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UNIVERSITY OF CALIFORNIA, IRVINE

Human Vestibular Signals Generated By Natural Locomotion

DISSERTATION

Submitted in partial satisfaction of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in Psychology

by

Andrew Zachary Wisti

Dissertation Committee: Professor Michael D'Zmura, Chair Professor Ramesh Srinivasan Professor Charles E. (Ted) Wright

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DEDICATION

То

my family and friends

without whom I would not be where I am today

I will find each and every one of you...

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ABSTRACT OF THE DISSERTATION

Human Vestibular Signals Generated By Natural Locomotion

By

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Sensory systems are believed to take advantage of the properties of natural stimuli. Natural images, for example, follow normality and a power-law which are reflected in the dynamics of visual cells. In order to better understand the vestibular system we examined natural human motion. We measured torso and head angular velocities of human subjects who walked, jogged, and climbed a staircase. Angular velocity distributions of the head and torso were fit well by Cauchy distributions, while power spectral densities did not follow a power law. We found that neither a power law nor a two-line-segment fit were sufficient to fit power spectral densities of angular velocity. Increases in power at the gait frequency and its harmonics are not well fit by lines. Differences between torso and head motion show a more evenly distributed reduction of angular velocities, presumably by the neck, in the semicircular canal frame of reference. Coherence between torso and head angular velocity did not show a linear relationship over all frequencies, but did suggest a linear relationship at the fundamental gait frequency and its harmonics. Reduction in angular velocity between the torso and head was then modeled by an adaptive linear filter. Results were mixed and depended on subject, condition, and axis. Qualitatively, predictions of

Х

angular velocity were good, capturing both the amplitude and periodicity of the actual head velocity. Finally, initial results were replicated while normalizing gait cycles using linear length normalization. Natural walking and running conditions were compared to treadmill walking and running. Subjects showed significantly different peak velocities during natural and treadmill conditions despite similar movement speeds. Coherence was also different between natural and treadmill conditions. These results provide evidence that natural and treadmill locomotion are treated differently, possibly due to the lack of visual input during treadmill locomotion. Subjects also walked with their heads turned to either the left or right, separating direction of motion and direction of the head. Angular velocity during these conditions show that head direction is not important for stabilizing the head, suggesting that efference copies play a role in head stabilization.

1 Introduction

Natural stimuli in vision and audition follow a power law, where spectral power is inversely proportional to frequency (Burton & Moorhead, 1987; Legge, 1981). These sensory systems are believed to be adapted to and take advantage of the statistical properties of the stimuli they encode. One common proposal is that neurons encode stimuli as efficiently as possible by maximizing information capacity (Atick, 1992; Attneave, 1954; Barlow, 1961; Burton & Moorhead, 1987). For example, large monopolar cells of the fly's compound eye have a contrast-response function that nearly matches the cumulative probability function of the contrast of natural scenes (Laughlin, 1981) (Figure 1.1).



Figure 1.1. Reducing Redundancy *Left, top*: A hypothetical distribution of stimulus intensity. *Left, bottom*: The intensity-response function that maximizes a neuron's information capacity by ensuring all response levels are used with equal frequency. As number of neurons reaches infinity, this curve becomes the cumulative probability function. *Right*: The contrast-response function of the large monopolar cells of a fly plotted next to the cumulative probability function of the contrast in natural images. From Laughlin (1981).

The vestibular system detects angular acceleration via three roughly orthogonal semicircular canals and linear acceleration via two otolith organs (Angelaki and Cullen, 2008). These organs measure self-motion generated from walking or running, through head movements during visual search, or through passive motion like that found when riding as a passenger in a vehicle. Groundbreaking work by Carriot and colleagues (2014) showed that vestibular stimuli are not distributed normally and do not follow a power law. These distinctive features of vestibular stimulation may be due to the nature of self-motion and biomechanical filtering of vestibular input by the body (Allum, Gresty, Keshner, & Shupert, 1997; Fard, Ishihara, & Inooka, 2004; Goldberg & Peterson, 1986).

The first project, which is described in Chapters 2 and 3, confirms that power spectral densities of angular velocity do not follow a power law, shows that the probability distributions of vestibular stimuli are modeled well by Cauchy distributions, and explores the differences between world-centered and vestibular-organ-centered velocities. The second project, described in Chapter 4, models and predicts the biomechanical filtering of the neck using a linear adaptive filter and looks at intersubject differences in angular velocity. The third project, described in Chapter 5, uses normalization techniques to reduce differences between subjects and replicates the results of Chapters 3 and 4. It also examines head stabilization of conditions with altered sensory feedback. Differences in natural and treadmill locomotion highlight the importance of visual feedback and the effects of its absence. Locomotion while the head is turned separates movement direction and head direction, and examines the roles of efference copies and measurement-feedback mechanisms during head stabilization.

Understanding the statistical properties of vestibular stimuli and the effects of biomechanical stabilization can also help in creating better virtual environments. Some users of virtual environments experience cybersickness, which includes symptoms similar to motion sickness such as nausea, eye strain, and vertigo, but is generally not caused by vestibular stimulation (LaViola, 2000). While there is no one exact cause for cybersickness (Kennedy & Fowlkes, 1992), motion sickness in general seems to occur from sensory mismatch where signals from the eves, vestibular system, and non-vestibular proprioception are at odds (Mark Stephen Dennison & D'Zmura, 2017; Krusienski et al., 2006; James T. Reason & Brand, 1975; J T Reason, 1978). Tracking and predicting head movements in space can lead to improved accuracy in visual presentation of virtual environments (LaValle, Yershova, Katsev, & Antonov, 2014). Improving the presentation of virtual environments should reduce symptoms related to cyber sickness by reducing sensory mismatch, and a better understanding of the properties of head movements should allow for better prediction of head movements. Physiological signals have been used in the past to predict motion sickness (Mark S. Dennison, Wisti, & D'Zmura, 2016), and understanding head stability during natural motion would provide a baseline to compare to for prediction of motion sickness and determining susceptibility to motion sickness.

2 Methods for Measurement of Vestibular Signals

The following section details methods common to the projects in Chapters 3 & 4.

2.1 Subjects

Angular velocity measurements for the torso and head were recorded for 13 subjects (11 male, 2 female) while they moved actively or sat passively in six conditions. All subjects were in good physical condition with no reported history of vestibular defects and with normal or corrected-to-normal vision.

2.2 Conditions

Angular velocities of the torso and head were measured while subjects performed 6 different activities: Walking, Running, Virtual Walking, Stair Climbing, Stair Descending, and Virtual Sitting. Each condition lasted two minutes, except for stair climbing and stair descending conditions, each of which lasted 1.5 minutes. Walking and running was done on a NordicTrack Commercial 1750 treadmill. No subject reported any sickness or discomfort during Virtual Walking or Virtual Sitting. The details of each condition were as follows:

Walking: Subjects used the treadmill to walk at 2 mph.

Running: Subjects used the treadmill to run at either 5 or 6 mph. Subjects were started at 6 mph and ran for a short period of time to determine if this speed was comfortable. Two subjects elected to lower their running speed to 5 mph.

Stair Climbing: Subjects climbed 5 flights of stairs set outdoors at a moderate, comfortable pace, one step at a time. The stairs spiraled up in a counter-clockwise fashion.

Stair Descending: Subjects descended the same 5 flights of stairs at a moderate, comfortable pace, one step at a time. The stairs spiraled down in a clockwise fashion.

Virtual Walking: Subjects walked on the treadmill while wearing an HMD. The virtual environment was comprised of a well-lit, bare hallway with textured walls. Subjects walked on the treadmill at 1.5 mph while the camera in the virtual environment moved down the hallway at a comfortable speed. Before recording, the camera height and movement speed was matched to the subject's satisfaction in order to feel as natural as possible while walking on the treadmill.

Virtual Sitting: Subjects sat in a chair and wore the HMD and viewed a tour through the solar system (Titans of Space for the Oculus Rift). Subjects were instructed to look around freely and progress through the tour at their own pace.

2.3 Measurements

Angular velocities of the torso and the head were recorded at 100 Hz using either two InertiaCube BTs, a 3 degrees-of-freedom orientation tracking system, or one InertiaCube BT and an Oculus Rift Development Kit 2 Head Mounted Display (HMD). Torso measurements were taken at approximately the sternum; head measurements were taken from the forehead. Each InertiaCube was attached by an elastic band. Both the InertiaCubes and the HMD recorded angular velocity around three axes: yaw (vertical), pitch (horizontal), and roll (forward-backward). Recall that rotation about a vertical axis produces left-right motion, often referred to as yaw. The torso cube malfunctioned for one subject during the Stair Climbing and Stair Descending conditions; data collected during those periods were not included in analysis. Figure 2.1 shows raw velocity measurements



from both the cubes and the HMD. Measurements from the two devices were nearly identical. No scaling was needed except for changing the sign of yaw angular velocity.

2.4 Data Analysis

Angular velocity measurements were first filtered using a 7-pole Butterworth filter with a low-pass cutoff of 25 Hz. This range includes the frequencies at which the

vestibuloocular reflex does not suffer from frequency-dependent nonlinearities (Huterer &

Cullen, 2002). It also includes the upper limit of harmonics produced while running

(Grossman, Leigh, Abel, Lanska, & Thurston, 1988).

The semicircular canals do not lie perfectly along the X-Y-Z axes used by the inertial measurement units, so angular velocity measurements were rotated onto the semicircular canal planes (left-anterior, right-posterior [LARP]; right-anterior, left-posterior [RALP]; semicircular canal yaw [scYaw]) using the following rotation matrix:

(3.1)
$$\begin{pmatrix} v_{LARP} \\ v_{RALP} \\ v_{scYAW} \end{pmatrix} = \begin{bmatrix} \cos(\theta) & -\sin(\theta) & 0 \\ \sin(\theta) & \cos(\theta) & 0 \\ 0 & 0 & 1 \end{bmatrix} \begin{bmatrix} \cos(\gamma) & -\sin(\gamma) & 0 \\ 0 & 1 & 0 \\ \sin(\gamma) & \cos(\gamma) & 1 \end{bmatrix} \begin{pmatrix} v_X \\ v_Y \\ v_Z \end{pmatrix}$$

where $\theta = 45^{\circ}$ and $\gamma = 18^{\circ}$ (Carriot et al., 2014; Della Santina et al., 2005; see Figure 2.2). Effectively, this is equivalent to taking an object and rotating in pitch 18° and in yaw 45° in world-centered yaw-pitch-roll. It is also important to note that while the horizontal canal pair (LH & RH) is approximately coplanar, the vertical canal pairs (LA & RP; RA & LP) are slightly less so. Measurements and analysis for the following project were calculated as if all three pairs of semicircular canals were exactly coplanar for ease of calculation.



3 Statistical Properties of Vestibular Signals

3.1 Introduction

The first project aimed to describe the vestibular signals experienced by the torso and head during self-motion. It also aimed to look at the differences between LARP, RALP, and scYaw rotation signals as well as their relationship to world-centered axes of yaw, pitch, and roll.

3.2 Data Analysis

Analysis was performed on angular velocity data in both the original sensor frame of reference (YPR-space) and the rotated, semicircular-canal frame of reference (LRY-space). This was done to compare the signals experienced by the torso and head both in an intuitive, world-centered coordinate system and in a coordinate system corresponding to the orientation of the semicircular canals (Della Santina et al., 2005).

