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Depth Judgment and Target Tracking from Eye Movements During
Self-Motion

A dissertation written in partial satisfaction for the degree

Doctor of Philosophy in Biomedical Engineering

by

Jared Rale Frey

2012

ABSTRACT OF THE DISSERTATION

Depth Judgment and Target Tracking from Eye Movements During

Self-Motion

by

Jared Rale Frey

Doctor of Philosophy in Biomedical Engineering

University of California, Los Angeles, 2012

Professor Dario Ringach, Chair

Here we investigate visuomotor integration in humans, in particular, eye movements occurring during head and body movement. While this self-motion poses a challenge for the visual system it can also provide valuable information. This is evident in the first study, which demonstrates that self-motion-derived parallax can elicit binocular eye movements in depth (vergence). The most notable result of this study is that this depth cue drives vergence even when binocular disparities indicate a flat surface. The second study explores the dynamics of visual tracking behavior with the head free to move. Most studies of visual tracking have restrained the head, therefore little is known about the interaction between the eye movement systems involved when the head is also engaged in tracking. Using a rich visual

stimulus and simultaneous tracking of the head and eye, we sought to close this gap in the literature. In particular, we were able to characterize not only the linear sensorimotor dynamics of smooth pursuit and head tracking during this task, but also the vestibular-ocular reflex as behaves during unrestrained pursuit. Sensorimotor integration is best understood in the context in which is has evolved to perform. Allowing the subject unrestrained self-motion is a step in that direction.

The dissertation of Jared Rale Frey is approved.

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TABLE OF CONTENTS

Chapter 1: Background

<i>1.1 The Importance of Eye Movements</i>	<i>1</i>
<i>1.2 Vestibulo-Ocular Reflex</i>	<i>2</i>
<i>1.3 Smooth Pursuit</i>	<i>4</i>
<i>1.4 Eye-Head Tracking</i>	<i>6</i>
<i>1.5 Binocular Vision and Vergence Eye Movements</i>	<i>8</i>
<i>1.6 Depth from Motion Parallax</i>	<i>10</i>
<i>1.7 References</i>	<i>14</i>

Chapter 2: Binocular Eye Movements from Self-Induced Motion Parallax

<i>2.1 Abstract</i>	<i>20</i>
<i>2.2 Introduction</i>	<i>21</i>
<i>2.3 Materials and Methods</i>	<i>23</i>
<i>2.4 Results</i>	<i>30</i>
<i>2.5 Discussion</i>	<i>33</i>

2.6	<i>References</i>	41
Chapter 3: Dynamics of Coordinated Head-Eye Visual Tracking		
3.1	<i>Abstract</i>	43
3.2	<i>Introduction</i>	44
3.3	<i>Materials and Methods</i>	47
3.4	<i>Results</i>	55
3.5	<i>Discussion</i>	60
3.6	<i>References</i>	73
Chapter 4: General Discussion		
4.1	<i>Future Work</i>	75
4.2	<i>Concluding Remarks</i>	81
4.3	<i>References</i>	82

TABLE OF FIGURES

Figure 2-1	Experimental Setup	36
Figure 2-2	Individual and Group Vergence Responses	38
Figure 2-3	Dynamics of Vergence Responses	39
Figure 2-4	Vergence versus Simulated Depth	40
Figure 3-1	Mean Velocity Traces for Eye-Head Tracking	68
Figure 3-2	Linear Temporal Filters	69
Figure 3-3	Estimated Frequency Response Functions	70
Figure 3-4	Predicted Velocity Traces	71
Figure 3-5	Predicted versus Measured Velocities	72

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There have been many hard choices and difficult problems along the way. I've been fortunate to have many great mentors and teachers. While there are too many to list, I would be remiss if I didn't single out Jon Stolk. I came to college without a strong sense of self, like most teenagers. I left with at least some understanding of what I had to offer and what gave life meaning. What's more is I learned that those things constantly change and that's a good thing.

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When I went to formally change my advisor, the graduate student affairs officer said, "Oh, Dario! Great! He's a true mentor." Though reassuring, I didn't really know what he meant until later. A mentor models how to do quality science. It's someone who holds up high standards, who considers your interests and development, and who volunteers their precious time. And a mentor is also patient. As I found out, not every PI is a true mentor.

I ended up with one that is. Thank you.

Chapter 2 is a version of Binocular Eye Movements Evoked by Self-Induced Motion Parallax *The Journal of Neuroscience*, 23 November 2011, 31(47): 17069-17073, reproduced with permission. Abtine Tavassoli assisted with experimental design and data analysis. Dario Ringach was the principal investigator.

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Chapter 1: Background

1.1 THE IMPORTANCE OF EYE MOVEMENTS

Human vision is active. That is, rather than passively receiving visual information, we move our eyes, heads, bodies and use our limbs to move objects in order to gain more information, which in turn informs more movement. Due to the relatively small area of high acuity, eye movements are especially important to turn the fovea toward the area of greatest need or interest. Additionally, we move and live in environments where many objects of interest move as well. Without compensatory eye movements, motion blur would compromise visual acuity. As a result, the eyes are almost constantly in motion, sometimes to stabilize the retinal image and sometimes to move it to a new location. Further, self-motion can be a rich source of extra-retinal information, which can aid in understanding incoming visual information. All of this requires incredible communication and integration between the visual, vestibular, proprioceptive and oculomotor systems. This chapter of the dissertation outlines some fundamental topics in eye movements as they relate to depth, object motion and self-motion. It will cover two topics in detail, which will be important to

the proceeding chapters, eye-head tracking (EHT) and motion parallax (MP). But first some introduction to related topics is in order.

1.2 VESTIBULO-OCULAR REFLEX

The vestibular apparatus, located in the inner ear is a fluid filled organ with specialized sensory cells (hair cells), which can detect flow within the fluid. The hair cells transduce motion into an electrical signal, which is carried on to the vestibular nucleus. The three semi-circular canals (in each ear) detect angular acceleration while the two otoliths detect linear acceleration. Vestibular signal is important for controlling posture, kinesiesthesia and eye movements. More specifically, the vestibulo-ocular reflex (VOR) generates motor commands to counter-rotate the eye during head movement in order to stabilize the retinal image.

The VOR is extremely fast, with latencies as low as a few milliseconds in humans and monkeys (Lisberger 1988; Maas, Huebner et al. 1989; Snyder, Lawrence et al. 1992; Angelaki and McHenry 1999; Lasker, Ramat et al. 2002). This is made possible by rapid signal transduction and the short, three-neuron reflex arc responsible for the sensory-motor transformation. However, this reflex must be labile. For instance, depending on the distance

of the fixation point, the gain of the VOR must be adjusted. These adjustments are very rapid, with some reports indicating that they occur as within a few milliseconds, or even before the movement begins (Gianna, Gresty et al. 1995; Crane and Demer 1998; Angelaki and McHenry 1999; Lasker, Ramat et al. 2002; Crane, Tian et al. 2003; Zhou, Xu et al. 2007). Experimental regimes have shown the VOR to be extremely adaptable to changes to in visual feedback – accommodating for phase changes, changes or even reversal of gain brought on by prisms, constant vestibular stimulation and exhibiting cross-axis plasticity, where VOR response direction is manipulated (for instance adding a vertical eye movement component to purely horizontal head rotation) (Leigh and Zee 2006).

When the target and head move in the same direction, however, the VOR is counter-productive since it drives the eye away from target. This can happen, for instance, when looking at something in your hand while walking. In the laboratory, a more pure example is to have a subject in a rotating chair, with the task to foveate on a target that is fixed to the chair. As the chair rotates, so does the target, and therefore the VOR must be cancelled to maintain fixation. Humans and monkeys are very good at this task and can even cancel about half of the VOR when imagining a target in

complete darkness (Jones, Berthoz et al. 1984). However, in all cases, cancellation is never quite complete, leaving a small residual VOR which is compensated for by small catch-up saccades.

1.3 SMOOTH PURSUIT

When it is the target that moves rather than the observer, there is no vestibular signal that can be used to generate compensatory eye movements for gaze stabilization. Instead, humans and many other animals have a specially adapted, visually-guided smooth pursuit (SP) system that controls eye movements for gaze stabilization during target motion (for reviews of SP see (Krauzlis 2004; Ilg and Thier 2008; Lisberger 2010). SP is reflex-like in that it has a relatively fast response and needs a stimulus in order to become engaged, the signal being retinal slip velocity (difference in angular velocity between eye and target) (Rashbass 1961). However some have argued that SP is more voluntary in that there is some cognitive control over which motion signals are pursued and that it can follow complex, gestalt, perceived motion rather than simply retinal motion (Steinbach 1976; Beutter and Stone 2000; Stone, Beutter et al. 2000). Using eye movement recordings to feedback to target velocity, it was found that once pursuit is engaged, it will continue at a constant velocity in absence of retinal slip (Morris and

Lisberger 1987). This is evidence that SP is not purely regulating retinal slip and that initiation of pursuit is different than maintenance.

SP has much longer latencies than the VOR because of the more numerous sensory processing steps and longer signal transduction, with reported latencies typically around 100 ms. From a controls standpoint, this significant closed-loop delay between output and feedback can cause problems. A fast, high gain controller would be unstable, constantly ‘overreacting’ to error signals that were generated from the previous ‘overreaction.’ However, a slower, lower gain controller is sluggish – responding too little and too late to changes in target motion. As described earlier, retinal slip alone is not enough to explain behavior, which has also been shown by analysis of the steady-state dynamics (Ringach 1995). Several signals could be utilized to help solve this problem this including image acceleration, efference copies of motor commands and internal models of feedback delays (i.e. Smith predictors) (Robinson, Gordon et al. 1986; Krauzlis and Lisberger 1994; Ringach 1995; Churchland and Lisberger 2002).

1.4 EYE-HEAD TRACKING

More naturally, visual tracking is not accomplished solely by SP but by a combination of eye, head and even torso movements. These additional joints offer greater range of motion and allow the eye to remain closer to the primary position, which permits saccades across a more symmetric area of visual space. On the other hand, the additional joints increase the complexity of the tracking task and make the execution of experiments and interpretation of results more difficult. As a result, joint eye-head tracking (EHT) is more poorly understood than SP.

Similar to the examples provided previously, the VOR must be cancelled during EHT. In the classic head-brake experiment (Lanman, Bizzi et al. 1978), it was found that the VOR isn't simply 'turned off' but actively suppressed by a cancellation signal. In this experiment, monkeys were trained to pursue a target with a combination of head and eye movements, and then suddenly and unexpectedly, a brake was applied to the head. With a latency of only a few milliseconds the eyes were able to compensate for the sudden loss of head movement. This response is far too fast to be visually mediated and therefore most likely originates from a still-active VOR. To

confirm this, monkeys with a vestibular lesion had response latencies that were over 100 ms, which is feasible for a visually mediated response.

When the head is manipulated by a torque helmet, vestibular chair or head brake (Lanman, Bizzi et al. 1978; Cullen, Belton et al. 1991; Tabak and Collewijn 1994; Paige, Telford et al. 1998; Demer and Crane 1999; Tangorra, Jones et al. 2003; Tangorra, Jones et al. 2004; Crane, Tian et al. 2005; Ramachandran and Lisberger 2006), it is more straightforward to discern which eye movements caused by the VOR because the experimenter can control the input signal (the head movement). However, active head movements are by definition not manipulated by the experimenter, and are therefore more difficult to tease apart from other eye movements.

