the stimulus frequency, the components at the stimulus frequency ± 1 bin were replaced by linear interpolation of the components at the neighboring frequency bins (i.e. stimulus frequency ± 2 bins). Then, the optic flow sway data were filtered using the coefficients determined from the model.

$$A(f) = a_0 + \sum_{q=1}^{p} a_q e^{-i2\pi f q \Delta t} \qquad (8)$$

$$X_{white}(f) = X(f)A(f) \qquad (9)$$

Matlab was used to design and apply the pre-whitening filter, using the following scripts:

```
A=lpc1(x,p,fs,f1);      % use lpc1 to find the filter coefficients for the pre-whitening filter
                        % A is the vector of filter coefficients
                        % x is the input signal
                        % p is the order of the linear predictor
                        % fs is the sampling frequency of the input signal
                        % f1 is a vector of stimulus frequencies

y=filter(A,1,x);        % y is the pre-whitened signal

%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%
function A=lpc1(x,p,fs,f1);
fN=fs/2;                         % fN is the Nyquist frequency
lx=length(x);                    % Determine length of input signal
```

```
if mod(lx,2)==1, lx=lx-1; end          % Make input signal have even number of values
X = fft(x(1:lx),lx);                   % Compute autocorrelation vector
X2=(abs(X).^2);               % Calculate PSD of x
LX=length(X)/2;               % Determine length of positive half of signal
deltaf=fN/LX;                          % Determine increment in frequency
fx = 0 : deltaf : fN-deltaf ; % fx is the frequency vector

% loop to get rid of peak at each stimulus frequency

for nfreq=1:length(f1),

%Determine frequency bins that correspond to stimulus frequency
g1(fx==f1(nfreq));            % positive half
g2=lx+1-g1;                   % negative half

                        % Find slope of line joining 2 points behind and ahead of stim. freq.
slope=(X2(g1+2)-X2(g1-2))/4;

                        % Replace the points around stim. freq. with the interpolated points
X2(g1-1:g1+1)= X2(g1-2)+slope*[1:3];        % positive half
X2(g2-1:g2+1)= X2(g2-2)-slope*[1:3];        % negative half

end

R = ifft(X2);                          % Return back to the time domain
R = R./(lx-1);                         % Biased autocorrelation estimate
[A,E] = levinson(R,p);                 %Levinson-Durbin recursion to solve the normal equations
that arise from the least-squares formulation


% Notes:
%   A = LPC1(X,N) finds the coefficients, A=[ 1 A(2) ... A(N+1) ],
%   of an Nth order forward linear predictor
%
%      Xp(n) = -A(2)*X(n-1) - A(3)*X(n-2) - ... - A(N+1)*X(n-N)
%
%   such that the sum of the squares of the errors
%
%      err(n) = X(n) - Xp(n)
%
%   is minimized.
%
%   LPC1 uses the Levinson-Durbin recursion to solve the normal equations
%   that arise from the least-squares formulation.  This computation
%   of the linear prediction coefficients is often referred to as the
%   autocorrelation method.
```

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