First, peak angular velocities were compared across subjects, conditions, and axes. To get peak angular velocities, head and torso data were split into epochs, consisting of a single gait cycle, which were determined manually for each subject and condition from sensor angular position. For example, one epoch would last from the moment the left foot first left the ground to the next time it left the ground. For each gait cycle, two peak angular velocities were extracted for analysis from the absolute value of angular velocity measurements. The first was taken from the first half and the second from the second half of the epoch, representing each step. No such analysis was performed for the virtual sitting condition.

Akaike's information criterion (AIC) was used to compare the fit of normal and Cauchy distributions to the empirical distributions of angular velocity data. For a model with k parameters and likelihood L, AIC = 2k - ln(L) (see Bozdogan, 1987, for review). This measure estimates the amount of information lost by the model (lower is better) and can be compared with an AIC calculated for a different model. Next, a likelihood ratio test was used to compare the fits of different Cauchy distributions from a full model with separate parameters for each combination of sensor, subject, condition, and axis to simpler models aggregating over one or more dimensions.

Power spectral densities (PSD) of the angular velocity time series were calculated by Welch's method with a window of size 512 samples (5.12 seconds) and 50% sample overlap. Following Carriot and colleagues (2014), two kinds of line-based fits were calculated for each PSD function. The first was a single line fit over the entire frequency range (0.2 to 25 Hz). The second was made of two lines, one fit over the low frequency range (0.2 to 2 Hz) and the other over the high frequency range (10 to 25 Hz) and combined at their intersection. A paired t-test was used to compare fits of these two models.

3.3 Results

3.3.1 Peak Velocity

Angular velocity data from each stride epoch were used to determine two peak angular speeds, one from the first half and one from the second half of the stride. Figure 3.1A and B shows mean peak speeds for the torso and the head for each condition combined over subjects and axes of rotation. Mean peak speeds for the head were lower

than for the torso overall (p<.001) and within each condition (each head-torso pair p<.001). Torso mean peak speeds were greatest while running, followed by stair descent and climbing.

The two walking conditions had the lowest mean peak speeds. Mean peak speeds for the head followed a similar pattern but with much smaller differences between conditions. LARP and RALP average peak speeds were about equal, with yaw smaller for both the torso and head (Fig. 3.2A). A repeated measures ANOVA showed significant main effects of sensor (p<.001) and axis (p<.001) and significant interaction effects of sensor by axis (p<.001).

Figure 3.3 shows that mean angular velocities were at or close to zero for all conditions except for the two stair conditions where subjects climbed a spiral staircase, ascending counterclockwise or descending clockwise. During stair climbing and stair descending, LARP and RALP angular velocities were more extreme for the head than for the torso, while scYaw angular velocities were more extreme for the torso than for the head (p<.001).



and D show mean peak angular speed of the torso and head separated by axis, combined over subjects and conditions. This highlights the reduction in angular velocity between torso and head for each axis. scYaw speeds were significantly lower than LARP and RALP speeds (p<.001). There was a significant difference in damping between yaw, pitch, and roll (p<.001).



Figure 3.2. Comparison of LARP, RALP, and scYaw peak angular velocity to raw sensor yaw, pitch, and roll peak angular velocity for the head and torso. Comparing A to B and C to D, changes in LARP and RALP are driven mostly by increases in pitch. Roll angular velocity is relatively small throughout all activities. In the torso, LARP, RALP, and scYaw are all almost equal for all conditions except running, whereas in the head scYaw is clearly damped.



canal axes (left column) vs. sensor axes (right column). Mean velocities were close to zer cases except for during the two staircase conditions where subjects turned clockwise or counterclockwise

The more extreme LARP and RALP head velocities may be due to the pitch of the head while moving up and down stairs, which would be split evenly between LARP and RALP but not appear in the yaw axis of rotation. The torso, however, does not experience such strong pitching motion and shows smaller LARP and RALP velocities. Speeds were not calculated during the VR Sit condition because subjects did not take any strides.



Overall angular velocity did not differ too much between sensor axes and semicircular canal axes (Figure 3.1A & B). However, damping between the different axes is clearly different. Pitch angular velocity contributes to both LARP and RALP angular velocity (Figure 3.1C & D, Figure 3.2 left vs. right column). Angular velocity in pitch is the most damped between the torso and head (p<.001, Figure 3.1D). Increase in pitch angular velocity is much greater than increase in yaw angular velocity when going from Walking to Running, while Stair Climbing and Stair Descending are much closer for pitch and yaw. Roll contributes relatively little to head angular velocity. The distribution of differences

between the torso and head are different in YPR-space with pitch having nearly twice the damping than yaw for Running, and roll damping being near zero. In semicircular canal space, LARP and RALP are nearly identical and have greater damping than scYaw (see Figure 3.4, previous page).

3.3.2 Distribution Fitting

Angular velocity distributions depend on movement condition (e.g. walking vs. running), subject, axis of rotation, and sensor location (torso vs. head). This can be seen by comparing different models using AIC and likelihood ratio tests. Table 3.1 shows the AIC of the full Cauchy and normal models as well as Cauchy models that aggregate data over one or more dimensions (lower is better).

| Table 3.1. Models and their AIC for LARP, RALP, scYaw | | | |
|---|------------------------|--|--|
| Model | AIC | | |
| Cauchy Full | 8.85 x 10 ⁵ | | |
| Cauchy Axes Combined | 1.08 x 10 ⁶ | | |
| Cauchy Subjects Combined | 1.18 x 10 ⁶ | | |
| Cauchy Sensors Combined | 1.33 x 10 ⁶ | | |
| Cauchy Conditions Combined | 2.23 x 10 ⁶ | | |
| Cauchy Subjects and Conditions Combined | 2.28 x 10 ⁶ | | |
| normal Full | 2.83 x 10 ⁶ | | |

Table 3.2 shows likelihood ratio tests comparing the full Cauchy model to various simpler models aggregating data over one or more dimensions.

| Table 3.2. Likelihood-ratio test of Cauchy fits, full models vs. various combinations for | | | | | |
|---|--|------------------------|-------|--|--|
| LARP, RALP, scYaw. 2 sensors * 13 sub | LARP, RALP, scYaw. 2 sensors * 13 subjects * 6 conditions * 3 axes – lost data of 2 conditions * 3 | | | | |
| axes for one subject = 930 degrees of fr | eedom in full model | | | | |
| Comparison | Degrees of | X2 | р | | |
| Full vs. Combined Subjects | 930 - 72 = 858 | 3.01 x 10 ⁵ | <.001 | | |
| Full vs. Combined Conditions | 930 - 156 = 774 | 1.35 x 10 ⁶ | <.001 | | |
| Full vs. Combined Axes | 930 - 312 = 618 | 2.05 x 10 ⁵ | <.001 | | |
| Full vs. Combined Sensors | 930 - 468 = 462 | 1.82 x 10 ⁵ | <.001 | | |

Neither head nor torso velocity distributions were fit well by normal distributions. The Δ AIC comparing the full-model Cauchy distributions and full-model normal distributions was -1.95 × 10⁶ in favor of the Cauchy model. This means that the normal model is exp(-1.95 × 10⁶/2) << .0001 times as likely as the Cauchy model to minimize information loss (Burnham & Anderson, 2002).

The best fit Cauchy and normal distributions can be seen plotted with the measured velocity distributions in Figure 3.5 (next page). The stair conditions show a slight skew in opposite directions. Subjects turned counter-clockwise while climbing and clockwise while descending, which caused velocities to skew in opposite directions.



combined across subjects for each condition. The solid black lines and gray shading show the means and standard deviations, respectively. Green dashed lines show the best-fit normal distributions. Magenta dash-dotted lines show the best-fit Cauchy distributions. These are better fit by Cauchy rather than normal distributions.

Variation in individual subject yaw angular velocity distributions is shown in Figure 3.6 for walking and running conditions. Color is used to code each subject's distribution. The bold black curve in each panel is used to show the average distribution. Individual subjects show large variation but follow the same general pattern. The angular velocity distribution during walking is more leptokurtic than during running; there are fewer extreme velocities while walking than while running. The angular velocity distribution for the head is more leptokurtic than for the torso; the head experienced fewer extreme velocities than the torso. Overall, this underscores individual differences in head stabilization and the difficulties in combining data over subjects.



Fits using raw sensor axes yaw, pitch, and roll yield mostly the same results: Cauchy distributions fit angular velocity distributions better than normal distributions, fits are best done with subjects and conditions kept separate, and head velocities are generally more leptokurtic. Tables 3.3 & 3.4 show AIC and chi-squared comparisons of model fits using angular velocity in sensor axes (yaw, pitch, and roll).

| Table 3.3. Models and their AIC for yaw, pitch, roll | | | |
|--|------------------------|--|--|
| Model | AIC | | |
| Cauchy Full | 3.40 x 10 ⁵ | | |
| Normal Full | 2.25 x 10 ⁶ | | |
| Cauchy Subjects Combined | 6.97 x 10 ⁵ | | |
| Cauchy Conditions Combined | 1.60 x 10 ⁶ | | |
| Cauchy Axes Combined | 7.06 x 10 ⁵ | | |
| Cauchy Sensors Combined | 5.64 x 10 ⁵ | | |
| Cauchy Subjects and Conditions Combined | 1.67 x 10 ⁶ | | |

Table 3.4. Likelihood-ratio test of Cauchy fits, full models vs. various combinations yaw, pitch, roll. 2 sensors * 13 subjects * 6 conditions * 3 axes – lost data of 2 conditions * 3 axes for one subject = 930 degrees of freedom in full model

| Comparison | Degrees of Freedom | X ² | р |
|------------------------------|--------------------|------------------------|-------|
| Full vs. Combined Subjects | 930 - 72 = 858 | 3.59 x 10 ⁵ | <.001 |
| Full vs. Combined Conditions | 930 - 156 = 774 | 1.35 x 10 ⁶ | <.001 |
| Full vs. Combined Axes | 930 - 312 = 618 | 2.05 x 10 ⁵ | <.001 |
| Full vs. Combined Sensors | 930 - 468 = 462 | 1.82 x 10 ⁵ | <.001 |



3.3.3 Power Spectral Densities

PSDs of the subject-averaged angular velocity time series for each condition and axis of rotation were calculated. Following Carriot and colleagues (2014), we fit two simple models to the PSDs. The first was a simple power-law fit (a single line over the entire frequency range). The second model was a two-line fit over two physiologically relevant frequency ranges (Massot, Schneider, Chacron, & Cullen, 2012) including the range where the vestibuloocular reflex has approximately unity gain (Gauthier, Piron, & Roll, 1984; Huterer & Cullen, 2002; Tabak & Collewijn, 1994). These two models are shown by the dashed lines in Figure 3.7, which shows PSD results for LARP rotations in the running condition.

Figure 3.8 (see next page) shows subject-averaged PSDs with best fit lines for both models for all conditions. LARP, RALP, and scYaw axes of rotation are shown in the columns, respectively, while conditions are separated by row. The range depicted covers the proposed neurologically relevant frequency ranges for the vestibular system (Massot et al., 2012) and the upper range of harmonics still visible in running (Grossman et al., 1988): the low range of 0.2 to 2 Hz and the high range of 10 to 25 Hz. The two models that were used to fit PSDs were 1) a power-law (single line) fit over the entire frequency range and 2) a two-line model with one line fit over the low range and one line fit over the high range.7



Walking PSDs show a clear peak at 0.8 Hz, the fundamental gait frequency, and its harmonics (~1.6 & 2.4 Hz). Running shows a similar set of peaks at about 1.3 Hz and its harmonics. Peaks for walking and running are visible in all three axes of rotation. While these same peaks are present during virtual walking at ~ .7 Hz, they are greatly reduced in LARP & RALP for the head; the vanishing point of the hallway may have acted as a sort of fixation point and reduced pitching of the head compared to walking and running where no fixation cross was provided. Stair climbing shows a clear peak at .9 Hz and its harmonics for both the torso and head for all axes of rotation. Stair descending has some weak peaks at approximately 1 Hz but they are not as clear as other conditions and mostly appear only in the torso. There is a particularly large peak at 2.15 Hz; this peak is unlikely to be the fundamental stride frequency considering running has a fundamental frequency of only 1.3 Hz. Because this peak is very strong in LARP and RALP but not as much in scYaw, this peak is probably the downward velocity from moving down a step and upward velocity from stabilizing on that same step, putting it at roughly twice the stride frequency.