As a result, there is relatively little characterization of how the VOR actually operates during active movement. We do know that the vestibular pathways of the brain stem treat active and passive head movements differently and that there seems to be a ‘cancellation signal’ derived from motor efference copies (Belton and McCrea 2000; Belton and McCrea 2000; Roy and Cullen 2001; Roy and Cullen 2002; Roy and Cullen 2003; Cullen and Roy 2004). Behaviorally, we know that the VOR is incompletely cancelled and that

cancellation can be anticipatory (Barnes and Lawson 1989; Barnes and Grealy 1992; Waterston and Barnes 1992; Barnes 1993; Barnes and Paige 2004; Ackerley and Barnes 2011)). However, we have almost no characterization of the dynamics of the residual VOR during EHT. Further, there is little direct comparison between how SP operates during EHT versus the more typical head-fixed situation. Finally, the full linear dynamics of the sensorimotor responses of the eye and head have not been described. The proceeding chapter addresses these points. The remainder of this chapter introduces additional topics important to the third chapter.

1.5 BINOCULAR VISION AND VERGENCE EYE MOVEMENTS

Front facing mammals observe spatial parallax due to the close, relative displacement of their eyes. That is, a given point in space will likely project to each retina, but only rarely projects to exactly the same corresponding point on each one because each eye has a slightly different view. The challenge is to appropriately match corresponding locations from eye to the other. This is often called the ‘correspondence problem’. The relative differences in retinal locations are called binocular disparities and are directly related to depth. Stereopsis results from solving the ‘correspondence problem’ and subsequently reconstructing depth. Stereopsis is very acute at

short distances, where small changes in depth result in large disparities and becomes less accurate as distance increases, simply due to geometry.

The vergence angle is defined by the relative angle between the lines of sight of the two eyes. If a subject perfectly fixates on a point, the eyes converge to that point and binocular disparities at that point are zero. Due to this tight relationship, it should come as no surprise that vergence is strongly driven by disparities. However, this need not be. The eyes could be yoked such that the vergence angle is always fixed or that the eyes could be independently controlled as in chameleons. In both cases, you would also have disparities and the possibility of stereopsis.

However, vergence seems necessary. First, there has found to be a limit to the degree of disparity tolerated before binocular fusion breaks down and diplopia occurs (Panum's area). Second, patients with eye movement deficits that do not allow proper control of vergence do not have stereopsis (Leigh and Zee 2006). From a functional standpoint, we can think of vergence as greatly reducing the overall computational complexity of stereopsis by constraining solutions to the correspondence problem to small disparities. As a result, it seems vergence is necessary for functional binocular vision and

serves as a measurable indicator of the depth a subject is viewing (or, perhaps, for which the oculomotor system estimates that depth to be).

Aside from disparities, several other cues to depth have been shown to drive vergence. These include retinal blur (Müller, 1843), changing size (looming) (Regan and Erkelens, 1986; McLin et al., 1988; Wismeijer et al., 2009), perspective, (Enright, 1987), and shape-from-shading (Hoffman and Sebald, 2007). However, when faced with a conflict between these cues and disparities, (e.g. during binocular viewing) disparities dominate. Therefore the effects of these cues have only been found during monocular viewing.

Vergence and the TVOR are intimately related and scale with one another. Causally, it seems that the TVOR gain is at least partially set by vergence state (Paige 1989; Busettoni, Miles et al. 1991; Schwarz and Miles 1991; Yang, Fitzgibbon et al. 1999; Lasker, Ramat et al. 2002; Medendorp, Van Gisbergen et al. 2002; Crane, Tian et al. 2003; Wei, DeAngelis et al. 2003; Zhou, Xu et al. 2007).

1.6 DEPTH FROM MOTION PARALLAX

A related topic is depth-from-motion, or motion parallax. If an object is viewed from two locations, the change in relative position (in terms of

angular displacement on the retina) depends strictly on the distance between the object and the observer and the viewing locations. Therefore, an observer moving through a static scene with knowledge of their velocity has not only relative but absolute depth information from optic flow alone. This makes motion parallax a particularly rich cue to depth. It is extremely similar to binocular disparities and the ‘correspondence problem’ discussed earlier, except instead of two views coming from the intraocular distance, there is a continuously changing view as the observer or object moves.

It has long been known that motion parallax is indeed used as a cue to depth by humans (Gibson, Gibson et al. 1959; Rogers and Graham 1979) and has been more recently implicated in updating spatial memory (Medendorp, Tweed et al. 2003; Li and Angelaki 2005). It has also been shown that depth perception from motion parallax does indeed scale with viewing distance (Ono, Rivest et al. 1986; Rivest, Ono et al. 1989). That is to say, the percept is appropriately calibrated so that the depth from parallax relates to absolute distance, rather than simply giving depth order information. For this to occur, an extra-retinal cue is needed because the same pattern of retinal motion could come from a near object moving slowly or a far object moving quickly.

Psychophysical experiments with humans and monkeys point to eye movement signals as an important source of this extra-retinal information (Nawrot 2003; Nawrot 2003; Nawrot and Joyce 2006; Nadler, Nawrot et al. 2009; Nawrot and Stroyan 2009; Stroyan and Nawrot 2012). The authors attribute SP in particular. However the origin of these eye movement signals is not straightforward. They result from changes in gain in the TVOR as viewing distance changes (Busetini, Miles et al. 1991; Schwarz and Miles 1991; Paige, Telford et al. 1998; Kawano 1999; Angelaki 2004) as well as visually mediated eye movement systems (namely SP, the optokinetic reflex (OKR) and the ocular following response). Further, the TVOR gain itself scales with vergence, independent of viewing distance, as referenced in the previous section.

All-in-all, it is difficult to tease apart cause and effect because there are several systems with overlapping dependencies working together and relying on each other, typically in reciprocal ways. Perhaps the extra-retinal cue for motion parallax is coming from eye movements (TVOR/OKR/SP) but these eye movements can depend on myriad sources: visual, vestibular, proprioceptive and reafferent.

However, not all of these sources are available in every case. Most notably, structure-from-motion that originates from object motion (rotation or translation) lacks the self-motion signals generated when the observer creates the parallax (recall that these signals are necessary to calibrate absolute depth solely from MP). Similar to the previously mentioned EHT case, there is a difference between the active versus the passive: when presented with visually identical MP stimuli, the parallax from observer movement results in a stronger depth percept than parallax from object movement (Wexler, Panerai et al. 2001). This seems to suggest that SP (a purely visual response) is not the only extra-retinal cue used in perceiving depth from MP.

In the previous discussion of vergence, several depth cues were described that can drive vergence. Structure-from-motion due to object rotation belongs on that list as well (Ringach, Hawken et al. 1996). It was found that humans tracking a target dot on a rotating, transparent sphere covered with such dots converged and diverged concurrently with perceived depth. In the third chapter we will investigate what happens when the observer is actively generating the motion parallax and suddenly has access to a richer set of extra-retinal information. From what we've discussed about the differences

between active and passive movement (see also (Britten 2008)), it certainly seems plausible that self-generated motion parallax may be a stronger cue for vergence just as it is for perception.

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Chapter 2: Binocular Eye Movements from Self-Induced Motion Parallax

2.1 ABSTRACT

Perception often triggers actions, but actions may sometimes be necessary to evoke percepts. This is most evident in the recovery of depth by self-induced motion parallax. Here we show that depth information derived from one's movement through a stationary environment evokes binocular eye movements consistent with the perception of three-dimensional shape. Human subjects stood in front of a display and viewed a simulated random-dot sphere presented monocularly or binocularly. A head-mounted eye tracker recorded eye movements, while a motion capture system monitored head movements. The display was continuously updated to simulate the perspective projection of a stationary, transparent random dot sphere viewed from the subject's vantage point. Observers were asked to keep their gaze on a red target dot on the surface of the sphere as they moved relative to the display. The movement of the target dot simulated jumps in depth between the front and back surfaces of the sphere along the line of sight. We found the subjects' eyes converged and diverged concomitantly with changes in the perceived depth of the target. Surprisingly, even under binocular viewing

conditions, when binocular disparity signals conflict with depth information from motion parallax, transient vergence responses were observed. These results provide the first demonstration that self-induced motion parallax is sufficient to drive vergence eye movements under both monocular and binocular viewing conditions.

2.2 INTRODUCTION

In humans the lines of sight of the eyes converge onto a point of interest in space. The location of this point with respect to the head determines the appropriate angle of vergence of the eyes. Vergence eye movements reduce binocular disparities allowing for fusion of the retinal images (Leigh and Zee, 2006). However, we know that monocular cues to depth are capable of evoking changes in vergence as well. These include retinal blur (Müller, 1843), changing size (looming) (Regan and Erkelens, 1986; McLin et al., 1988; Wismeijer et al., 2009), perspective, (Enright, 1987), shape-from-shading (Hoffman and Sebal, 2007) and shape-from-motion in the kinetic depth effect (KDE) (Ringach et al., 1996). It is fairly well established, however, that when binocular disparity signals are available, they provide the main drive to vergence, with monocular cues to 3D depth rarely being

able to compete if their signals are in conflict with binocular disparity information (Leigh and Zee, 2006).

Human ability to perceive depth from motion parallax has been studied before (Rogers and Graham, 1979; Rogers, 2009; Braunstein, 2009, Durgin et al., 1995, Medendorp et. al., 2003; Wexler, 2001), but whether such percepts can trigger vergence eye movements has never been assessed in detail. One of the goals of our study is to close this gap in the literature. Based on our prior study using the kinetic depth effect (Ringach et al., 1996) we hypothesized that motion parallax would be able to evoke vergence eye movements as well. Indeed, we report that during monocular viewing of a motion-parallax display the eyes change vergence in a way that correlates with perceived depth. Remarkably, even under binocular viewing conditions, when disparity information is unambiguous and indicates the stimulus lies flat on a fronto-parallel plane, motion parallax was able to evoke vergence responses (albeit with a smaller amplitude and transient in time). This result contrasts with our prior study of shape-from-motion, where binocular viewing completely abolished vergence responses (Ringach et al, 1996). These findings indicate that information about depth from self-induced motion parallax can be used by the brain to control binocular eye

movements, and it is strong enough to do so even when in conflict with binocular disparity signals.

2.3 MATERIALS AND METHODS

A computer simulated, transparent random-dot sphere was displayed on a video monitor (Panasonic High Definition Plasma Display, TH-50PF10UK, 1920x1080 pixels, 100 Hz refresh rate) mounted at eye level, one meter away from the subject, in a dimly lit room (Figure 2-1). The locations of the dots were determined by perspective projection of a simulated, stationary sphere. Subjects stood, unrestrained and viewed the display either binocularly or monocularly. As the subject moved, information obtained from a motion capture system was used to continuously render the sphere from the subject's vantage point (the point midway between the eyes) with one video frame delay. The display subtended 67° in the horizontal direction and 37° in the vertical direction. In the first experiment, the simulated sphere was 20° in diameter (35.2 cm in space) and covered by 800 identical white dots (0.13° radius), uniformly distributed on the surface, which were replaced on each trial. One of the dots was designated as a tracking target and indicated in red. The initial position of the target dot was in the center of

the display and located randomly on the front or back surface of the simulated sphere.

Subjects wore a head-mounted eye tracker (Eyelink II, SR Research, Mississauga, Ontario, Canada) that sampled the position of both eyes at 250 Hz. Three infrared LED markers were affixed to the head-mounted eye tracker and four additional markers were affixed to the corners of the screen. The marker locations were tracked by an Optotrak Certus Motion Capture System (NDI, Waterloo, Ontario, Canada), which allowed us to determine head position with sub-millimeter resolution. This data was used by a dedicated machine running MatLab (Mathworks, Natick, MA) with PsychToolbox (Brainard, 1997; Pelli, 1997; Kleiner et al, 2007) to update the display by rendering the sphere from the last recorded viewing point.

Each trial consisted of 24 seconds of voluntary, self-motion while subjects tracked the target dot on the surface of the sphere. The only motion on the display was due to the self-motion of the observer relative to the simulated sphere. A sample record of the head trajectory in one trial is shown in Figure 2-1c,d. At random intervals (uniformly distributed) between one and four seconds, the target dot jumped to the opposite side of simulated sphere

along the line of sight (Figure 2-1b). This experimental design prevented displacements of the projected position of the red dot on the screen during a jump. Such a strategy was adopted to prevent saccadic eye movements accompanying the changes in vergence we wanted to measure. The occurrence of the jump was tagged by a TTL pulse that was time-stamped by the eye recording acquisition system.

We ran experiments under monocular and binocular viewing conditions. In the monocular condition each subject performed one block of 30 trials, yielding approximately 270 depth jumps per subject. Since we anticipated lower signal-to-noise ratios for the binocular condition, two blocks of 30 trials were run in this condition. In both conditions, trials beginning with the target dot in front surface were randomly interleaved with trials starting with the target dot in back. The eye tracker was calibrated with a nine-point calibration display at the beginning of each block and after the 15th trial. Calibration was always binocular. Fixed to the eye tracker was an occluder that covered one eye during the monocular viewing condition without interfering with the operation of the eye tracker, so the movements of both eyes could be recorded.

In a second experiment, subjects viewed monocularly six different sphere sizes (diameters subtending 27.2° , 22.16° , 18.3° , 13.14° , 7.91° , 2.64° or, in space, 48.4 cm, 39.2cm, 32.2 cm, 23.03 cm, 13.83 cm, 7.9 cm and 4.6 cm, respectively) to test if changes in vergence scaled with the physical size of the simulated jumps in depth. The number of dots for each sphere (11025, 7225, 4900, 2500, 900, 100, respectively) was chosen to maintain constant dot density on the surface of the sphere. The dot density was higher in this experiment because at the smallest diameter, a minimum number of dots were needed to create a compelling impression of a rigid sphere. The dots were smaller in size (0.066° radius) to reduce visual clutter at higher dot densities. Additionally, the brightness of the white dots decreased with sphere size so as to maintain constant luminous flux across the display. In this experiment subjects ran one block of 30 trials (five trials for each of the six sphere sizes, randomly interleaved).

Subjects

Experiments were approved by the UCLA IRB and subjects provided their informed consent for participation. Subjects had normal or corrected to normal vision. Some subjects participated in more than one experiment. In

the first experiment, the monocular viewing condition was performed by the two authors (JF and DR, both male) and four subjects with little or no previous experience with oculomotor experiments and naïve as to the objectives of the study (females: JC, RB; males: JM, DS). The binocular condition was performed by three subjects that had previously participated in the monocular condition (JF, RB and DS) and three new subjects (males: JP, GD, female: DG) with little or no previous experience with oculomotor experiments and naïve as to the objectives of the study. In the second experiment, which examined vergence responses as a function of sphere size, one of the authors (JF) participated along with two new naïve, inexperienced subjects, ES and CO (both female). Naïve subjects were given the following instructions: "At the beginning of each trial, you will first see a cross in the center of the screen. When you are ready to begin the trial, fixate on the cross and press the button to begin the trial. Many white dots and one red dot will then appear on the screen. These dots will move on the display as you move side-to-side. Your task is to follow the red dot as you move continuously until the dots disappear." Further clarifications and a sample trial were provided to naïve subjects as necessary, but there was no suggestion that the dots represented depth or three-dimensional shape. All

our subjects reported a vivid 3D percept when debriefed after the experiment.

During the analysis of the data we noticed that the vergence responses of one of the authors, DR, were consistent with perceived depth but approximately four times larger in magnitude than the other subjects. This subject was aware of the goals of the study in advance and his responses, while large, were also substantially slower than the other subjects, suggesting the possibility of top-down control (although he reported not being consciously aware of any intention to modulate his vergence state.) Based on these considerations we excluded this subject's data from subsequent analyses.

Data Analysis

The vergence angle was calculated from head-referenced eye position data and aligned to the occurrence of the target jump in depth for averaging across trials. Data points with a velocity above three standard deviations were clipped to eliminate saccades. Since intervals between the jumps were as short as one second, segments were truncated at the occurrence of the next jump to prevent contamination from adjacent segments. The mean vergence angle of each jump segment was subtracted from that segment.

Finally, the segments were averaged across simulated jumps having the same direction (front-to-back or back-to-front) to yield a mean change in vergence over time according to sign of depth change.

To estimate the latencies of the responses we first subtracted the mean back-to-front response from the mean front-to-back response. From this differential signal we then subtracted its baseline during the 500 ms prior the onset of the jump and fitted the initial segment of the signal (from 500 ms before to 360 ms after the target jump) response with the empirical function:

$$\alpha(t) = \begin{cases} 0, & t < d \\ c(t - d), & t \geq d \end{cases}$$

Here α is the vergence angle and t is time. The fitting parameters are the slope, c , and the latency, d . To find the optimal parameters we used the MatLab functions *nlinfit* and *nlparci* which find nonlinear least-squares fit using the Levenberg–Marquardt algorithm and confidence interval for the parameters, respectively. A similar approach was adopted earlier by Busettoni et al. (2001).

For the second experiment, in which we measured the responses to spheres of different sizes, we compared the geometrically expected versus measured

changes in vergence for each jump the target made in depth. For each case, we first computed the *expected* change in vergence for each simulated change in depth. This is calculated as the vergence change required to shift gaze between the two points on the simulated sphere intersected by the line joining the vantage point (middle of the eyes of the observer) and the red target. We then computed the *measured* change in vergence as the difference between a ‘pre-jump’ vergence angle obtained as the mean of the 125 samples (500 ms of data) immediately before the target jump, and a ‘post-jump’ vergence angle obtained as the mean of the 125 samples from 2 seconds after the jump to 2.5 seconds. This window was selected from the analysis of the mean responses (Figure 2-2), which saturate around 2 seconds after the jump. Finally, we calculated the correlation coefficient between the measured and expected vergence changes and its statistical significance.

2.4 RESULTS

In the monocular viewing condition, motion parallax information to depth was sufficient to evoke convergence of the eyes when the target dot jumped from back-to-front and a divergent movement when the target jumped front-

to-back (Figure 2-2a). The magnitude of the response was significant and robust in all subjects tested (Figure 2-2b). The effect was also significant under binocular viewing of the same stimuli (Figure 2-2c). Here, however, the responses were clearly smaller in magnitude and transient in time. In addition, we noted a larger individual variability in the binocular condition, with some subjects showing little or no effect (such as subjects RB and SS in Figure 2-2d).

We then took a closer look at the early dynamics of the average responses in the monocular and binocular conditions. The average responses to jumps in opposite depth directions were subtracted to produce a differential response (Figure 2-3a). The monocular response raises and saturates reaching a steady-state value at ~ 1.5 s after the target jump, while the binocular response peaks at a lower amplitude at ~ 1 s after the target jump and decays back to baseline shortly after.

To ensure that these results were not due to individual differences, the data were reanalyzed using only the three subjects who performed the task under both viewing conditions (JF, RB, DS). While the pooled responses for the

three subject group were more variable, they were not noticeably different than the average responses of the entire subject group (data not shown).

To look for differences in response delay between the two conditions we analyzed the initial 500 ms (Figure 2-3b). The estimated latencies from the fits (d in the first equation) were 226 ± 33 ms and 192 ± 37 ms ($\pm 95\%$ confidence intervals) for the monocular and binocular responses, respectively. The binocular responses were thus slightly faster than monocular ones.

To determine if the vergence response scaled with changes in the simulated depth jumps of the target we plotted the measured versus expected changes in three subjects (Figure 2-4). We found a modest but statistically significant correlation between the expected and measured change in vergence ($r = 0.12$, $p < 0.005$, best fitting line $y = 0.1x - 0.02$). Thus, while the evoked response was much smaller than expected (the slope of the line is 0.1 instead of unity), the magnitude of the response was nevertheless correlated with the magnitude of the simulated change in depth.

2.5 DISCUSSION

The goal of the present study was to find out if depth information derived from self-motion through a static scene can be used by the brain to evoke binocular eye movements in accordance with a 3D percept. Indeed, we found changes in vergence evoked in both directions of simulated motion parallax, consistent with perceived jumps in depth in both naïve and experienced subjects. The size of the effect was larger and more robust across subjects in the monocular viewing condition. The magnitude of the response correlated with the size of the simulated object. When the stimulus was viewed binocularly, a weaker and transient response was nevertheless detected. This was a surprising result. Typically, when monocular cues to depth are in clear conflict with binocular disparity, the latter dominates. However, our results show that the perception of depth from motion parallax is so compelling that it can transiently evoke vergence movements that are in conflict binocular disparity.

The estimated response latencies to motion-parallax information are in general agreement with those reported earlier for vergence changes in response to other monocular cues without anticipation (Erkelens and Regan, 1986; Leigh and Zee, 2006; Ringach, et al., 1996). The initial raising phase

of the vergence response is similar under both monocular and binocular viewing. However, around 150 ms after the response begins (~350 ms after the target jump), the two conditions diverge. The monocular response continued to rise for several hundred milliseconds, while the binocular response reached an inflection point and soon began to decline back to baseline. This is likely the result of increased binocular disparity signaling the error incurred by the evoked movement. This interpretation is consistent with the observed 150 ms delay, which is similar to the one obtained by driving vergence with changes in binocular disparity (Erkelens and Collewijn, 1991; Leigh and Zee, 2006; Rashbass and Westheim, 1961).

These findings demonstrate, for the first time, that vergence control can be influenced by self-induced, motion parallax information. A previous report using a KDE stimulus (Ringach et al., 1996) did not evoke a vergence response during binocular viewing. The main difference is that in motion parallax the retinal motion is induced by one's voluntary movement through the environment, while in the KDE it is generated by the rotation of an object and a static observer. In the case of KDE, depth sign is ambiguous. A rigid, rotating object could be moving clockwise or counter-clockwise and nothing about the motion itself distinguishes from these two possibilities. As

a result, the percept is bistable, sporadically switching between the clockwise and counterclockwise interpretations (Nawrot and Blake, 1989). Self-induced motion parallax, on the other hand, is unambiguous as the observer also has information about his/her own motion (from both efference copy and vestibular signals). Further, if the relative velocity between object and observer is known, motion parallax can provide an absolute indicator of distance independent of other cues (Ferris, 1972; Ono et al, 1996). These qualities make self-induced motion parallax a potentially stronger source of depth information compared to KDE. In agreement with this idea, Wexler et al. (2001) compared depth perception from motion parallax and KDE directly and found that motion parallax yielded a stronger percept. Similarly, we show here that motion parallax is perhaps the strongest of the monocular cues to vergence, and capable of driving binocular eye movements even when in direct conflict with binocular disparity information.