For the low frequency range, there is reduced power in the head compared to the torso for most conditions and axes of rotation. All axes of rotation for running as well as yaw for walking and virtual walking show reduced power in the head at the fundamental stride frequency. Virtual walking does not have as pronounced peaks at the fundamental stride frequencies when compared to walking. This may be due to the slightly slower speed and because many subjects used the treadmill armrests for balance and support. For the high frequency range, there is reduced power in the head compared to the torso for all conditions and axes of rotation. Overall, head PSDs stay at around the same power regardless of condition while torso power changes up to 2 orders of magnitude. This is
especially evident when comparing walking to running. Just as in Figure 3.1A, torso power varies greatly by condition while head power stays roughly the same.

The virtual sitting condition is much different than any of the other conditions, which comes as no surprise because it did not involve periodic motion and instead was mostly active head movements. There is greater power at low frequencies for the head than for the torso, but it declines more rapidly at high frequencies.

One-line and two-line models were fit to the PSDs, as described in the Methods. In all cases, the two-line model fit better than the one-line model, especially for the virtual sitting condition. An F-test with subjects averaged rejects the null hypothesis (F(108,12204)=16.55, p<.0001) that PSDs for the head and torso follow a power law. The same procedure performed on the full data set (with subjects not averaged) also rejects the null hypothesis (F(1404,158652)=7.87, p<.0001) that PSDs of the head and torso velocities follow a power law. Despite the improvement in fit using the two-line model, it is unable to capture the spectral peaks at the fundamental gait frequency and its harmonics.

3.4 Discussion

The current study continues the efforts of previous head stabilization studies that have use both passive (Fard et al., 2004; Goldberg & Peterson, 1986; E. A. Keshner, Cromwell, & Peterson, 1995; Emily A. Keshner, Hain, & Chen, 1999; Tabak & Collewijn, 1994) and active (Carriot et al., 2014; Grossman et al., 1988; Pozzo, Berthoz, & Lefort, 1990) conditions to provide a clearer picture of head stabilization and of natural vestibular stimuli. In addition to determining characteristics of vestibular neurons, head and torso motions can be used to study movement disorders such as Parkinson's disease (Latt, Menz, Fung, & Lord, 2009) or motion-sickness from perceived movement in virtual environments.

The statistical properties of vestibular stimuli should shape the way vestibular neurons respond to such neurons, just as in other modalities (Atick, 1992; Attneave, 1954; Barlow, 1961; Burton & Moorhead, 1987; Laughlin, 1981). In the present study, torso angular velocities show non-power-law and non-normal properties. In contrast, active motion of feet during locomotion as well as passive motion (such as the seat of a bus) both follow power-law distributions (Carriot et al., 2014). This suggests that biomechanical filtering (e.g. passive absorption of motion by bones and flesh and/or active movements to counteract motion) takes place in addition to neck stabilization. Body-balancing systems like the neural networks involved in the cervicocollic reflex must deal with non-power-law, non-normal signals from body motion. In any case, even though there were large changes from task to task in torso angular velocity, there was relatively little variation in the head (Figure 3.2). Compared to the walking condition, there were huge increases in torso velocity during running and only moderate increases during stair climbing/descent.

Angular velocity was not fit well by a normal distribution as the empirical distributions tended to be far too peaked with relatively high kurtosis values. This agrees with previous work (Carriot et al., 2014) where relatively high kurtosis values were found for the distributions of the head's angular velocity. We show in the present work that Cauchy distributions capture better the shapes of the angular velocity distributions than do normal distributions. Also, subjects clearly differed from one another, as shown by the high intersubject variability and the increase in goodness of fit when fitting individual distributions as opposed to subject-averaged distributions.

Vestibular stimuli do not follow a power-law. In agreement with Carriot and colleagues (2014), there is greater power at lower frequencies (0.2 to 2Hz) than at high

frequencies (10-20 Hz), with the change in power over frequency not consistent with a power law. This follows the results of Massot and colleagues (2012), who found that gain of central vestibular neurons was significantly lower over 0-5 Hz compared to 15-20 Hz when vestibular stimulation had both low- and high-frequency components. This type of frequency response would allow the detection of high frequency stimuli despite the power of the low frequency band, especially in the 1-2 Hz range. In order to efficiently detect high-frequency signals, neurons would have to be more sensitive to high frequency than to low frequency signals.

A model that uses one- or two-line segments to model PSDs fails to capture the increase in power at gait frequencies and their harmonics. This differs from previous results (Carriot et al., 2014) where a two-line fit worked well to capture angular velocity PSDs. However, this result is almost certainly the result of combining subject data and the types of conditions used. Subjects show large individual differences in head and torso motion as well as peaks in their PSDs at gait frequencies, especially during walking and running. In addition, because gait varies by condition, power increases at gait frequencies become difficult to see after averaging across conditions.

Angular velocities in scYaw are reduced the most through head stabilization, although LARP and RALP reduction are not much less. Peak velocities were smaller for the scYaw axis (left-right motion) than for the LARP or RALP axes, and LARP and RALP velocities increased greatly for running whereas scYaw velocity increased only slightly. Raw sensor data show that these differences are a result of changes in pitch.

Head movement in pitch has been studied in some detail (Fard et al., 2004; Hirasaki, Moore, Raphan, & Cohen, 1999; Pozzo et al., 1990). Angular velocity measurements from

the present study match previous work (Pozzo et al., 1990) pitch angular velocity was measured during a number of self-motion activities including walking (30+-8 deg/s), running (72+-20 deg/s), and hopping (72+-15 deg/s). During running, where there was the most damping of velocity from torso to head, the differences in velocities for yaw, pitch, and roll clearly stand out. Figure 3.4 shows that there is approximately twice as much damping in pitch than there is in yaw. There is very little damping in roll, possibly due to the lack of roll angular velocity in general.

It has been suggested that the size of semicircular canals is related to the type of locomotion of the animal. For primates and other mammalian species, those that are agile and have fast, jerky locomotion have significantly larger canals relative to body size than those that move more cautiously (Spoor et al., 2007). Humans have larger vertical canals (LARP and RALP) and a somewhat smaller lateral canal than the great apes, which may be due to the bipedal nature of human locomotion (Spoor, Wood, & Zonneveld, 1994). If canal size is related to type of locomotion, then the orientation of the canals may also depend on the movement of the organism.

The distribution of head angular velocities and their relative levels of damping shed some light on why the canals are oriented the way they are. Rather than having the canals in axes corresponding to left-right, forward-back, and up-down, the canals are rotated 45° in yaw and 18° in pitch (Della Santina et al., 2005, see Figure 2.2). Yaw, pitch, and roll angular velocities are quite different from each other (Figures 3.1 & 3.2). However, angular velocities in the semicircular canal planes are much more similar, with LARP and RALP being nearly identical. Having the semicircular canals rotated 45° splits up pitch rotations to LARP and RALP, instead of just a hypothetical pitch canal. While sensitivity may be

roughly equal for each semicircular canal axis, because pitch contributes to both LARP and RALP signals there are twice as many neurons available to detect changes in pitch. It is possible that this would lead to greater sensitivity to changes in pitch as well as better head stabilization in pitch compared to other axes. Whereas in semicircular canal coordinates damping from torso to head is roughly equal for the three axes (lines are roughly parallel in Figure 3.1C, distributions are roughly equal in Figure 3.4), damping in world-centered coordinates is greatest for pitch, less for yaw, and least for roll (Figures 3.1D & 3.4). A comparison with other species would be informative for answering this question. Cats (Blanks, Curthoys, & Markham, 1972) and pigeons (Dickman, 1996) have similarly oriented canals but very different methods of locomotion. It may be the case that these two species face similar challenges in that pitch velocity during locomotion is significantly greater than yaw or roll and needs to be damped at a much greater level.

3.5 Summary

Replicating and enhancing previous work (Carriot et al., 2014), this work shows that vestibular stimuli do not follow normal distributions nor do they follow a power law in their PSDs, unlike visual and auditory stimuli. It was previously postulated (Carriot et al., 2014) that passive filtering of the flesh and bones were responsible for these properties. This is supported by the non-power law and non-normal distributions of torso angular velocity. The neck further shapes angular velocities experienced by the head. The current study shows that it is inappropriate to combine subject and condition data; subjects, conditions, and axes all show distinct patterns of angular velocity and are best fit when kept separate. Significant increases in power at gait and step frequencies and their harmonics further shape angular velocity statistics. Finally, differences in sensor-centered

and semicircular canal-centered coordinates show that the orientation of the semicircular canals may be due to the requirements of human locomotion. Most head motion is in pitch, followed by yaw, with little motion in roll as measured by mean peak velocity. The same pattern is true of damping, with pitch damping roughly twice that of yaw damping, and roll damping being close to zero. When rotated to semicircular-canal coordinates, LARP and RALP canals experience roughly equal stimulation and damping is roughly equal for all three axes. Pitch angular velocity, which is the source of most of the angular velocity changes, gets split roughly evenly between two canals per vestibular organ instead of one and may benefit from twice the measurement power, leading to its significant damping compared to yaw and roll.

4 Models of Head Stabilization and Intersubject Clustering

4.1 Introduction

Head stabilization involves many components and includes biomechanical filtering of the flesh and bones as well as short latency reflexes such as the vestibulocollic reflex (VCR), the cervicocollic reflex (CCR), and the vestibuloocular reflex (VOR)(Angelaki & Cullen, 2008; Goldberg & Peterson, 1986; Hirasaki et al., 1999; Peterson, Goldberg, Bilotto, & Fuller, 1985; Wilson, 1991; Wilson & Schor, 1999). While decerebrate cats and lower mammals rely principally on the VCR and CCR to stabilize the head on the body (Goldberg & Peterson, 1986), it is less clear this is the case for primates, especially humans. Bizzi and colleagues (1978) estimated that the contribution to head stabilization by VCR and CCR amounted to only 10 – 30%. Instead, voluntary actions seem to contribute a great deal to head stability. Mechanical properties of the neck muscles (stiffness, viscosity, elasticity) that can be adjusted by subjects voluntarily seem to contribute more to head stabilization than reflexes such as VCR (Allum et al., 1997; Emily A. Keshner et al., 1999). When distracted by a mental arithmetic task, subjects showed a reduced ability to stabilize their head in space (Guitton, Kearney, Wereley, & Peterson, 1986). This may be because CCR and VCR both act to prevent instability of the head relative to the body but not necessarily to provide stabilization in space.