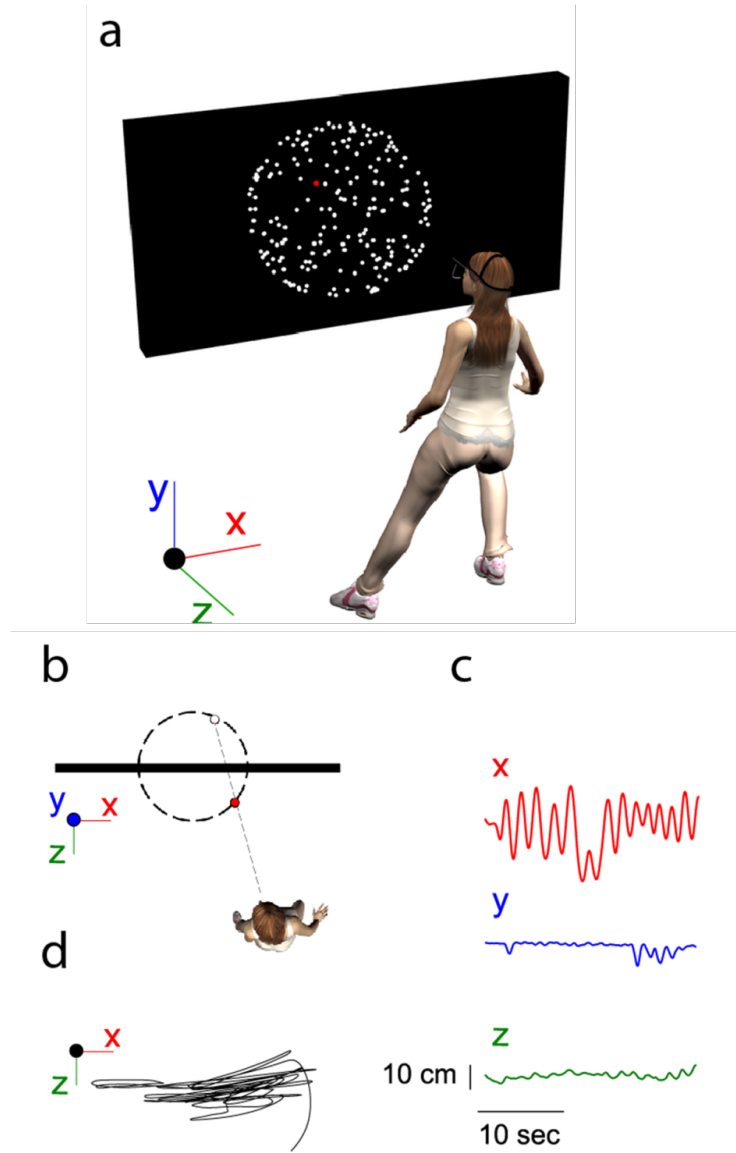


Figure 2-1 Experimental Setup. (a) Subjects wore a head-mounted eye tracker and stood about 1 m from a computer display depicting a random dot sphere. Head movements were tracked by a motion capture system. The display was updated continuously to render the projection of a static, transparent sphere from the observer's vantage point (the point midway between the eyes). (b) The task consisting of visually tracking a red target

dot that intermittently jumped between the front and back of the sphere along the subject's line of sight. (c,d) Sample traces of self-induced subject movement during one trial in the experiment.

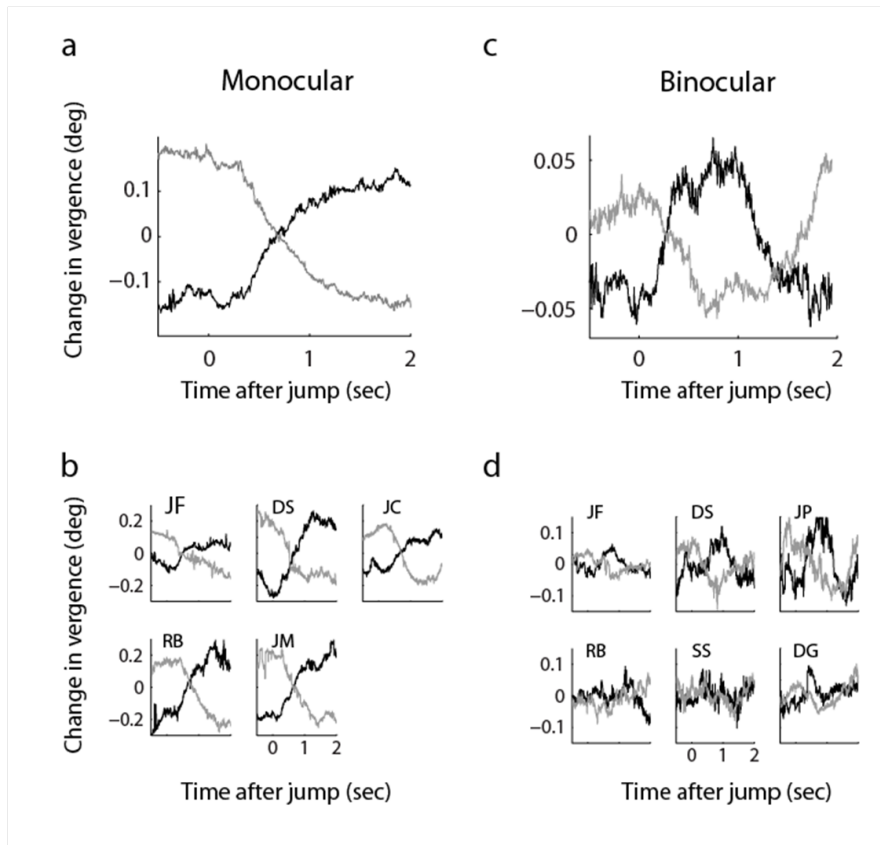


Figure 2-2 Individual and Group Vergence Responses. Vergence signals were aligned to the occurrence of target jumps and the mean was subtracted. The segments were then separated by direction of jump (front-to-back and back-to-front) and subsequently averaged. Black traces are changes in vergence when the target jumped from the back of the sphere to the front (when we expect the eyes to converge), while the gray traces show the vergence change when the target jumps from front-to-back (when we expect the eyes to diverge). Average responses were different in both monocular and binocular conditions (a,c). The effect was clear in all individuals during monocular viewing (b), but more variable and weaker to non-significant in the binocular viewing condition (d).

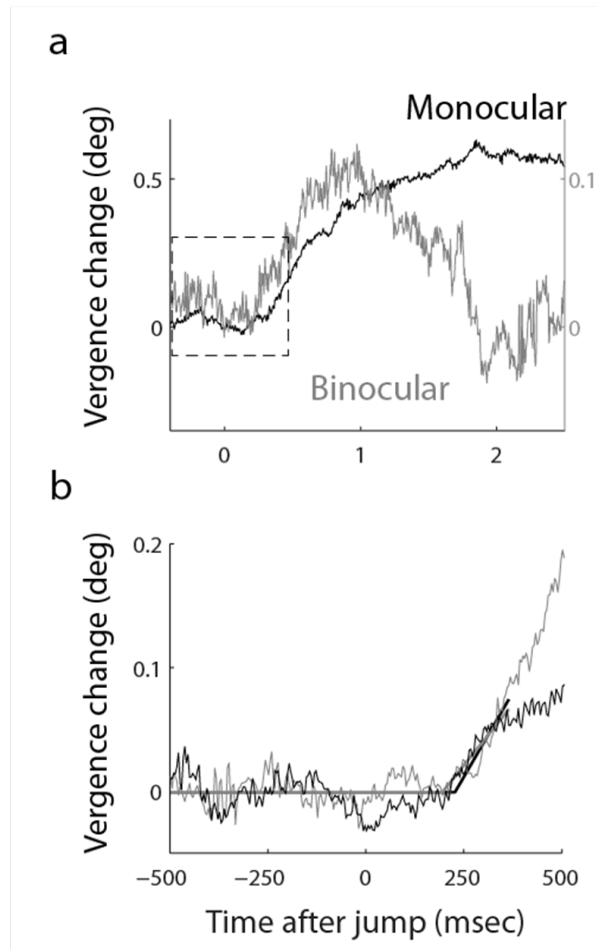


Figure 2-3 Dynamics of Vergence Responses. Average responses from previous figure (a,c) were subtracted to compare the dynamics of binocular and monocular conditions. (a) The difference between back-to-front and front-to-back is shown in black for monocular viewing and gray for binocular viewing. Note the binocular response is plotted at one fifth the scale of the monocular and shows the entire time-course of the response. (b) An expanded view of the early phase of the responses (dashed square in panel a) along with their fits in solid black and gray lines (which overlap before response onset). Note the initial responses up to 350 ms after the target jump are very similar in both cases.

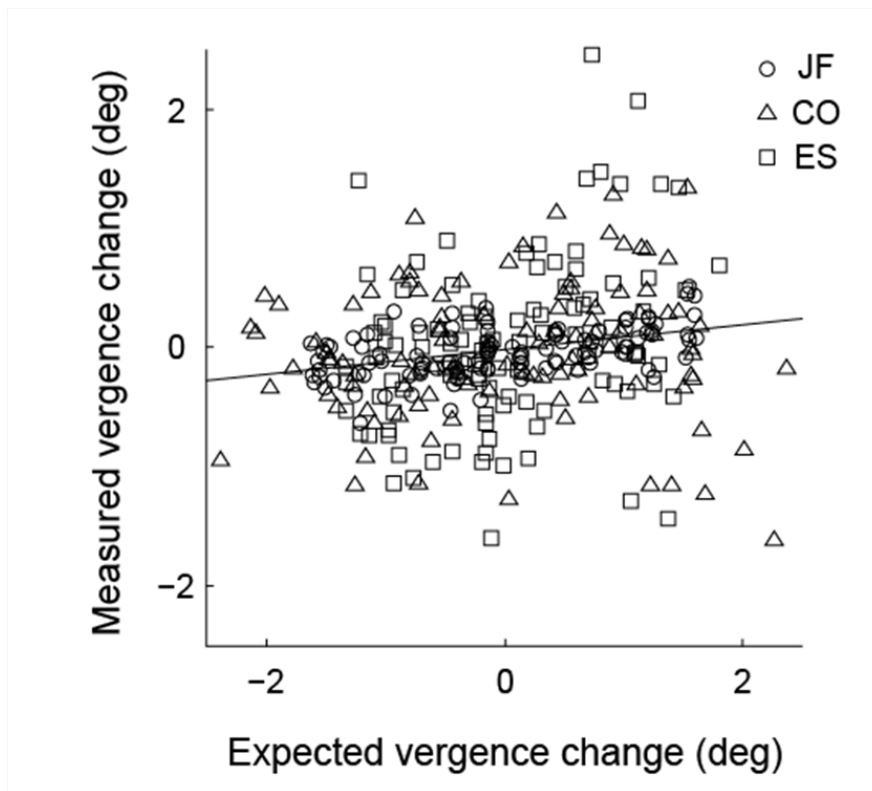


Figure 2-4 Vergence versus Simulated Depth. Data from three subjects show a correlation between the measured and expected change in depth. This implies the size of the vergence changes correlate with the simulated size of the objects being simulated.

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Chapter 3: Dynamics of Coordinated Head-Eye Visual Tracking

3.1 ABSTRACT

When visually tracking a moving object over an extended region of the visual field we use a combination of eye, head and body movements. To reduce the retinal velocity tracking error the brain must generate commands to different parts of the body in a well-coordinated fashion. How such coordinated planning of motor commands takes place is not fully understood. Here we studied the dynamics of joint head and eye movements while observers tracked a target moving at a constant speed plus a white-noise velocity perturbation. Measured movements in these experiments allowed us to estimate the optimal, temporal linear filters that linked perturbations in target velocity to fluctuations in the velocity of the eyes and the head, as well as any potential link between head and eye velocities. By simultaneously extracting stimulus-driven and head-driven components of the eye's response, we could, for the first time, separate the VOR during active head movement from smooth pursuit in combined head and eye tracking. Stimulus-dependent eye filters were similar to previous reports (Tavassoli and Ringach, 2009) with the head-fixed, suggesting that the

smooth pursuit system is operating in a similar manner in both conditions. We found a substantial contribution from an incompletely cancelled VOR with very fast dynamics, which was also demonstrated by a negative covariance between eye and head movements in response to a fixed stimulus. Additionally we show that the covariance between head and eye movements during EHT can be explained by head motor variance and the extracted VOR filter. This suggests that covariance is not appreciably influenced by other sources of noise, such as sensory error. To our knowledge, this is the first time a full estimate of such filters is offered along with an assessment of the goodness of fit of the resulting linear model during the maintenance phase of combined head-eye tracking.

3.2 INTRODUCTION

Keeping our gaze on a moving target can be accomplished in multiple ways. We can voluntarily decide to keep our bodies still and track the target with our eyes alone or, as is more natural in most cases, we can execute combined head and eye movements. The planning of smooth head-eye tracking (EHT) must be carefully coordinated to achieve a reduction in retinal slip velocity. How the brain achieves this feat is not fully known. We do know, however,

that during EHT the head and the eye often move in the same direction. This means that the vestibulo-ocular reflex (VOR), which normally acts to stabilize the retinal image during fixation by moving the eyes in the opposite direction of the head, must be cancelled during EHT (Robinson 1982). Evidence for a cancellation signal was obtained in a now classic head-brake experiment where a target jumps to one side of the fixation point and immediately begins moving towards the opposite side. A brake is then unexpectedly applied to the head during the tracking movement. The eye movements evoked by the brake have a very short-latency $< 15\text{ms}$ (Lanman, Bizzi et al. 1978). As such short-latency response cannot be visually mediated, we must conclude the VOR must be engaged during head-eye tracking and actively cancelled. Neural correlates for VOR cancellation during active head movements have been found in the vestibular nucleus of macaques (Roy and Cullen 2004). However, during EHT it is difficult to differentiate the VOR from visual pursuit. While these can be accomplished directly, by passively rotating the head, as in a vestibular chair or torque driven helmet, it is well known that the VOR behaves differently to active head movements, such as those that naturally occur during EHT (reviewed in (Cullen 2004) and (Angelaki and Cullen 2008)).

We studied the dynamics of EHT by having human subjects track a target moving at a constant speed, perturbed by unpredictable, pseudo-random noise. We measured head and eye movements in response to these stimuli, and then estimated the optimal linear filters linking perturbations in target velocity to evoked fluctuations in head and eye velocity as well as a filter linking head fluctuations to eye fluctuations. By simultaneously estimating these filters, we could appropriately separate the VOR from pursuit-related eye movements. We show that the resulting filters can be used to predict both head and eye velocity to novel stimuli with reasonable accuracy, demonstrating the approximate linear behavior of EHT during steady-state. The method is an extension of the technique we previously used to study the dynamics of smooth pursuit when the head is fixed (Tavassoli and Ringach 2009) and is also related to a general class of techniques that minimize predictability of stimuli by using sum-of-sinusoids and pseudo-random noise either applied to the stimulus or head (Gresty and Leech 1977; Collewijn, Conijn et al. 1982; Barnes and Lawson 1989; Waterston and Barnes 1992; Keshner and Peterson 1995; Tangorra, Jones et al. 2004).

3.3 MATERIALS AND METHODS

3.3.1 Stimulus and task. Observers stood facing a Panasonic High-Definition Plasma Display (1920x1080 pixels, refresh rate of 100 Hz, model TH-50PF10UK) mounted approximately at eye level at a distance of one meter. The monitor subtended 67° in the horizontal direction and 37° in the vertical. The stimulus was a white disk, 0.3° in diameter, against a black background created using the Psychophysics toolbox (Brainard 1997; Pelli 1997; Kleiner, Brainard et al. 2007) for MatLab (Mathworks, Natick, MA) on a dedicated machine.

Each trial began with a central fixation cross and a visual prompt to press a button on a hand-held wireless input device. Following the input, the target would appear, with random delay between zero and one second, on either the left or right of the display (Figure 3-1a). The initial displacement of the stimulus was always thirty degrees from center in the horizontal direction and zero degrees in the vertical. Following the initial horizontal displacement, the stimulus would immediately begin moving towards center of the screen and continue until it moved off-screen. Trials starting on the left and right were randomly intermixed.

The target moved at a mean velocity of $10^\circ/\text{s}$, to which we added filtered Gaussian noise (low-pass filter with a cut-off frequency of 25 Hz) with a standard deviation of $5^\circ/\text{sec}$ (Figure 3-1b). As we will show, this stimulus is nearly white within the band of frequencies in which gaze tracking operates. Each subject ran a total of 400 trials, of which 160 contained different noise signals and 240 contained "frozen noise" patterns that repeated themselves. The trials with a unique added noise pattern were used to extract the linear filters. The repeated noise patterns (six different patterns repeated 40 times each) were used to compute mean responses and assess the goodness of fit of the predictions. The unique and "frozen noise" trials were randomly intermixed within each 100 trial block. Subjects were instructed to visually track the stimulus, moving their heads freely while keeping their torsos still. Observers did not have difficulty voluntarily fixing the torso, in agreement with previous studies (Collewijn, Conijn et al. 1982).

3.3.2 Subjects. Five observers participated in the experiments, all with normal or corrected to normal vision. Three observers were experienced with oculomotor tasks (DR, AT, JF) and two naive (CR, AY). The four male observers were aged 46 (DR), 31 (AT), 23 (JF) and 28 (CR) and the female

observer was 22 (AY). Each observer performed 4 blocks of 100 trials with no more than two blocks per day and no more than eight days between the first and last block. All the observers provided their informed consent and all experiments were conducted with the approval of the Chancellor's Office for the Protection of Research Subjects at UCLA. Data from subject CR was removed from analysis due to a previous head trauma.

3.3.3 Data Collection. An Eyelink II (SR Research, Mississauga, Ontario, Canada) head-mounted, video-based eye tracker was used to collect head-referenced eye position. Both eyes were monitored, but there was no appreciable difference between the analyses of the eyes. Here, we present data only for the left eye. A nine point calibration was performed before each block and after every 25 trials.

To determine head movement, an Optotrak Certus motion capture system (NDI, Waterloo, Ontario, Canada) was used. Three LED position markers were fixed to the Eyelink headband and four to the corners of the screen. Using the NDI Rigid body builder, the angle between head and screen was computed directly by NDI First Principles and logged to disk.

At the beginning of each trial, a TTL pulse was sent to both the motion capture device and eye tracker from the display host, and data from both devices were sampled at 250 Hz. The TTL pulse triggered recording for the motion capture host and was collected by the EyeLink system and later used to align eye tracker data offline. Both the head and eye position data were differentiated to obtain angular velocity traces.

3.3.4 Estimation of Linear Filters. We estimated the linear temporal filters linking stimulus velocity to eye and head velocities with minimal mean-squared error. All reported velocities are angular, in the horizontal plane (yaw). The stimulus moved purely horizontally and movements in other directions were negligible. We also considered that due to a partially cancelled VOR, the eye velocity may also be influenced by head movement. It would have also been possible to reconstruct retinal slip from the measured movements and instead used this as the input to the system as this is the actual velocity signal coming into the eye and long known to be the principle driver of smooth pursuit (Rashbass 1961). However, considering the visual processing delays, it is impossible to create a stable feedback

controller that adequately describes the dynamics of the behavior by regulating retinal slip alone. It is unclear what and how other signals are involved (retinal image acceleration, reafferent motor commands, etc.), though several models exist (Robinson, Gordon et al. 1986; Ringach 1995; Churchland and Lisberger 2001; Nuding, Ono et al. 2008). Instead of assuming one of these models, we assume that the objective of visual tracking is to follow the target velocity and that the visuomotor system can do this with reasonable fidelity.

When the input is approximately white within the range of frequencies a single-input single-output system operates, the standard method of estimating the linear filter linking the variables is by cross-correlation. In the discrete case, this is equivalent to a least-squares linear regression problem, where the regressor is a Toeplitz matrix, A , consisting of the time-shifted versions of the inputs, the regressand, y , is the output and the parameter vector, x , is the linear filter. To find the minimum norm least-squares solution we pre-multiply by the Moore-Penrose pseudo-inverse to get our estimate $\hat{x} = A^+y$.

Because of the possibility of a residual VOR we considered eye velocity as depending on the recent history of two variables, the stimulus velocity *and* the head velocity. To accommodate both variables the matrix A contains two parts, one for the stimulus and one for the head. The resulting regression coefficients, then, are estimated linear filters which appropriately separate the relative contributions of each variable to predict eye velocity. To reduce noise, we added a regularization term (ridge regression) consisting of a finite difference matrix multiplied by a coefficient. This changes the least-squares problem from finding $\min_x \|Ax - y\|^2$ to $\min_x \|Ax - y\|^2 + \|c\Gamma x\|^2$, where Γ is the difference operator and c is a constant. The regression equation then becomes: $\hat{x} = (A^*A + c\Gamma^*c\Gamma)^{-1} A^*y$. The regularization term, then, penalizes solutions by their mean-squared derivative. In a Bayesian context, the regularization term can be thought of as a prior that favors a temporally smooth filter. The effect of adding this term is that higher frequencies in the filter are reduced. This is favorable because there is little response at higher frequencies so power in these frequencies is dominated by noise. Due to the fact that these frequency cutoffs are different for the head and eye, the coefficient was different for each partition, but the same for all subjects. To find appropriate values for the coefficients, we sought to

maximize the correlation coefficient between the predictions as (described below) by performing an exhaustive search over a logarithmic range. Near the maxima, a second exhaustive search was performed over a finer, linear range. In both cases, the maxima were broad and there were no discernible discontinuities, so no further optimization was performed. From the linear filters we estimated the time-to-peak (defined as the time at which the maximum gain is achieved), the integration time (calculated by the full-width half maximum), and a pure delay (calculated by the method previously described in (Tavassoli and Ringach, 2009)). These filters are a ‘black box,’ statistical description of the average response; they do not contain any physical modeling of the mechanics and lump the plant and controller into a single filter.