In passive vestibular perturbation studies, previous work has suggested VOR had unity gain up until 10 Hz and suffered from serious phase lag at frequencies of 15 Hz and higher (Gauthier et al., 1984; Tabak & Collewijn, 1994; Tabak, Collewijn, Boumans, & van der Steen, 1997), but there has also been evidence to the contrary. Huterer and Cullen (2002) showed that VOR in monkeys was highly compensatory even up to stimuli up to 25 Hz. The authors argue that problems with equipment explained the results of previous experiments. As shown in the previous chapter, head stabilization still shows power at harmonics up to approximately 20 Hz in yaw, pitch, and roll. Cremer and colleauges (1998) looked at VOR in both healthy subjects and patients who had undergone surgery to alter their semicircular canals. For healthy subjects, VOR retained a gain of .9 or greater to low-amplitude (15-30°), high velocity ($200 - 400^{\circ}/s$), high-acceleration ($2000 - 4000^{\circ}/s$) head rotations. A VOR with these characteristics is more than enough to compensate for the head velocities experienced by subjects during locomotion.

This project aims to model head stabilization by trying to predict head motion from torso motion, effectively modeling the action of the neck during self-motion. Although the previous project showed that subjects had very large individual differences overall, this project attempts to find any underlying links between subjects.

4.2 Data Analysis

A linear adaptive filter (Widrow & Stearns, 1985) was used to determine the characteristics of the neck in filtering angular velocity from the torso, $T(\tau)$, to the head, $H(\tau)$ (see Figure 4.1, next page).

Given the most recent 100 torso signal samples $T(\tau) = [x(\tau), x(\tau - 1), x(\tau - 2), ..., x(\tau - 100 + 1)]^T$ and a vector of weights $W(\tau) = [w_1(\tau), w_2(\tau), w_3(\tau), ..., w_{100}(\tau)]^T$, the prediction of the head signal at time τ was calculated by:

(4.1)
$$\widehat{H}(\tau) = W^T(\tau)T(\tau)$$

Error was calculated as

(4.2)
$$e(\tau) = H(\tau) - \hat{H}(\tau)$$

where $H(\tau)$ was the recorded head signal. Weights were updated at using the least

mean squares (LMS) algorithm:

(4.3)
$$W(\tau+1) = W(\tau) + \mu(\tau)e(\tau)T(\tau)$$

where $\mu(\tau)$ was step-size. Weights of a filter are equivalent to its impulse response

in time.



Trial data from the experiment described in Chapter 3 were split into 11 chunks of data. The first 10 chunks were used to train the filter weights via 10-fold cross validation. The mean estimated filter weights were then used to predict head motion on the 11th chunk of data. Filter fit and prediction was calculated using R²_{prediction} by

(4.4)
$$R^{2} = 1 - \frac{\sum_{i=1}^{N} (h_{i} - \hat{h}_{i})^{2} / (N-1)}{\sum_{i=1}^{N} (h_{i} - \overline{h}_{i})^{2} / (N-1)} = 1 - \frac{MSEP_{head}}{Var[h]}$$

where *h* was the actual recorded head velocity and \hat{h} was the predicted head for $R^{2}_{prediction}$. Correlation was calculated by taking the dot product of the normalized predicted and recorded head velocity measurements. In other words,

(4.5)
$$correlation = \frac{H \cdot \hat{H}}{\|H\| \|\hat{H}\|}$$

The relationship between torso and head angular velocity was estimated using magnitude squared coherence. Coherence is a frequency-dependent measure of similarity between two signals. For two signals x(t) and y(t), coherence is calculated as:

(4.6)
$$C_{xy}(f) = \frac{|G_{xy}(f)|^2}{G_{xx}(f)G_{yy}(f)}$$

where G_{xy} is the cross-power spectrum of x(t) and y(t) and G_{xx} and G_{yy} are the auto-power spectrum of x(t) and y(t), respectively. A linear, noise-free system will have unity coherence, whereas introducing noise or nonlinearities reduces coherence (Bendat & Piersol, 1993; Thomas, 2015). When calculated for torso and head angular velocity, coherence gives an idea of how much noise is present and whether there are nonlinearities as vestibular signals pass through the neck from the torso to the head. Finally, cluster analysis was used to determine if subjects could be separated into any number of subgroups. A k-means clustering approach was used on parameters from Cauchy fits of the previous experiment. Because k-means clustering is sensitive to scaling, each set of parameters was normalized by dividing by its standard deviation across subjects, conditions, and axes. A normalized mean squared distance to cluster centroid was used to determine the optimal number of clusters. This can be thought of a mean squared error, where cluster centroid positions are the prediction and Cauchy solutions are the observed values. Hierarchical clusters based on Euclidean space were also computed using MATLAB's *linkage* command. This clustering was used as comparison to the k-means clustering.

4.3 Results

4.3.1 Coherence

Coherence was calculated between torso and head angular velocity for yaw, pitch, and roll. Figure 4.2 shows subject-averaged coherence and Figure 4.3 a single subject's coherence for yaw, pitch, and roll for all 6 conditions. Coherence is low except at gait & step frequencies and their harmonics. Yaw and roll show relatively high coherence at gait frequency (from left foot off to left foot off) and its harmonics whereas pitch shows high coherence at the step frequency (double the gait frequency) and its harmonics. Coherence is greatest for Walking, Running, and Virtual Walking, with some coherence in Stair Climbing and Stair Descending. Virtual Sitting, as expected, showed little coherence between torso and head.



Stair Climbing and Stair Descending have high coherence at low frequencies in yaw for due to the spiral staircase used in this study. A constant clockwise or counterclockwise turn shows up as a low-frequency component. Because the turn was the same direction and magnitude for torso and head, it has a high coherence. These two conditions also have moderate peaks in yaw and roll at the gait-frequency. Only Stair Descending has a peak in pitch at twice the gait-frequency which may be due to the faster and jerkier motion when descending stairs compared to when climbing stairs. In the single subject case, Stair Climbing and Stair Descending have coherences that do not show the same clear peaks as Walking or Running. It is very likely that because subjects had very different styles of climbing and descending stairs that these coherences were averaged out in the subjectsaveraged coherence.

Harmonics in coherence were present up to 20 Hz during the Running condition, similar to what was found by Grossman and colleagues(1988) for angular velocity. In the subjects-averaged case, coherence drops off from 5-10 Hz and is in general low above 10 Hz. However, coherence remains high at harmonics up to and past 10 Hz for Running for individual subjects. Coherence slowly drops off to moderate levels past 10 Hz for Walking and Virtual Walking.



frequency (twice the gait-frequency). Walking, Running, and Virtual Walking show clear and strong coherence at gait and step frequencies and their harmonics. In general, individual subject coherence has greater coherence at gait and step frequency harmonics than subject-averaged coherence.

4.3.2 Adaptive Linear Filter

Adaptive filter weights for each condition and axes followed some patterns between subjects (see Figure 4.4, next page). LARP and RALP weights were very similar to each other and dissimilar to yaw. Running showed greater variation in weights compared to walking and virtual walking. Filters for yaw tended to weigh recent samples positively while filters for LARP and RALP weighed them negatively. Running weights were lower overall than for Walking or Virtual Walking, which matches the result shown in Figure 3.2 that the reduction of peak angular velocity from torso to head was greater for Running than for Walking or Virtual Walking. Just as in the project on the statistical properties of vestibular stimuli, there were some general patterns but there was great variation between subjects, condition, and axes. Filter weights converged to roughly the same values for each of the 10 folds. This means subjects kept a steady pattern for the duration of a trial and that filter weights converged to values that minimized least squared error.



while scYaw is different.

Linear filter R²_{prediction} values are summarized in Tables 4.1 and 4.2. Filters varied in

their performance from great to very poor, with great individual variation. The linear filter

had the highest R²_{prediction} values for yaw and scYaw, with LARP and RALP being roughly

equal. R²_{prediction} values averaged over subjects and conditions were -0.06, 0.06, and 0.25 for

LARP, RALP, and yaw, respectively. Among conditions, Walking and VR walking had the

highest R²_{prediction} values, followed by the stair climb/descent conditions, with running

having the lowest R²_{prediction} values, except for in yaw.

Table 4.1. R² values averaged over subjects for the 10-fold cross-validation procedure and correlation for values for the predicted and actual head in semicircular canal axes, LARP, RALP, and scYaw.

| | | - | | | | - |
|----------------------------------|---------|---------|----------|------------|---------|---------|
| R ² prediction | Walking | Running | Stair | Stair | Virtual | Mean |
| | | | Climbing | Descending | Walking | |
| LARP | 0.2477 | -0.8823 | 0.0813 | 0.05 | 0.2193 | -0.0563 |
| RALP | 0.2156 | -0.3894 | 0.1299 | 0.10 | 0.2382 | 0.0608 |
| scYaw | 0.3891 | 0.1691 | 0.1414 | 0.24 | 0.3224 | 0.2527 |
| | | | | | | |
| Correlation | | | | | | |
| LARP | 0.4974 | 0.4304 | 0.2979 | 0.29 | 0.4634 | 0.3977 |
| RALP | 0.4627 | 0.4522 | 0.3375 | 0.30 | 0.4800 | 0.4074 |
| scYaw | 0.6142 | 0.5530 | 0.4020 | 0.45 | 0.5570 | 0.5157 |

| Table 4.2. R ² values averaged over subjects for the 10-fold cross-validation procedure and | |
|--|--|
| correlation values for the predicted and actual head in sensor axes, yaw, pitch, and roll. | |

| | , | | | | | |
|---------------------------|---------|---------|----------|------------|---------|---------|
| R ² prediction | Walking | Running | Stair | Stair | Virtual | Mean |
| | | | Climbing | Descending | Walking | |
| Yaw | 0.4741 | 0.2775 | 0.1947 | 0.2043 | 0.2349 | 0.2771 |
| Pitch | 0.2469 | -2.3279 | 0.1732 | 0.1839 | 0.3834 | -0.2681 |
| Roll | 0.3227 | 0.3949 | 0.1914 | 0.0758 | 0.3037 | 0.2577 |
| | | | | | | |
| Correlation | | | | | | |
| Yaw | 0.6795 | 0.5700 | 0.4619 | 0.4379 | 0.4545 | 0.5208 |
| Pitch | 0.4858 | 0.3828 | 0.3989 | 0.4523 | 0.6066 | 0.4653 |
| Roll | 0.5699 | 0.6294 | 0.3874 | 0.2964 | 0.5609 | 0.4888 |

When looking at individual subjects, one reached a maximum $R^2_{prediction}$ value of during the walking condition (Figure 4.5), followed by 0.76 for the same subject during the running condition, both in scYaw. This same subject showed the highest mean $R^2_{prediction}$ value across subjects in scYaw at 0.62. Filters that had low $R^2_{prediction}$ values (meaning they did not explain much of the variance in the signal) still did a good job qualitatively, and correlations tended to be higher than $R^2_{prediction}$ values. Figure 4.6 compares a filter with high $R^2_{prediction}$ and a filter with low $R^2_{prediction}$. Again, even with a negative $R^2_{prediction}$ the predicted angular velocity seems to capture the essence of the recorded head angular velocity. The correlation of the "low" $R^2_{prediction}$ filter is 0.693.



Figure 4.5. Top: Recorded torso (green), recorded head (blue), and predicted head velocity (magenta) for Subject 2, with $R^{2}_{prediction} = 0.85$. Bottom: The 10 sets of filter weights determined by the adaptive filter algorithm and 10-fold cross-validation procedure. The weights spanned the most recent 100 samples (1 second) of data. The 10 sets of filter weights for each trial had little variation, meaning each fold of data was similar to the other folds.