3.3.5 Linear Predictions. The velocity traces of the repeated white noise trials were averaged to produce mean responses. To remove transients caused by saccades and blinks, data points within 25 ms of crossing a three standard deviation velocity threshold were removed (as described in more detail in (Tavassoli and Ringach 2009)). Eye velocities were low-pass filtered with a cutoff frequency at 25 Hz. Predicted fluctuations in head

velocity were obtained by convolving the estimated filter with the fluctuations in target velocity. Predicted fluctuations in eye velocity are the sum of two components. A stimulus-driven component obtained by convolution of the corresponding linear filter with the fluctuations in target velocity, and a head-driven component, which was computed by convolving the measured head velocity for each trial with the head-driven filter. The predictions were compared to the average responses by computing correlation coefficients between the two. Both the predictions and the mean responses were used to compute residual velocities for each repeated noise trial. The residual eye and head velocity traces were cross-correlated, resulting in the cross-covariance. One subject (AY) exhibited constant head acceleration in their mean responses during the trial, which was removed by linear de-trending. We believe this is justifiable as the purpose is to study pursuit maintenance and the dynamics of the response to velocity perturbations around a constant tracking velocity. Finally, the mean-squared coherence between the predictions and mean responses was calculated across subjects.

3.4 RESULTS

Subjects performed stereotypical movements to track the target (Figure 3-1b). The head and the eye made an initial fast movement to bring the target into the center of gaze after which it was tracked smoothly up to the point it reached the end of the display. Our analysis concentrates on the steady-state portion of the tracking, after the initial transient and before gaze begins to decelerate towards the end of the trial. The mean gaze velocity across subjects was 9.87 deg/s, very close to that of the target. The head compensated for most of the mean speed of the target, moving at an average of 8.86deg/s, while the mean velocity of the eyes was smaller but still in the direction of the target, at an average speed of 1.01 deg/s.

We then estimated the optimal linear filters linking head and eye velocity to those of the target (Figure 3-2a). These filters also represent the average response of the head and eyes to a brief impulse in target velocity. Across observers we note that the stimulus-driven eye movement filters (Figure 3-2a, black curves) are dominated by an early peak at 164 ± 8 (1 SD) ms with a narrow integration time (40 ± 8 ms) and a pure delay of 106 ± 9 ms. In contrast, the head dynamics is much slower with its response peaking at 347 ± 50 ms and with an integration window of 260 ± 101 ms and a delay of 179 ± 47 ms

(Figure 3-2a, gray curves). One can calculate the DC gain by integrating the filters over time. The stimulus-driven filters for the eye had a DC gain of 0.18 ± 0.09 , while the head had a DC gain of 0.78 ± 0.40 . These gains are another way to quantify how much of the constant velocity is tracked by each component.

The different dynamics of the eye and the head are also evident when we compute the Fourier amplitude of the associated kernels (Figure 3-2b). The gain of the head at frequencies below 1 Hz attains values that are more than four-fold higher than those of the eyes, but the situation reverses at temporal frequencies at 6 Hz, where the difference between the gain of the eyes and the gain of head at its maximum. At this frequency, the gain of eye is five-fold higher than that of the head (Figure 3-2b, population average, right panel). The cross-over frequency where the average gain of the eyes equals that of the head is 3.4 Hz (Figure 3-2b, right panel, dashed vertical line). A head/eye coordination strategy that is in agreement with these data consists in splitting the retinal velocity error into low and high temporal frequency channels, with the former driving head movements and latter driving corrective eye movements.

The simultaneous regression of the eye velocity on the recent history of the target and head velocities also yields a kernel that shows the contribution of head velocity to the movement of the eyes (Figure 3-2c). Here the kernels are very fast (integration time of one time sample, 10 ms), with extremely short delays (10 ms) and negative gains (-0.13 ± 0.03). We note that the peak absolute magnitude ranged from 0.05 to 0.15 which is comparable to that of the temporal filters for the eyes (Figure 3-2a), implying the contribution of the this term during coordinated tracking is substantial and cannot be ignored.

To assess the linearity of EHT we used the filters to predict responses of the eye and head during steady-state tracking for a novel velocity perturbation. By "novel" we mean this is a different noisy velocity pattern that was not used for the calculation of the temporal filters but is only used to assess their goodness-of-fit. Directly comparing the actual mean responses to the predicted responses shows that many of the temporal features are well captured by a linear system (Figure 3-3). On average, correlation coefficients between measured and predicted eye velocities were slightly higher than for the head. We can also form predictions for eye velocity by

ignoring the contribution of fluctuations of the head velocity to eye velocity. When only target velocity is used to predict eye velocity the average correlation coefficient is 0.54 ± 0.08 . When only the head-dependent filter is used, it is 0.50 ± 0.13 . For all subjects, the fraction of variance explained by each component separately adds up to the fraction they explain together. This means there is negligible covariance between the predictions formed from the two filters and their respective inputs. To examine this further, the correlation coefficients between the estimates for each subject were computed. The resulting coefficients were: -0.06, DR; 0.03, AT; -0.04, JF; 0.007, AY. Scatter-plots between predicted and measured velocities show that there are no obvious static nonlinearities between the two under the conditions of our experiment (Figure 3-3, insets, dashed line represents unity line.)

A plot of the coherence between the predicted and measured responses show correlations over relevant frequencies (Figure 3-4). Predictions of the head movement fall to half the maximum coherence at 4.8 Hz while the predictions of the eye fall to half maximum at 8 Hz. These cutoffs are not unexpected considering the frequency response functions shown in Figure 3-

2. These graphs also demonstrate our stimulus, which had a high-cut of 25Hz, was approximately white in the relevant range of the spectrum.

Finally, we explored if there was any relationship between fluctuations in the velocities of the head and the eyes while tracking the same visual stimulus over repeated trials (frozen noise velocity profiles). Indeed, when the residuals are computed by subtracting the mean velocity response to multiple presentations of a fixed stimulus, we find that the covariance between head and eye velocity during steady-state tracking exhibits a strong negative peak centered near zero (Figure 3-5, black curves). This means that variations in the head velocity are negatively correlated with variations in the eye velocity on short time scales — when fluctuations of the head velocity exceed its mean, those in eye velocity are below its mean. However, when residuals are computed from the predictions, this negative peak is no longer present (Figure 3-5, grey curves). This is because the predictions of the eye velocity incorporate a component that depends on the head velocity on each individual trial. The absence of structure in the covariance of the predictions means that the negative peak in the covariance was indeed caused by fluctuations in head velocity from trial to trial and its influence on eye movements. A slightly different analysis reinforces this result. To each

trial, the head velocity, convolved with the head-dependent eye velocity filter, was subtracted from the eye velocity. The covariance of the resulting signals is flat as well.

3.5 DISCUSSION

We used a linear systems approach to study the dynamics of joint eye-head tracking. The method involves the introduction of a perturbation to the velocity of a target and the subsequent estimation of linear filters that explain how fluctuations in the velocity of a visual target influence tracking movement. The method was previously used to study the dynamics of human smooth pursuit with the head restrained (Mulligan 2002; Mulligan 2003; Osborne and Lisberger 2009; Tavassoli and Ringach 2009) and optomotor responses in *Drosophila* (Theobald, Ringach et al. 2010). Here we used the technique to measure the dynamics of eye and head movements during EHT, and to assess its linearity in more detail than prior studies which employed sum-of-sinusoids velocity profiles (Gresty and Leech 1977; Miles and Lisberger 1981; Collewijn, Conijn et al. 1982; Barnes and Lawson 1989; Waterston and Barnes 1992). Our results add to these previous findings by providing the first estimation of the full temporal filters linking

target velocity to eye and head velocities, an estimation of the residual VOR in individual human subjects, and an assessment of the goodness of fit of the linear model in coordinated head-eye tracking movements. Consistent with previous reports (Gresty and Leech 1977; Barnes 1993; Chen, Keshner et al. 2002), our findings indicate that movements of the head are unable to track frequencies above 5 Hz. As expected from the larger inertia, the head also has a longer latency than the eye. Overall, the shapes of the filters and frequency responses indicate that the eye is faster and responds to higher frequency components of the target velocity while the head is slower and does the bulk of the constant velocity and low frequency tracking.

The filters were similar in shape across subjects, containing a monophasic peak with similar pure delays, but some individual differences were evident. Primarily, there is much individual variation in the relative contribution of eye and head to the tracking movement which has been noted elsewhere and is likely due at least partially to cognitive factors (Gresty and Leech 1977; Collewijn, Conijn et al. 1982; Dubrovsky and Cullen 2002). Using our methods these differences can easily be quantified and compared using metrics such as latency, time-to-peak, full-width half-maximum, and gain. This could be useful for studies of individual variation or differences

between groups (e.g. patient populations) or behavioral contexts. One could quantify how sensorimotor performance is affected by disease, aging, cognitive state, task demands or treatment. For instance, measures of these filters could be used in concussion diagnosis or monitoring recovery (Heitger, Jones et al. 2009).

As previously discussed, it is difficult to separate eye movements resulting from visual tracking from eye movements resulting from the VOR. By using a rich stimulus and simultaneously regressing the head and stimulus velocities, we believe we have appropriately separated these two responses. When one compares the stimulus-dependent eye movement filters from this paper to the filters from the head-fixed condition, there are very similar in shape (Mulligan 2002; Mulligan 2003; Tavassoli and Ringach 2009). The longer latencies found here are likely due to differences in stimulus properties (e.g. size (Pola and Wyatt 1985) and shape (Masson and Stone 2002)). In particular, the stimulus was quite small. Since tracking relies on visual motion processing and is ultimately a visual task, it is not surprising that stimulus properties would affect tracking dynamics and be incorporated into the estimated filters. Latency aside, the stimulus-dependent eye filters are extremely similar to the smooth pursuit only filters found previously.

This seems to suggest that these filters are in fact isolating the linear component of smooth pursuit.

The recovered head-dependent eye movement filters contain a dominant negative peak of about 0.2 with delay and integration time equal to the sampling period (10 ms). This means that very soon after the head moves, the eye moves in the opposite direction, but not as much. These characteristics would be expected in an incompletely cancelled VOR, which has been previously theorized and for which there is experimental evidence (reviewed in (Angelaki and Cullen 2008) and (Roy and Cullen 2004)). However, it is worth exploring alternative explanations for the origin of this filter. The delays are too short to be visually mediated so it cannot be an artifact of feedback. If it were due to sensory processing or errors one would expect to see the eye respond more quickly due to the smaller plant rather than more slowly. Additionally, sensory errors should positively correlate with eye and head movement rather than positively with one and negatively with the other since both are clearly involved in tracking the target (covariance would be positive). It may be possible that a shared motor controller could result in such a behavior, but again, it is odd that the head would lead the eye and therefore seems highly unlikely. It seems that the

simplest explanation is that this filter is characterizing the average linear response of the VOR during EHT. To our knowledge, this is the most complete of such characterizations to date. This conclusion is further supported by the predictions and covariance analysis as described below.

Considering the complexity of turning visual input into coordinated motor output, the linear approximation is surprisingly good. Predictions formed from convolving the recovered impulse responses with novel stimulus motion accounted for, on average, more than half of the variance of the eye (57% explained variance). We can further divide this into the contribution by each input. The linear response to the stimulus accounts for 30% of the variance, while 27% can be explained by a constant gain VOR alone. That these values approximately sum to the total fraction of explained variance is evidence that we have successfully separated the contribution of stimulus (smooth pursuit) and head (VOR), as there is negligible covariance between the estimates. That there is little covariance between the estimates is borne out through direct measure as well, as described in the results. This seems strange considering that the head itself is driven by the stimulus. However, analysis of the filters and cross-covariance sheds light on this predicament.

First, it has been previously noted that the head tracks low frequencies and the eye tracks high frequencies. Similar to a radio, dividing a single channel into frequency bands allows multiple, independent signals to be carried over that channel. In this case, the single ‘channel’ is the visual tracking task/retinal slip while the ‘signals’ are the head and eye movements. Inspection of the temporal filters comes to a similar conclusion. Due to the difference in delays and sharp peak of the SP filter, by the time the head begins to respond, the eye is almost back to baseline. This suggests that the linear portion of the velocity response of the eye to a velocity perturbation is temporally split in two: first the smooth pursuit response, then the VOR response, with little overlap.

The cross-covariance curve, showing how trial-by-trial variations between eye and head velocities were associated temporally, contained a large negative peak for all subjects. As shown in Figure 5 and described in the results, the linear filter linking head velocity to eye velocity could account for this. The result is partly surprising because if there was a significant source of shared sensory noise contributing to motor variability during the steady-state phase of tracking as seen during pursuit initiation (Osborne, Lisberger et al. 2005), one would expect a positive covariance as

fluctuations in the estimated velocity of the target would drive head and eye in the same direction. To illustrate, imagine the sensory system overestimates the retinal slip; this should cause both the head and eye to overcompensate since both are tracking the target. However, this was not the case: the covariance between the signals after the subtraction of the VOR component was essentially flat.

One potential complaint with the assumption that the head-eye filter we extracted truly characterizes the VOR is that the filter is essentially an average response and therefore, may poorly characterize the actual response at any one time. Most notably, the VOR operates differently during a saccade (Lefevre, Bottemanne et al. 1992; Cullen, Huterer et al. 2004). However we see a very similar filter for subjects who exhibit a large number of saccades (e.g. AY) versus those who exhibit almost none (e.g. DR). Further, since the time window around saccades have been removed, it is reasonable to assume that modulations of the VOR response near a saccade are not included. Further, the proof is in the pudding-the filters themselves display the fast dynamics one would expect and do a reasonably good job of predicting new responses, so it at least represents a real dynamic link between the head and eye which cannot be explained by the stimulus. That

being said, there's no proof here that the VOR response is indeed static throughout the trial even though we treat it as such. However, due to similarity between subjects and between sessions, it is reasonable to assume that the linear portion of the response varies little.

We analyzed the velocity responses of the head and eye to velocity perturbations of the target during tracking. We were able to separate what we believe to be the average VOR response from the average smooth pursuit response to such perturbations. Our data leads to a surprising conclusion -- the visuo-motor responses of the head and eye to the same stimulus are relatively independent once the VOR is taken into account. That the head tracks low frequencies and the eye tracks higher frequencies has been noted before and is not surprising considering the large inertia of the head. However, the independence of the predicted smooth pursuit and head pursuit movements suggest that this may actually be a strategy to simplify the task of dividing target tracking into head and eye components in a frequency multiplexing-like manner.

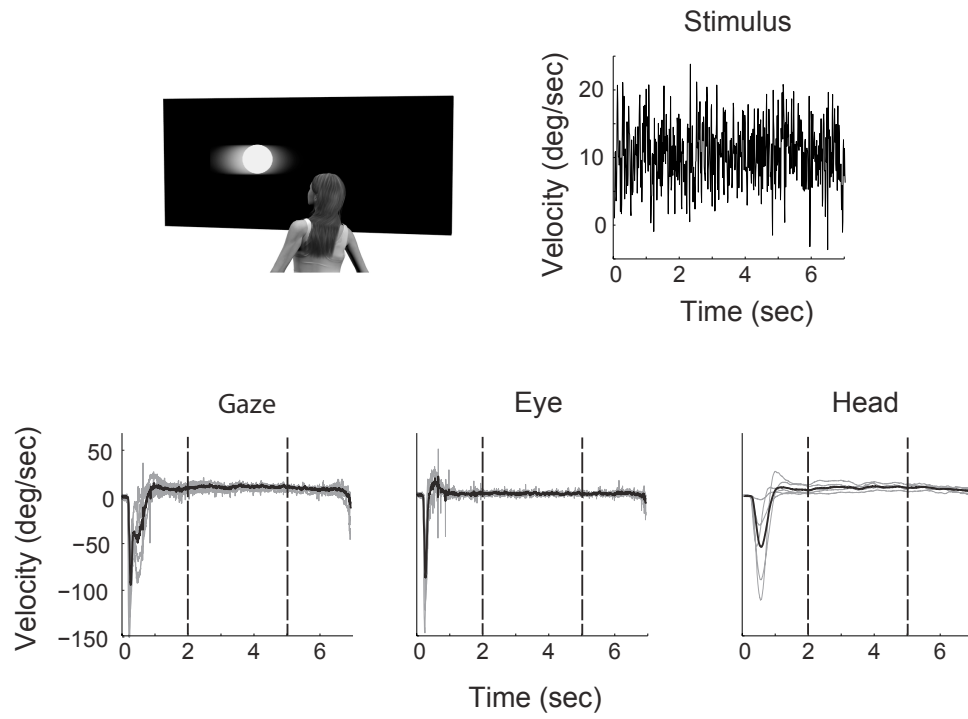


Figure 3-1 - Mean Velocity Traces for Head-Eye Tracking. Observers followed a tracking target across a total of about 60° . Target velocity was entirely horizontal with a mean of $10^\circ/s$. Added to the mean was a broad-band noisy perturbation term with a standard deviation of $5^\circ/s$. Mean head, eye and gaze (eye+head) velocities over the course of a trial are plotted for each subject (gray curves) with the group average in black. We are concerned with steady-state tracking, which begins after a large gaze shift and initiation of tracking and continues until near the end of the trial.

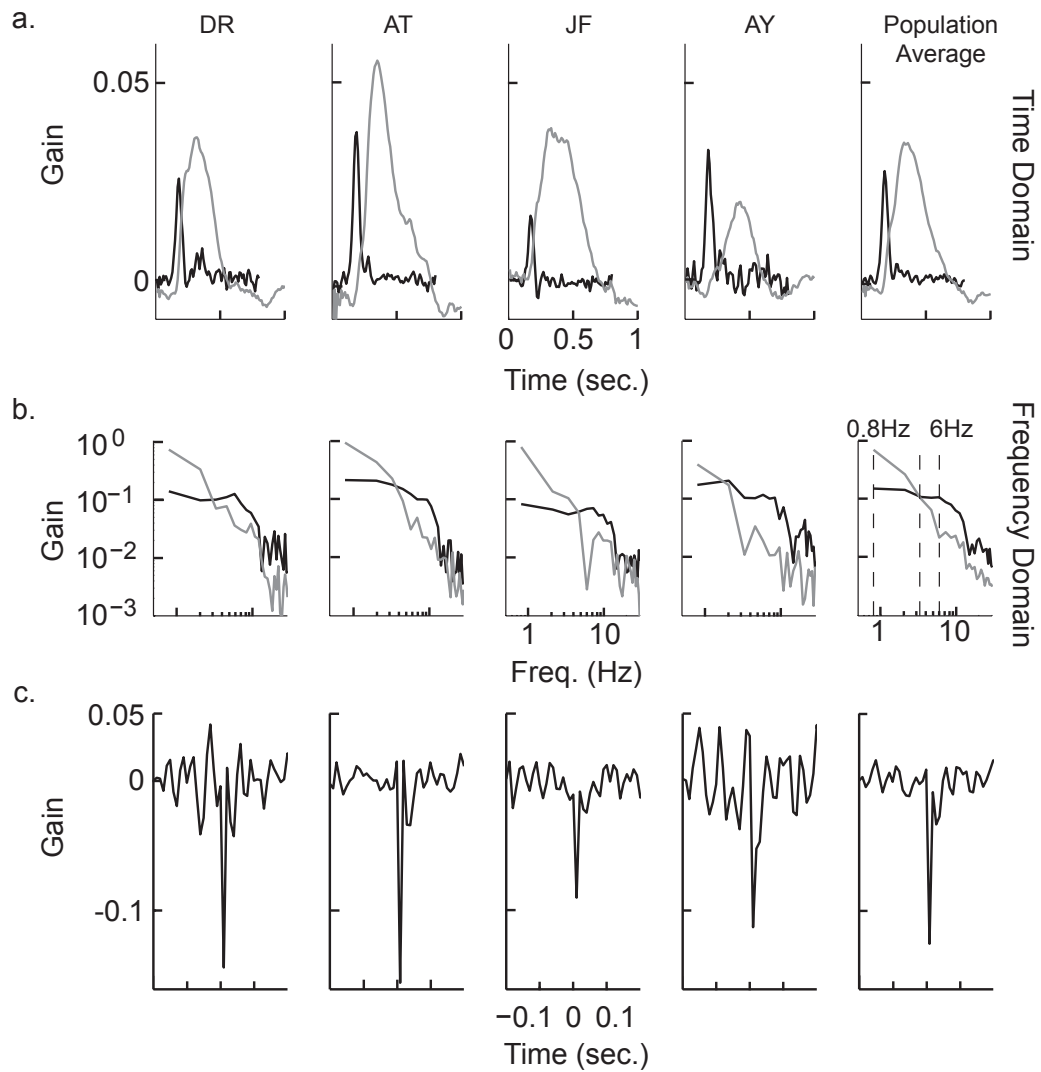


Figure 3-2 - Linear Temporal Filters, characterizing the velocity response of the head and eye to a sudden impulse in target velocity were recovered for five subjects. The eye (black) exhibits a strong, sharp, dominate peak after a delay of about 100 ms. The head (gray) follows with a broader and later peak.

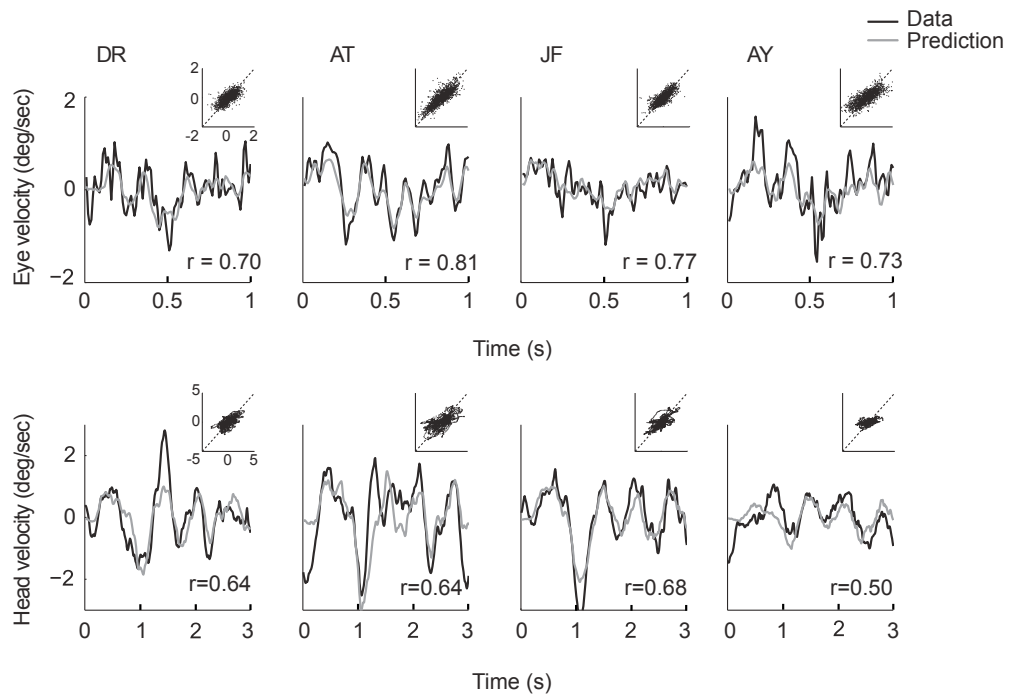


Figure 3-3 - Predicted versus Measured Velocities. Predicted velocity is plotted against measured velocity for each time point and for each subject. Eye is on the top, head on the bottom.