(magenta) velocities. The top panel shows a prediction for a well-fit filter that accounts for roughly half of the variation in the original signal (head velocity). The middle panel shows a prediction for a poorly-fit filter that has more variation than the actual head signal. Even though it is "poorly" fit, the predicted head velocity signal captures the amplitude and periodicity of the recorded head velocity signal. Bottom: filter weights for subject 3's (blue) and subject 9's (red) filters. While slightly different, similarities remain.

4.4 Discussion

Active, voluntary motion surely plays an important role in head stabilization, not only during passive perturbations (Allum et al., 1997; Guitton et al., 1986) but during active motion. Unlike many previous studies that used these passive perturbations to study head stabilization, the present study examines head stabilization during voluntary, rhythmic actions. Reflex control may play a vital role in head stabilization (Hirasaki et al., 1999; Peterson et al., 1985; Wilson, 1991; Wilson & Schor, 1999) as reflex control operates in the 1-2 Hz range (Keshner et al., 1995), overlapping with gait frequencies. However, head stabilization during locomotion may rely instead on efference copies of motor command signals.

The idea of efference copies (also known as corollary discharge) has its origins with von Helmholtz (1925) and was later expanded upon by von Holst and Mittelstaedt (1950). Motor commands can cause changes in sensory afference but are somehow accounted for and generally do not affect one's perception of the world. For example, moving one's eyes during a gaze shift causes the image on the retina to move without the perception of the world moving whereas poking one's eye seemingly causes the world to jump around. Von Holst and Mittelstaedt (1950) proposed that a copy of a motor command, the efference copy, is used to predict the reafference that would be caused by that command. This reafference is then compared to the actual afference received by the sensor and the resulting difference is the exafference. The exafference represents the sensory input from the outside world. Assuming no change in the outside world, a perfect efference copy would fully negate the sensory reafference and the resulting exafference would be zero. The suppression of reafference from self-generated behavior has been shown in many

animals and sensory systems including the electrosensory systems of mormyrid fish (Bell, 1981; Mohr, Roberts, & Bell, 2003), the mechanosensory system of crayfish (Edwards, Heitler, & Krasne, 1999; Krasne & Bryan, 1973), and the auditory system of crickets (Poulet, 2003, 2006).

Spinal central pattern generator-derived efference copies in tadpoles have been shown to drive compensatory eye movements (Combes, Le Ray, Lambert, Simmers, & Straka, 2008; Lambert, Combes, Simmers, & Straka, 2012; von Uckermann, Le Ray, Combes, Straka, & Simmers, 2013). Theoretical models of tadpole, teleost fish, and horse locomotion have shown that head displacement during locomotion (whether aquatic or terrestrial) shows strong spatio-temporal correlation to potential predictive values for compensatory eye movements (Chagnaud, Simmers, & Straka, 2012). In other words, stereotyped locomotion involves efference copies that could be used to predict head motion and consequently generate compensatory eye movements. This motion prediction can be combined with sensory feedback from VCR and CCR during rhythmic motion to maximize stability. This matches previous work with VOR where vestibular neurons were able to encode and compensate for voluntary gaze shifts during motion (see Angelaki and Cullen, 2008, for review).

4.4.1 Coherence

Fard, Ishihara, & Inooka (2004) used a spring-mass-damper model to accurately model head pitch motion during passive perturbations. In the frequency range of 0.8 Hz to 3 Hz, the mean values of 98% of their coherence functions were greater than 0.7 (see Figure 4.8).

Because they found consistently high coherence over their relevant range of frequencies, they decided it was appropriate to use a linear model. In the present study, coherence between torso and head angular velocities are close to one at step/gait frequencies, suggesting that linear models may work for predicting the relationship between the torso and head at those frequencies, but overall a purely linear approach may not do well. Figures 4.2 and 4.3 show subject-averaged coherence and a single subject's coherence. All conditions except for Virtual Sitting showed a similar pattern of coherence, where there were strong spikes at gait frequency but heavy noise and/or nonlinearities elsewhere. Overall, this pattern of coherence points to a non-linear system where gait frequencies pass through but other frequencies are not linked in a linear fashion between torso and head. Predicted velocity has coherence of near unity across the frequency range, unlike actual head velocity, and thus will fail to explain much of the variance in the actual head angular velocity in many cases even if amplitudes are reproduced.

Results could be improved by reducing sensor noise with better experimental procedure and equipment, much as Huterer and Cullen (2002) did to improve upon previous VOR experiments. Results may also be improved by considering nonlinear, active prediction of the neck. A model that uses predicted torso motion or has an existing model of possible head motion would likely do better to predict head motion than a purely passive model. It is very possible that efference copies originating from the spinal pattern generator or motor cortex could be used to predict head motion and the required neck muscle activation to counter that head motion. A simple modification of the linear filter may improve its prediction. This could be achieved by training a non-causal version of the

filter with prerecorded data then using a prediction of torso motion in addition to past torso motion to predict head motion in real-time.

4.4.2 Adaptive Linear Filters

Filter weights did not vary much from epoch to epoch during the 10-fold cross validation procedure (Figure 4.5), meaning subjects kept a stable pattern of motion during each task. In addition, LARP and RALP filter weights tended to be similar to each other while scYaw weights differed. This intuitively makes sense since scYaw velocities were different from LARP and RALP velocities in general and in their reduction from torso to head. In addition, most of the rotation experienced by subjects in this experiment was symmetrical in the LARP and RALP axes and different in the scYaw axis due to the natural left-right sway in gait.

The two walking conditions had the best R²_{prediction} and correlation values for each axis, which may have been related to the amount of motion of the torso and the jarring nature of faster movements, i.e. some subjects may have been smoother runners than others. Any jarring motion may have not only caused differences in how the neck anticipated incoming motion, but also may have created extra noise in the IMUs. Each sensor was attached by a strap to the head and torso which allowed some movement independent of the body, especially during changes in velocity like during the bottom or top of a stride. During the more rigorous conditions (running/stairs) the torso sensor may have bounced independent of the body in a way that they did not during the calmer conditions. The head sensor probably did not experience this problem as the head was stabilized by the neck and did not experience such large changes in acceleration.

The VR condition had slightly lower prediction that the walking condition which could be explained in several ways. Subjects were also may not have been perfectly matched in speed and height in the VR condition which may have affected their balance and movements. For safety and comfort reasons, some subjects held onto the treadmill's hand rails or relied on the safety strap placed behind them to guide their movements, which may also have affected their movements. Although the VR walking pace was slightly slower and had slower peak head velocities, there was probably no significant difference in sensor noise. Finally, they may have also been distracted by the novelty of the VR environment. Many subjects were new to VR in general and seemed excited to explore the world around them.

Qualitatively, the filters predicted head motion well, especially in terms of the amplitude range and general shape of the angular velocity curve. Sensor noise and high frequency perturbations from the sensor as it jostled independently from the torso/head could explain the low percent of variance explained and introduction of more variance than actually experienced for certain conditions. As previously mentioned, conditions with lower movement speed had better prediction in general. As Huterer and Cullen (2002) discovered, the fit of the sensors can significantly alter results, especially at high amplitudes and frequencies.

The linear filter does not account for voluntary movements subjects may have made to look around their environment. Subjects had high individual differences when it came to prediction. One subject had very high R²_{predicted} values for yaw at a mean 0.63 across conditions and an average correlation of 0.8. Two other subjects had R²_{predicted} values of 0.45 and 0.41 across conditions. Other subjects had very poor fits and were not modeled

well. This matches the statistical modeling in that individuals varied greatly from each other and were best fit separately.

Several factors could explain this inter-subject difference. Subjects varied greatly in their style of motion, with some subjects determined to look straight ahead while on the treadmill and others not so diligent (subjects were not specifically instructed to fixate their gaze, especially during conditions that took place outdoors). Some subjects also held onto the hand rails of the treadmill and/or stairs for stability, which may have affected their natural gait or caused some other unexpected alteration to their head velocity. Differences in gait and stabilization may also simply be due to intrinsic differences between subjects such as sex, height, weight, and athleticism.

4.5 Summary

The relationship between torso and head angular velocities was examined and a linear adaptive filter was used to predict head motion from torso motion. Just as in the previous project, subjects varied greatly between each other. Different movement conditions had different patterns of coherence. While all showed peaks in coherence at the fundamental gait frequency, some conditions showed peaks in coherence at each harmonic while others did not. This suggests that a linear or mostly linear relationship may exist between the torso and head. Linear adaptive filters had varying success which depended on subject, condition, and axis. In some cases, linear adaptive filters worked well to capture the filtering of the neck and predict head motion from torso motion, having both high correlation and high percent of variance explained. In other cases, the filters did not capture the noise of head motion, resulting in low percent of variance explained or even predicting greater variance than what the head actually experienced. Even in these cases,

however, there was still a considerable amount of correlation between predicted and actual head motion. A filter that took into account planned movement may be more accurate. One possible way of implementing this would be to train a non-causal filter or use a model to predict future torso movement and negate it, much like an efference copy is used to generate a prediction of change in sensation and is used to negate reafference. In any case, the active portion of head stabilization must be considered when trying to predict head motion during locomotion.

5 Head Stabilization During Natural Motion with Normalization

5.1 Introduction

Experiments 1 and 2 are repeated with modification. New angular velocity measurements were recorded from 20 subjects in eight conditions that included those from the previous chapters, except for virtual reality conditions. Outdoors walking and running conditions were added to allow analysis of gait in a more natural setting, rather than on a treadmill. Stair climbing and stair descent conditions were improved to only include actual stair-stepping rather than including turns between flights on the staircase. Two head turn conditions, where subjects walked with their heads turned approximately 45° to the left or right, were added to examine stabilization in situations where head and eye facing were different from direction of motion.

Custom sensors were built for this project to measure foot acceleration, which allowed analysis of gait cycles duration and normalization of data based on gait cycle. Methods from Chapter 3 on peak velocity of the torso vs. head, fitting angular velocity distributions, and power spectral density analysis were repeated with the new, gaitnormalized data and the additional conditions. Methods from Chapter 4 on coherence and using linear adaptive filters to predict head motion were repeated for the gait-normalized data and the additional conditions. Finally, the relationship between coherence and filter performance was examined.

5.2 Methods

5.2.1 Subjects

Angular velocity measurements for torso, head, and feet were recorded for 20 subjects (13 male, 7 female) while actively moving in eight conditions. All subjects were in good physical condition with no reported history of vestibular defects.

5.2.2 Conditions

Eight conditions were used to study gait: walking, jogging, head turned right walking, head turned left walking, stair climbing, stair descent, treadmill walking, and treadmill jogging. Participants were recorded for two minutes while performing each activity. Walking, jogging, and the two head turn walking conditions were performed in an outdoor corridor. Recording was paused as subjects reached either end of the corridor and turned around. For each head turn condition, subjects were instructed to turn their head so their nose was approximately 45° to the side, but otherwise walk as normal. The reason for this was to disentangle head direction (and vision) from the body's direction of motion. Turning the head approximately 45° in either direction moves the semicircular canals closer to the YPR-frame (see Figure 5.1). For Head Right, torso pitch corresponds to head LARP while torso roll corresponds to head RALP. These pairs are swapped for Head Left. If the head is being stabilized in a "measure and react" fashion, then there might be a difference in pitch reduction between Walking and head turn walking. If, however, efference copies are being used to stabilize the head, this head turn will be taken into account and velocity reduction should be the same as Walking.



For the two stair-climbing conditions, subjects were instructed to climb and descend the same flight of stairs at a moderate pace, one step at a time, for approximately 5 minutes. Recording was paused when subjects reached either landing at the top or bottom of the stairs and resumed after subjects turned around and resumed climbing. The two treadmill conditions were performed continuously for 2 minutes each, walking at 2.5 mph and running at 5mph. One subject elected to run at 4mph. Subjects were instructed to look at a fixation cross presented to them directly in front and slightly above the treadmill.

5.2.3 Measurements

Angular velocities of the torso and head were recorded at 1000 Hz using two InertiaCube BTs, a 3 degrees-of-freedom orientation tracking system. Instead of using an elastic band to hold the InertiaCube BTs in place, an inelastic nylon webbing was attached and tightly fastened to subjects. One InertiaCube was attached around the head with the sensor resting on the forehead just above the eyebrows. The other InertiaCube was attached to the torso, with the webbing wrapping just under the armpit and above the bust.

Two custom-built sensors (see Figure 5.2) were attached to the legs to measure angular velocity of the feet at 300 Hz. Each sensor was built using an ESP8266 microcontroller and an LSM9DS1 9 degree-of-freedom IMU. Custom software allowed wireless communication with the sensor and the labstreaminglayer protocol (UCSD Swartz Center for Computational Neuroscience, 2017). Each sensor was attached to the feet, facing outwards, and measured angular velocity in three axes: vertical (up-down), linear (forward-back), and lateral (left-right). The sensors were used to detect gait cycles.



Figure 5.2. The custom IMU system that was built for this project and used to detect gait cycles. This IMU is depicted with the case open for detail. A sensor was attached to each foot, facing outwards, each measuring angular velocity in three axes: vertical, linear, and lateral. Data was recorded at 300 Hz, which was then down-sampled to 128 Hz for analysis.

5.2.4 Data Analysis

Much of the data analysis was identical to previous chapters so only new or modified analyses will be described in this section.

Angular velocity data were filtered using a 16th order bandpass Butterworth filter with passband frequency of 0.2 to 25 Hz. Torso and head angular velocity data were downsampled to 256 Hz whereas feet angular velocity data were down-sampled to 128 Hz.

Steps were marked using foot angular velocity. The major peak in vertical angular velocity was used to mark steps during stair-climbing (representing the lifting and landing of one foot), and linear angular velocity was used to mark steps in all other conditions (representing the forward motion and halting of one foot). One gait cycle was the time from one major peak in acceleration to the next major peak, e.g. the time from when the right foot took off to the next time the right foot took off. Angular velocity measurements were then normalized in time by spline interpolation using the MATLAB *interp1* function. This step-normalized data was used to calculate PSDs. Gait cycles were phase-locked by taking the median gait cycle for each subject and condition, finding the phase angle (sample number) of the maximum point, then shifting the cutoff point so that each gait cycle started at the maximum acceleration value.

Peak velocities tended to be positively skewed, partly due to being the magnitude of velocity, so a Kruskal-Wallis test was used to compare peak velocity samples combined across subjects. Instead of looking at means as in Chapter 3, medians were examined instead, although this change did not change previous results (see Results, below). For the two head turn conditions, YPR-frame data from the torso was compared to LRY-frame in addition to the within-frame comparisons. This is because pitch velocity from the torso

would approximately be measured as RALP velocity in the Head Right condition and LARP in the Head Left condition. Roll velocity from the torso would approximately be measured as LARP velocity in the Head Left condition and RALP in the Head Right condition (see Figure 5.1).

Chapter 4's methods were also reproduced, and coherence and prediction by an adaptive linear filter were performed. In contrast to Chapter 4, the adaptive linear filter was performed on normalized data. Additionally, to examine the relationship between coherence and performance by the adaptive linear filter, a correlation coefficient was calculated. Two different measures of coherence were used to calculated this correlation. The first was the peak value at the fundamental gait frequency and the second was peak coherence below 10 Hz. Filter performance was measured by R²_{predicted} and filter correlation.

5.3 Results

5.3.1 Gait Cycle Duration

Gait cycle duration variability was generally small within subjects and conditions. Table 5.1 shows the average gait duration and standard deviation of in milliseconds across all subjects and for a single representative subject. Individual subjects showed very little variability in their gait cycle durations. The two stair conditions showed the greatest variability in gait cycle duration.

| Table 5.1. Mean gait duration in milliseconds with standard deviation in parentheses. | | | | | | |
|---|---------------------|-----------------|-----------------|-----------------|--|--|
| Condition | Duration (ms) | Variability (%) | Duration (ms) | Variability (%) | | |
| | Average of Subjects | | Subject 2 | | | |
| Walking | 1110.10 (28.09) | 2.53 | 1073.79 (21.37) | 1.99 | | |
| Running | 759.08 (31.81) | 4.19 | 741.79 (18.58) | 2.50 | | |
| Head Turn Right | 1098.67 (40.79) | 3.71 | 1051.07 (20.70) | 1.97 | | |
| Head Turn Left | 1104.23 (41.00) | 3.71 | 1073.57 (18.78) | 1.75 | | |
| Stair Climb | 1183.01 (74.33) | 6.28 | 1050.23 (55.28) | 5.26 | | |
| Stair Descent | 1107.15 (71.79) | 6.48 | 981.69 (76.17) | 7.76 | | |
| Treadmill Walking | 1140.92 (22.47) | 1.97 | 1108.69 (19.26) | 1.74 | | |
| Treadmill Running | 778.03 (25.24) | 3.24 | 796.54 (13.37) | 1.68 | | |



Figure 5.3 shows foot linear acceleration for all subjects. After normalization and phase alignment, a clear pattern is visible in foot linear acceleration even across all subjects. This shows that subjects move their feet in a very similar manner. Figure 5.4 shows gait cycle data for all subjects for the Walking conditions. This was done mostly as a visual check to ensure gait cycle detection and alignment was working correctly. Foot acceleration shows a relatively clear pattern of motion across subjects. Gait cycles within a condition for individual subjects show clear patterns with relatively little variation across gait cycles, but subject-averaged data comes out to mostly noise around a mean of zero.



Figure 5.4. Walking scYaw data split by gait cycle, means in black and medians in green. Top left: Head scYaw angular velocity for subject 15, all gait cycles. Top right: Torso scYaw angular velocity for subject 15, all gait cycles. Most subjects & conditions showed identifiable patterns for individuals, showing that gait cycle identification was successful. Bottom left: Head scYaw angular velocity for all subjects. While head motion, especially for walking, was relatively small, averaging across subjects eliminated any identifiable patterns. Bottom right: Torso scYaw angular velocity for all subjects. Again, averaging over subjects removed much of the identifiable information and left mostly noise around the mean.

5.3.2 Peak Velocity

Subject-averaged median peak angular velocity is summarized in Figure 5.5. Median peak velocity was used in contrast to mean peak velocity as in Chapter 3 because of the use of the Kruskal-Wallis test in analyzing peak velocity. Peak velocity distributions show enough rightward skew that they do not follow normality. This is partly because of taking the magnitude of angular velocity in order to include both halves of the gait cycle.



torso are in the bottom two plots. LRY-frame velocities are in the left column and YPR-frame velocities are in the right column. Just as previously examined in Chapter 3, YPR-frame velocities are greatest in pitch, followed by yaw, and finally least in roll for most conditions.

For both the LRY-frame and the YPR-frame, velocities are generally greater for the torso than the head, and the two running conditions have the greatest peak velocities. In the YPR-frame, peak velocity is greatest in pitch, followed by yaw, and least in roll. In the LRY-frame, peak velocity is more evenly distributed between the semicircular canal axes. Just as before, it seems that pitch and roll are split between LARP and RALP, while yaw and scYaw are roughly equal.

The two stair conditions show increased yaw and scYaw compared to pitch, LARP, and RALP. Peak velocities of the four walking conditions combined over subjects are shown in Figure 5.6. For all conditions, reduction in velocity from torso to head is statistically significant (p<.0001). For Walking and Treadmill Walking, head scYaw velocity was significantly different from LARP and RALP velocities (p<.0001). For Treadmill Walking, torso scYaw was significantly different from torso LARP and torso RALP (p<.0001) and it was significantly different from torso scYaw in Walking (p<.0001). Treadmill Walking RALP and LARP were significantly greater than Walking RALP and LARP (both p<.0001). scYaw was different between Treadmill Running and Running for both the torso (p<.0001) and head (p<.0001). Distributions of differences between torso and head angular velocity are summarized in Figure 5.7. Overall, reduction of scYaw velocity is significantly greater than LARP (p<.0001) and RALP (p<.0001). Velocity reduction for LARP and RALP are not significantly different (p=.65).



Figure 5.6. Median peak velocity of the torso and head in the LRY-frame for all walking conditions. A Kruskal-Wallis test was used to compare peak velocities between axes within each condition and sensor. In the treadmill walking condition, torso scYaw is significantly different from torso and torso RALP LARP (p<.0001); head scYaw is significantly different than head LARP and head RALP (p<.0001). In the walking condition, head scYaw is significantly different than head LARP and head RALP (p<.0001). In the head turn conditions, RALP and LARP show complementary patterns. In Head Left, LARP and scYaw are significantly different from RALP (p<.0001) but not from each other. In Head Right, RALP and scYaw are significantly different from LARP (p<.0001) but not from each other.


Reduction in the head turn conditions was performed by comparing torso YPRframe velocities with head LRY-frame velocities. With the head turned to the right, pitch and roll of the torso correspond more closely to LARP and RALP of the head, respectively. With the head turned left, left, pitch and roll correspond to RALP and LARP, respectively. For both, torso yaw is unaffected and corresponds to head scYaw as normal. Median peak angular velocity is shown in Figure 5.8. Head Right LARP peak velocities are not significantly different from Head Left RALP. Walking yaw peak velocity is not significantly different form Head Right RALP (p = .15) or scYaw (p = .997). Head Left LARP and scYaw are both significantly greater than Head Right RALP and scYaw and greater than Walking yaw and roll (all p<.0001). Walking pitch is significantly greater than all peak velocities for Head Right and Head Left.

Reduction of torso pitch to its corresponding head axis follows the same pattern for Head Right and Head Left as it does for Walking in the YPR-frame (Figure 5.9). Torso roll is



Figure 5.8. Left, Middle: Median peak velocity of the torso and head for the two head turn conditions. Because the head was rotated, the semicircular canals were oriented approximately to match yaw, pitch, and roll axes. Torso peak velocities are taken from the YPR-frame values whereas head peak velocities are taken from the LRY-frame values to examine how the neck stabilizes incoming motion from the body. Right: Median peak velocity of the torso and head for Walking in YPR-frame only.

near zero or slightly negative (meaning there was more roll in the head), and pitch and yaw are roughly equal. Head Right RALP differences were not significantly different from Head Left LARP differences (p=.92), and Head Right LARP differences were not significantly different from Head Left RALP (p=.42). However, Walking roll differences were around the same magnitude but still significantly greater than Head Right RALP (p<.001) and Head Left LARP (p<.0001). Walking Pitch differences were significantly less than Head Right LARP (p<.0001) and significantly less than Head Left RALP (p<.0001).



Figure 5.9. Left, Middle: Distribution of differences between torso and head angular velocity for the two head turn conditions. Velocity for the torso was taken from the YPR-frame, velocity for the head was taken from the LRY-frame. In the Head Right condition, pitch velocity is measured by LARP, roll is measured by RALP, and yaw is measured by scYaw, approximately. For the Head Left condition, roll is measured by LARP, pitch is measured by RALP, and yaw is measured by scYaw (approximately). For Head Right, reduction in pitch-LARP velocity is significantly less than in roll-LARP and in yaw-scYaw (both p<.0001). For Head Left, reduction in roll-LARP differences are significantly less than in pitch-LARP and in yaw-scYaw (both p<.0001). Torso roll velocities were often actually less than their head counterpart, leading to the peak at a negative angular velocity value. Right: Distribution of differences between torso and head for Walking in the YPR-frame alone.