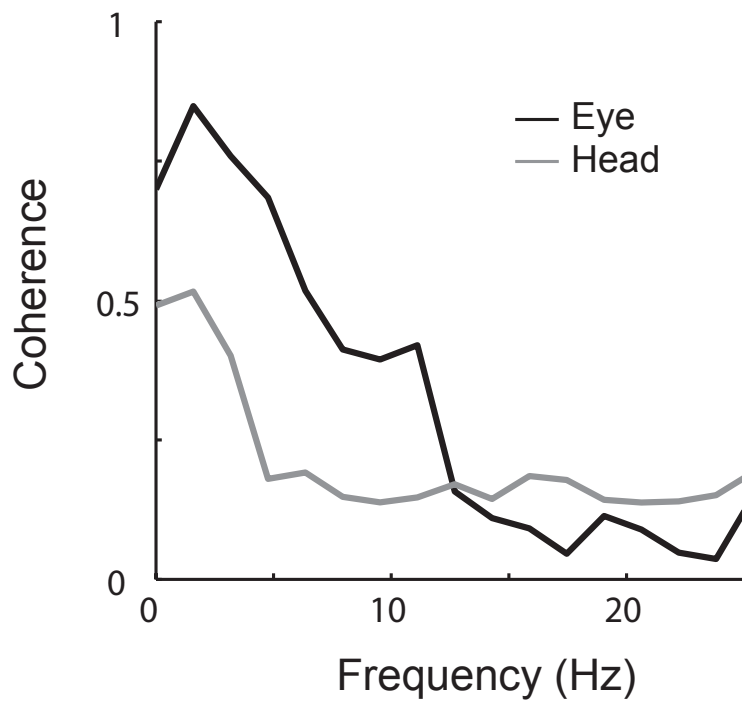


Figure 3-4 - Predicted velocity traces. We compared predicted versus measured mean ponses of head and eye to novel, white noise target velocity traces. Black lines are measured mean responses for the same stimulus pattern for each subject. Predicted responses were created by convolving stimulus velocity with the recovered filters from Figure 3-2 and shown in gray. For each subject, top plot is eye, bottom is head.

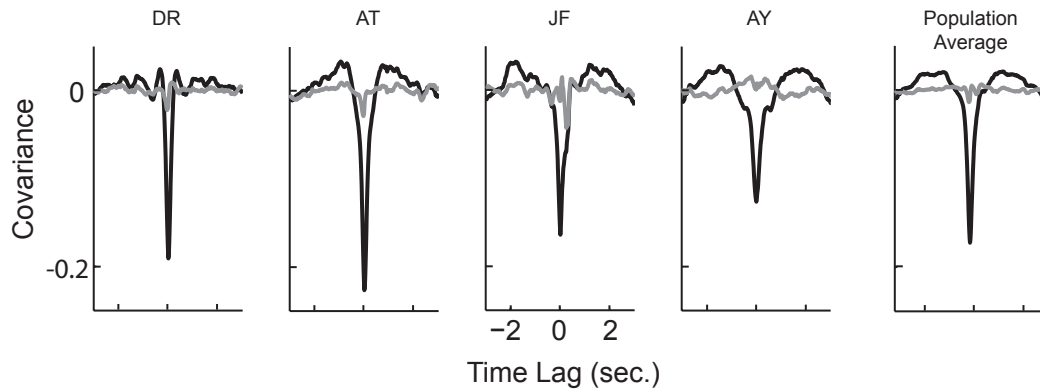


Figure 3-5 - Cross- Covariance between Head and Eye. The cross-covariance curve in black was calculated from trial-by-trial variations in velocity from the same stimulus. The large, negative peak near a time lag of zero indicates that if the head is going faster than average at a given time, the eye is likely moving slower and vice versa. The cross-covariance curves in gray were computed from errors in our predictions. In this case, there is very little covariance, indicating that our predictions account for the covariance between head and eye.

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Chapter 4: General Discussion

4.1 FUTURE WORK

Vergence and Perception

The work described and referenced in the second chapter begs for further investigation of the relationship between conscious size, depth and motion perception and vergence. In that vein, I'll briefly describe a couple ideas for future work.

Currently, collaboration is underway with the lab of Prof. Mel Goodale, examining the 'Taylor Illusion' (Taylor 1941; Ramsay, Carey et al. 2007) and the role of vergence and proprioception. In the Taylor Illusion, a subject in a dark room looks at their palm, where a brief flash is delivered. After the flash, the afterimage remains and as the subject moves their palm nearer or farther, the perceived size of the afterimage changes accordingly.

This illusion demonstrates that self-motion can influence conscious perception of size, but it is not clear which signals are being used. Recordings of vergence during the illusion indicate that while tracking the hand, vergence does indeed modulate. To eliminate motor efference as a source, the experimenter moved the hand passively as a condition. To eliminate the effects of vergence, we had the subject fixate away from the hand as a condition. The effect of the illusion diminished by half when the subject fixated away from the hand, suggesting that vergence plays a role but is not necessary. There was a small but non-significant difference between the active vs passive conditions, suggesting that proprioception is more important than motor efference for this illusion (Sperandio I 2012).

Another idea is to look at depth cue combination. Using a Bayesian approach, it is possible to estimate the weight a subject ascribes to individual depth cues by presenting multiple cues to depth and modulating them independently. If the cues conflict, the subject will more heavily weigh the cue they believe to be more reliable.

These techniques could be extended to vergence, using a similar quantification as found in chapter two. A stimulus could be shown, followed by a modulation in one of multiple depth cues, the change in vergence could then be compared to modulation of the cue as well as reported change in depth. This could show if depth perception and vergence do or do not use the same information and strategies for determining depth.

Neural Correlates of Motion Parallax

As discussed earlier, structure-from-motion due to object rotation is ambiguous when the axis of rotation is in the frontoparallel plane. The object could be rotating clockwise or counter clockwise and there is nothing about the motion itself which indicates which is the case. When viewing stimuli with only such motion as a cue to depth, the object is perceived to unambiguously rotate in one direction at any given time, sometimes flipping

from one direction to the other. Interestingly, activity from single units in area MT has been shown to predict the perceived direction of motion (Dodd, Krug et al. 2001; Born and Bradley 2005). MT is also implicated in the control of SP (Newsome, Wurtz et al. 1985; Lisberger and Movshon 1999; Recanzone and Wurtz 2000; Priebe, Churchland et al. 2001; Priebe, Cassanello et al. 2003; Priebe and Lisberger 2004; Yang and Lisberger 2009; Lisberger 2010). Further, MT also seems to carry the requisite eye movement signal to encode depth from MP (Nadler, Nawrot et al. 2009). Considering that MT is also responsive to stereoscopic depth (DeAngelis, Cumming et al. 1998), it seems that area MT does much more than encode 2D motion (Maunsell and Van Essen 1983), but may be a principle source of motion and depth information for guiding movement and forming perception.

A neighboring visual area, MST, is also a compelling candidate for such a role. As opposed to MT, the motion signals here are in a more earth-fixed reference frame (Dursteler and Wurtz 1988; Ilg and Thier 2003), at least partially due to the vestibular input it receives (Gu, DeAngelis et al. 2007; Takahashi, Gu et al. 2007; Fetsch, Rajguru et al. 2010), making it an excellent candidate for controlling the maintenance phase of SP (Newsome,

Wurtz et al. 1988; Squatrito and Maioli 1997; Collins and Barnes 1999; Dicke and Thier 1999; Ilg and Thier 2003; Krauzlis 2004; Nuding, Ono et al. 2008) and for constructing earth-centric perceptions of motion, such as heading (Fetsch, Wang et al. 2007). From these observations, one theory is that MP from self-motion may be more related to area MST while MP due to object motion may be more associated with area MT. This could be tested using recordings of MT and MST during observer-generated vs. object-generated parallax.

Temporal-Spatial Relationship Between LFP and MUA

The local field potential (LFP) refers to a temporally low passed electrical signal believed to originate from local network activity. However, the spatial-temporal size of this network and the relationship to individual neural and synaptic events is under debate (Logothetis, Pauls et al. 2001; Kreiman, Hung et al. 2006; Katzner, Nauhaus et al. 2009; Rasch, Logothetis et al. 2009; Linden, Tetzlaff et al. 2011). Understanding these properties could enrich interpretation of LFP for future research in areas such as epilepsy (Magill, Sharott et al. 2004), Parkinson's disease (Brown and Williams

2005) and brain-computer interfaces (Andersen, Musallam et al. 2004; Courtemanche and Lamarre 2005; Heldman, Wang et al. 2006).

I propose to use the techniques described in the previous chapter in conjugation with recordings of spontaneous activity from dense electrode arrays (e.g. (Du, Riedel-Kruse et al. 2009)) to characterize the linear, spatial-temporal relationship between the multi-unit activity (MUA) and LFP. We can extract first-order kernels linking the MUA from multiple electrodes to the LFP from a single electrode and vice-versa. This has previously been attempted (Rasch, Gretton et al. 2008; Rasch, Logothetis et al. 2009), however the authors only looked at pair-wise correlations (e.g. MUA from electrode A and LFP from electrode B) from relatively sparse electrode arrays. This may have resulted in overestimation of the effective spatial extent of the origin of the LFP. Simultaneously regressing across multiple electrodes could correct this potential error and provide a more complete characterization of the spatial-temporal relationship between LFP and MUA. Further, performing this analysis for different animal models and brain areas could help determine how the MUA/LFP relationship changes, aiding in future comparisons across species and brain area.

As before, we could use the kernels to form predictions and quantify the accuracy of the linear approximation. In this case, we could predict LFP from MUA or the MUA from LFP. This project could examine the connection between two fundamental signals used in neuroscience.

4.2 CONCLUDING REMARKS

This dissertation has focused on the relationships between motion and depth, movement and perception, sensory and motor systems. In practice these are more difficult to disentangle than it may seem from first blush. Perception informs action, but the reverse is also true. Movement generates sensory signals that must be dissociated from signals originating from the environment, but they also aid in interpreting these environmental signals. Experimentally, we can often manipulate one of these variables and fix the others. This approach has been successful but does not tell us about the interaction that can occur in more complicated and naturalistic cases.

Here we have attempted to leverage what is known from more isolated conditions by extending that knowledge to increasing unconstrained ones. In the case of the EHT, we investigated how SP and the VOR interact when the observer is free to move the head naturally. In the case of depth processing,

we investigated MP generated from free self-motion and found that it can generate vergence even when disparities indicate no change in depth- indicating that extra-retinal, non-SP signals are used to control vergence from MP. It is my hope that we continue to investigate not only how our sensory and motor systems operate in isolation, but to use that knowledge to investigate how they interact and coordinate as this will ultimately lead to a greater understanding of how we operate in the real-world.

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