5.3.3 Angular Velocity Distribution Fits

Cauchy and normal distributions were fit to angular velocity distributions just as in Chapter 3. Table 5.2 shows the AIC of each model. Again, the full Cauchy model performs better than the normal model. Additionally, the full model has a better (lower) AIC than the model with data combined over any dimension. The Δ AIC comparing the Cauchy model to the normal model is 8.2 x 10⁶ in favor of the Cauchy model, which means the normal model is much less than .0001 times as likely to minimize information loss as the Cauchy model (Burnham & Anderson, 2002).

Figures 5.10 and 5.11 show subject-combined angular velocity distributions and their best Cauchy and normal fits for head and torso LARP and scYaw. For the two running conditions in LARP and RALP the normal model fits as well or better than the Cauchy model, but for all other conditions and axes of rotation the Cauchy model is better fit. In those two conditions, there is a valley at 0°/sec angular velocity instead of a peak. In general, angular velocity distributions are leptokurtic, but more so for the head than the torso.

| Table 5.2. Models and their AIC for LARP, RALP, scYaw | | | | | | |
|---|------------------------|--|--|--|--|--|
| Model | AIC | | | | | |
| Cauchy Full | 1.04 x 10 ⁷ | | | | | |
| Cauchy Axes Combined | 1.13 x 10 ⁷ | | | | | |
| Cauchy Sensors Combined | 1.14 x 10 ⁷ | | | | | |
| Cauchy Subjects Combined | 1.15 x 10 ⁷ | | | | | |
| Cauchy Conditions Combined | 1.26 x 10 ⁷ | | | | | |
| Cauchy Subjects and Conditions Combined | 1.32 x 10 ⁷ | | | | | |
| Normal Full | 1.86 x 107 | | | | | |



subject averaged data is in black with standard deviation shaded in grey. In all cases the Cauchy distribution does a better job capturing the empirical angular velocity distributions.



Figure 5.11. Angular velocity distributions for torso LARP and scYaw. Cauchy fits are in magenta, normal fits are in green, and subject averaged data is in black with standard deviation shaded in grey. In all cases except for running LARP the Cauchy distribution does a better job of capturing the empirical angular velocity distributions.



meaning subjects experienced less motion. Head angular velocities are also more leptokurtic than torso angular velocities, as is expected, because the head is presumably more stabilized and thus experiences less motion.

As was previously shown in Chapter 3, angular velocity distributions of individual subjects show large variation, but follow common trends for each condition and sensor. Shown in Figure 5.12, this finding replicates previous results (see Figure 3.6). Each colored line represents one subject, with mean plotted in black. One difference to note is that torso velocities are smaller on average (more clustered around 0) here than in Figure 3.6. The walking condition from Chapter 3 was from the treadmill which has lower yaw (and scYaw) angular velocity than walking outdoors (see Figure 5.6).

5.3.4 Power Spectral Density

PSDs of full and subject-averaged angular velocity time series were calculated for each condition and axis of rotation. Just as in Chapter 3, we fit two simple models to the PSDs. The first was a single line, power-law fit, over the low (0.2 to 2 Hz) and high (10 to 25 Hz) range. The second model used two lines, one each for the low and high range. Figures 5.13 and 5.14 show subject-averaged PSDs with both the power-law (single line) and twoline fit. PSDs of angular velocity were much cleaner as a result of using gait-normalized data. All the walking conditions had a fundamental gait frequency of 0.875 Hz. This matches the previously computed mean gait cycle duration for each walking condition which came out to approximately 0.9 Hz (see Table 5.1).

The two-line model was a significantly better fit than the one-line (power law) model for the full set of PSDs not combined over any dimension (F(2880,125760) = 9.16, p<.0001) and for PSDs of subjects combined (F(144,6288) = 11.55, p<.0001). However, just as before, increases in power at the fundamental gait frequency and its harmonics were not well captured by either model. Power in LARP was greater for the head below 0.8 Hz for the walking conditions. Above 1 Hz, head power was generally lower than torso power (Figure 5.13). Power in the torso was greater over the whole frequency range during running. Power was about equal in the stair conditions below the fundamental gait frequency. Power in scYaw was greater for the head in walking conditions below and greater for the torso above the fundamental gait frequency. For the running conditions, power was about equal throughout the whole range. For the stair conditions, power was slightly greater in the head for almost the whole range, evening out near the gait frequency (Figure 5.14).



Figure 5.13. PSDs of LARP angular velocity. LARP is generally greater in the torso than head, except for very low frequencies (<1Hz) in the walking conditions. Each walking condition and stair condition had its fundamental peak in power at 0.875 Hz, which matches the normalized gait cycle duration. Running had a fundamental gait frequency of 1.375, with Treadmill Running slightly lower at 1.25 Hz. As a result of the gait cycle normalization, the peaks in power are much smoother compared to Figure 3.7. Again, single line fits of PSDs fail to capture increases in gait power at fundamental gait frequencies and their harmonics. For the stair climbing conditions, the two-line fit fails to cross in the depicted range.



Figure 5.14. PSDs of scYaw angular velocity. Each walking condition and stair condition had its fundamental peak in power at 0.875 Hz, which matches the normalized gait cycle duration. Running had a fundamental gait frequency of 1.375, with Treadmill Running slightly lower at 1.25 Hz. As a result of the gait cycle normalization, the peaks in power are much smoother compared to Figure 3.7. Again, single line fits of PSDs fail to capture increases in gait power at fundamental gait frequencies and their harmonics. For the stair climbing conditions, the two-line fit fails to cross in the depicted range.

5.3.5 Coherence

Coherence was calculated for the YPR- and LRY-frame between torso and head angular velocity, just as in Chapter 4, and results were largely the same. Subject-averaged coherence was quite poor, never exceeding 0.4 at the fundamental gait frequency for any condition-axis pair. Figure 5.15 shows single-subject coherence in the LRY-frame, which is in contrast to the single subject coherence in the YPR-frame as in Figure 4.3.

Coherence for normalized data was much cleaner than for the non-normalized data from Chapter 4. Peaks are much more recognizable at the fundamental frequency and its harmonics. Coherence is generally greater at lower frequencies and drops off as frequency increases, but patterns beyond this are subject-dependent. For example, subject 1 shows



Figure 5.15. Coherence between the torso and head in the LRY-frame for a subject 1. Peaks in coherence occur at the fundamental gait frequency and its harmonics. Coherence for scYaw was generally the highest. Peaks in coherence remain visible through 10 Hz.

strong peaks in coherence at the fundamental gait frequency and its harmonics up to 10 Hz during Treadmill Walking and Treadmill Running (Figure 5.15), while subject 7 (see Figure 5.16) shows a quick falloff in coherence over that same range.



5.3.6 Adaptive filter

Average linear filter R²_{prediction} values are summarized in Table 5.3. Head velocity predictions by the adaptive filter are shown in Figure 5.17. In the LRY-frame, prediction was roughly equal for all three axes except for scYaw in Walking and Treadmill Walking. In the YPR-frame, the highest R²_{prediction} values were for roll, followed by yaw, and were lowest for pitch head motion. The four walking conditions had the greatest R²_{prediction} values, followed by the two stair conditions, and finally was lowest for the two running conditions. Mean values were lower than in Chapter 4, but this may be due to the Running condition, where predicted head velocity had much more variance than actual head velocity. Treadmill Running in this experiment also had worse subject-averaged R²_{prediction} values. Out of the 20 subjects, only 3 had positive scYaw R²_{prediction} values for Running. Filters for Treadmill Running fared better, with half of the subjects ending up with positive scYaw R²_{prediction} values. Just as before, individuals had large variation in R²_{prediction} and qualitative filter performance.

Correlation between the predicted head velocity and actual head angular velocity were higher (see Table 5.4). Higher correlations mean that predicted head velocities are more similar in shape to actual head velocities, regardless of amplitude. Walking conditions generally had the greatest correlation between predicted and actual head velocity. In the YPR-frame, pitch had the lowest correlation overall, with yaw and roll being roughly equal. In the LRY-frame, correlation was more evenly split between axes but slightly greater in scYaw. Individuals also had large variation in correlation within each condition.

| cross-validation procedure for yaw, pitch, roll, LARP, RALP, and scYaw. The values in parentheses for the mean row are the mean without using the outliers from Running. | | | | | | | | |
|--|--------------|--------------|-----------|-------------|-------------|-------|--|--|
| R ² prediction | Yaw | Pitch | Roll | LARP | RALP | scYaw | | |
| Walking | 0.28 | 0.16 | 0.41 | 0.23 | 0.23 | 0.34 | | |
| Running | -4.03 | -0.95 | -0.03 | -0.47 | -0.67 | -4.26 | | |
| Head Right | 0.22 | 0.2 | 0.27 | 0.26 | 0.24 | 0.22 | | |
| Head Left | 0.18 | 0.21 | 0.27 | 0.28 | 0.29 | 0.24 | | |
| Stair Climb | 0.11 | 0.1 | 0.31 | 0.20 | 0.20 | 0.15 | | |
| Stair Descent | 0.16 | 0.19 | 0.24 | 0.22 | 0.26 | 0.19 | | |
| Treadmill Walking | 0.44 | 0.24 | 0.32 | 0.26 | 0.27 | 0.45 | | |
| Treadmill Running | -0.51 | -1.13 | 0.34 | -0.44 | -0.42 | -0.36 | | |
| Mean | -0.39 (0.13) | -0.12 (0.00) | 0.27 (31) | 0.07 (0.15) | 0.05 (0.15) | -0.38 | | |

Table 5.3. Average of individual R²_{prediction} values averaged over subjects for the 10-fold

Table 5.4. Average of individual correlations of filter prediction with actual head for the 10-fold cross-validation procedure for yaw, pitch, roll, LARP, RALP, and scYaw.

| Correlation | Yaw | Pitch | Roll | LARP | RALP | scYaw |
|-------------------|------|-------|------|------|------|-------|
| Walking | 0.67 | 0.41 | 0.62 | 0.48 | 0.45 | 0.69 |
| Running | 0.23 | 0.23 | 0.34 | 0.24 | 0.22 | 0.22 |
| Head Right | 0.59 | 0.44 | 0.49 | 0.50 | 0.48 | 0.59 |
| Head Left | 0.58 | 0.46 | 0.5 | 0.51 | 0.53 | 0.59 |
| Stair Climb | 0.7 | 0.36 | 0.56 | 0.45 | 0.46 | 0.69 |
| Stair Descent | 0.65 | 0.47 | 0.48 | 0.49 | 0.50 | 0.65 |
| Treadmill Walking | 0.67 | 0.48 | 0.55 | 0.49 | 0.49 | 0.67 |
| Treadmill Running | 0.39 | 0.28 | 0.58 | 0.34 | 0.30 | 0.45 |
| Mean | 0.56 | 0.39 | 0.52 | 0.44 | 0.43 | 0.57 |



Correlation was calculated between filter R²_{prediction} and filter correlation to peak coherence at the fundamental gait frequency. Gait frequency coherence had a correlation coefficient of 0.03 for R²_{prediction} and a correlation coefficient of 0.42 for filter correlation when not using the running conditions. The running conditions had large outliers for R2, and removing them gave correlation coefficients of 0.18 and 0.46 for R and filter correlation, respectively (see Figure 5.18). An example of this can be seen by comparing the linear filter predictions from Figure 5.17 to coherence in Figures 5.15 and 5.16. The top half of Figure 5.17 shows the actual and predicted head scYaw velocities of subject 1 during Treadmill Walking, which was one of the better-performing filter predictions. Figures 5.15 shows coherence for subject one, with Treadmill Walking in the bottom left. Coherence is very high at the fundamental gait frequency (0.875) and there are clear, strong peaks at its harmonics through 10 Hz. The bottom half of Figure 5.17 shows the actual and predicted head scYaw velocities of subject 7 during Treadmill Running, which had moderate performance with low R²_{prediction} but high correlation. There is one strong peak in scYaw at the fundamental gait frequency, but coherence quickly drops and does not have peaks at gait frequency harmonics.



5.4 Discussion

This project aimed to confirm previous results while applying gait normalization techniques to subject data. It also replicated previous results while attempting to control for gait cycle differences between subjects. There are several methods of normalization which are each useful for different applications such as linear length normalization, dynamic time warping, and piecewise versions of each (Helwig, Hong, Hsiao-Wecksler, & Polk, 2011). For this project, a linear length normalization was used, linearly adjusting each gait cycle is to have equal length. While different normalization methods warp data in different ways, using a more complicated method may not have been appropriate or helpful for the present work.

5.4.1 Gait Duration

Overall mean gait cycle durations and variability are comparable to previous work (Brisswalter & Mottet, 1996; Kurz, Wilson, & Arpin, 2012) but notably have smaller gait duration variability. This may be because previous work averaged across subjects whereas here an average of subject averages was taken. When averaging with subject data combined, variability becomes comparable to previous work.

Figure 5.4 shows the variation in torso and head angular velocity of gait cycles for all subjects combined and for a single subject. The overall structure of foot acceleration was still visible after averaging subjects, and torso velocity for a single subject still clearly followed the pattern of individual gait cycles. The loss of structure for head and torso velocity across subjects might just be due to differences between subjects and not a failing of the gait normalization method. Using one of the more advanced normalization methods outlined by Helwig and colleagues (2011) may or may not have given better results. The

shape of foot acceleration was largely similar across all subjects after normalization, but there was plenty of noise across subjects. Using a piecewise method where subsections of gait are normalized in length instead of just overall length may have improved results by reducing noise, but differences between subjects makes subject-averaged data average out to noise around the mean (see Figure 5.4). Variation within subjects was so small that improvements were likely to have been minor.

5.4.2 Peak Velocity

Peak velocity does not rely on the shape of the gait cycle and thus results were largely unaffected by normalization. In contrast to Chapter 3, median peak velocities instead of mean peak velocities were analyzed. This is because peak velocity distributions tended to not follow a normal distribution and instead were positively skewed. Replicating results from Chapter 3, angular velocity was greatest in pitch and least in roll, and transforming data to the LRY-frame more evenly distributed velocity among the three semicircular canal axes. Peak angular velocity by sensor and axis, however, differed from previous results. Compare Figure 5.6 with Figure 3.1 C and D. Results from Chapter 3 show that LRY-frame angular velocity reduction is more even across the three axes (LARP, RALP, scYaw) than for reduction in the YPR-frame, seen as three roughly parallel lines for LRYframe data compared to clearly non-parallel lines for YPR-frame data. In the current work, the relationship between axes and sensors is more nuanced. One key difference was in scYaw peak velocities and reduction.

Natural walking and running differed from Treadmill walking and running. Yaw and scYaw of the torso between Walking and Treadmill Walking were significantly different. This is especially notable as peak torso scYaw velocities were the same as LARP and RALP

peak velocities during Walking, but peak torso scYaw velocities were significantly greater than RALP and LARP peak velocities during Treadmill Walking. Reduction in scYaw was also significantly greater than LARP and RALP, as opposed to the even reduction found in Chapter 3. It is unlikely that differences in walking speed were the cause of this, as LARP and RALP angular velocities were not significantly different between Walking and Treadmill Walking. Differences in walking outside vs. on a treadmill such as a forced speed, lack of optic flow, or lack of forward linear acceleration may account for these differences in torso angular velocity. Lacour and colleagues (1997) found that their group of subjects seemed to weigh visual and vestibular input differently while measuring body sway. Approximately half of their subjects (both healthy and patients with a vestibular disorder) swayed more with eyes closed while the other half swayed less with eyes closed. It may be the case that the presence or absence of visual cues of motion like optic flow and vestibular cues of motion like linear acceleration may affect torso and head stabilization.

The two head turn conditions separate direction of motion and head direction. It also causes the semicircular canals to be oriented in such a way that pitch velocity no longer is split evenly between LARP and RALP canals. Instead, rotation in pitch of the torso becomes rotation in RALP of the head and rotation in roll of the torso becomes rotation in LARP of the head during the Head Right condition (and vice versa for Head Left).

Peak velocities for Head Right and Head Left followed the same pattern as Walking YPR-frame velocities. For Walking, peak pitch velocity was the greatest, with peak yaw velocity being only slightly greater than peak roll velocity. For Head Right, peak LARP velocities were greatest, with peak RALP and peak scYaw velocities roughly equal. For

Head Left, RALP and LARP switched places, as would be expected. Head Right and Head Left are not quite equal in scYaw or their roll equivalents (RALP for right, LARP for left).

Reduction of head velocities for the head turn conditions follow the same pattern of reduction as Walking in the YPR-frame. In these conditions, instead of two pairs of canals measuring pitch and roll, only one pair measures each. If head stabilization were completely reflexive, measuring incoming signals and counteracting them as quickly as possible, then using measurements from a single set of canals rather than two sets should reduce the stability of the head. Instead, reduction is about the same with the head turned in either direction, consistent with the hypothesis that head stability depends on signals generated by the torso (supporting efference-copy driven stability), as it has been shown to drive eye-movements in tadpoles (Combes et al., 2008; Lambert et al., 2012; von Uckermann et al., 2013) and be correlated to head displacement in tadpoles, telecost fish, and horses (Chagnaud et al., 2012). It may also be that perturbation from walking does not reach the limit of a single set of canals.

These results do not follow exactly what would be expected if the canals were rotated 45°. If subjects had held their heads at exactly 45° from center, each head turn condition should have shown results closer to the YPR-frame Walking results. In fact, subject mean head turn was 39.5° for Head Right and -38.1° for Head Left, meaning subjects had not turned and kept their heads at 45° for the entire trial. This means pitch and roll velocities were slightly split between RALP and LARP. Peak velocity distributions show this pattern, where peak velocities of RALP and LARP values of the head turn conditions are closer to each other than peak pitch and roll velocities of Walking.

5.4.3 Power Spectral Densities (PSDs), Coherence, and Filters

Power Spectral Densities

PSD graphs are much cleaner because of the normalization compared to the PSD graphs from Chapter 3 (see Figure 3.7). Overall results are the same, showing that the twoline fit is indeed better that a simple power-law fit. However, increases in power at fundamental gait frequency and its harmonics are not well-described by a power law. *Coherence*

Coherence results mostly replicated those from Chapter 4 except for the low coherence for subject-averaged data, likely due to larger individual differences and/or gait cycle normalization. Coherence for scYaw was generally greatest, and all three axes showed peaks in coherence at the fundamental gait frequency and/or its harmonics. For some conditions (especially the two treadmill conditions), some subjects showed peaks in coherence up to 10 Hz while others had very weak or no peaks at gait frequency harmonics. This shows that walking and running outside vs. on a treadmill can be very different for some people and is another factor to consider when examining gait data.

Filters

The adaptive linear filters showed mostly the same results as in Chapter 4. There was overall poor proportion of variance explained (R²_{predicted}), but filters for some individual subjects did very well. While roll showed higher R²_{predicted} than Yaw or pitch, this is likely because there was very little roll velocity to begin with. Gait normalization does not seem to affect filter performance, although smoothing of input velocity does. A lowpass filter with lower cutoff (e.g. 5 Hz instead of 25 Hz) results in greater R²_{predicted} performance, but this is to be expected as there is less high frequency variation. This may be desirable as

high frequency components are likely to come from sensor noise such as movement of the sensor against the skin that does not correspond to gait. Gait cycles had a fundamental frequency of around 1 Hz, so even a 5 Hz cutoff allows the first several harmonics to be represented in the data. Correlation is possibly a better measure of filter performance, and these values are much higher than R²_{predicted} values with an average of 40 – 50% correlation. Just as in Ch 4, the amplitude and shape of head motion is generally represented well by the filter prediction, even if the more minute variations are not. Filters for some subjects perform much better than for other subjects.

There was a positive correlation between coherence and filter performance. Given that the filter is a linear combination of data, data that have high coherence (i.e. linear relationship) will be more accurately represented by a linear relationship. Figure 5.15 shows coherence for one of the better performing subject-condition pairs. The prediction of this filter is shown in the top half of Figure 5.17.

5.5 Summary

Results from the first two projects in Chapter 3 and 4 were reexamined using gait cycle normalization techniques. Several conditions were added or modified to further examine gait, and to do so more optimally. Finally, a closer look was taken at results from Chapter 3 and Chapter 4 methods on new data.

Gait cycle normalization showed that subjects had very low variation in gait cycle duration. After normalization, gait cycles showed relatively little variation in foot acceleration, showing that a simple linear warping performed very well for healthy subjects during single gait types.

Modifications to the conditions include the staircase conditions and the two head turn conditions. The staircase conditions were modified to only record actual stair climbing and stair descent. Unlike Chapter 3 and 4, stair climbing did not include the turns that occurred between flights of stairs, and thus was a more accurate representation of gait cycles during stair climbing. Two additional outdoors conditions, Walking and Running, were added to contrast with the treadmill versions from Chapters 3 and 4, which were replicated with the Treadmill Walking and Treadmill Running of Chapter 5. Peak angular velocities as well as reduction in angular velocities were different between the outdoor and treadmill walking/running conditions. These differences may be due to the lack of optic flow, lack of linear acceleration, or the more controlled fixation point for the treadmill conditions.

The head turn conditions aimed to examine what happens when the canals are oriented in a YPR-frame relative to the direction of motion. Results from these conditions resemble those of YPR-frame Walking, with some differences. These differences may be because subjects did not turn their heads far enough to reach 45° during these trials. Results are consistent with the hypothesis that head stabilization is driven by efference copies of gait, although stronger perturbations of the head may be needed to fully answer this question. Using a motorized platform to apply rotations to subjects, one could theoretically record a subject's torso motion and "play it back" to them by rotating the platform in an identical manner. Differences in head rotation between this condition and from when they were actually moving could provide evidence of the importance of efference copies in head stabilization.

Previous model fitting results were mostly replicated. Distribution fitting was unaffected by gait cycle normalization. Cauchy distributions fit empirical distributions better than normal distributions, except for Torso LARP and RALP during running conditions. Full models that did not combine over subjects, conditions, or axes outperformed all other models. Results on PSD fitting were unaffected, other than the generation of cleaner PSDs. While the two-line model was a better fit for PSDs, power increases at the fundamental gait frequency and its harmonics were much clearer and were not captured by either model.

Coherence again showed large peaks at the fundamental gait frequency and its harmonics, although the decay over frequency differed between subjects and conditions. Linear adaptive filters again proved to have a wide range of success in predicting head velocity from torso velocity. However, this time, the performance of the filters was found to be correlated with coherence at the fundamental gait frequency, providing evidence that filter performance is dependent on the gait cycle of subjects.

6 References

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