Movement Function Follows Spatial Form: Coordinate System Implications for Online Visual Feedback Control of the Hand

Justin Brooks
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Movement Function Follows Spatial Form: Coordinate System Implications for Online Visual Feedback Control of the Hand

by

Justin Ryan Brooks

A dissertation presented to the Graduate School of Arts and Sciences of Washington University in partial fulfillment of the requirements for the degree of Doctor of Philosophy

May 2012

Saint Louis, Missouri
ABSTRACT OF THE DISSERTATION

Coordinate system implications for visual feedback control of the hand.

by

Justin Ryan Brooks

Doctor of Philosophy in Biology and Biomedical Sciences

Neurosciences

Washington University in St. Louis, 2012

Professor Kurt Thoroughman, Chairperson

Closed loop visual feedback control of the hand is essential for accurate reaching movements. Without visual signals of either the hand or target position, reaches are inaccurate and imprecise; therefore the brain uses a relative positional signal to control movements online. Previous studies suggest that movements are planned and represented in a polar coordinate system and that the dimensions, direction and extent are independently specified and processed. We were interested to find out whether there was behavioral evidence for the independent control of hand direction and extent as a movement unfolded. We asked subjects to make a reaching movement in a virtual reality environment in which we singularly removed the visual presentation of direction and extent information of the moving hand. Results from this experiment suggest that people control the direction and extent of hand position independently during the course of a movement. With that in mind, we reasoned that if these two dimensions were controlled independently then human responses to actual visuomotor perturbations would reflect
that processing. Therefore we asked subjects to perform point to point reaching movements with a visuomotor displacement and recorded their hand positions. The trajectories were then compared to model predictions of visuomotor control to determine what type of coordinate system and control architecture most closely mimicked human behavior. We chose 2 model systems, the Next State Planner (NSP) which could be implemented in different coordinate systems, and the Stiff-Viscous (SV) model which implements control by generating corrective feedback torques. We used systems engineering metrics to evaluate human and model responses. Results from this study suggest that feedback responses of humans to visuomotor perturbation are most closely modeled by a controller than compares spatial locations of the hand and target in a polar coordinate system. Our final investigation into the numerical underpinnings of this type of control system demonstrates that using a polar coordinate system to represent movement space naturally optimizes feedback control of point to point reaches. Taken together our works suggests that the brain has evolved to represent this particular movement space in polar-like coordinates in part to efficiently enact closed loop control of the hand.
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# TABLE OF CONTENTS

General Abstract … ii-iii

Acknowledgements … iv

Table of Contents … v

List of Figures, Tables, and Equations … vi

Introduction: The planning and control of reaching movements … 1

Chapter 1: Evidence for independent online control of direction and extent … 3
  Abstract … 8
  Introduction … 9
  Methods and Materials … 11
  Results … 14
  Discussion … 25

Chapter 2: Feedback responses suggest polar based corrective control in humans … 29
  Abstract … 29
  Introduction … 30
  Methods and Materials … 32
  Results … 40
  Discussion … 51

Chapter 3: Polar based feedback control is optimal for point to point reaching … 56
  Introduction … 56
  Implementation … 59
  Discussion … 67

Discussion: Implications of findings and future directions … 71

Citations … 78
LIST OF TABLES, FIGURES, AND EQUATIONS

CHAPTER 1

Figure 1. Experimental layout for Chapter 1 … 11
Figure 2. Raw trajectories for experiment 1 … 14
Figure 3. Endpoint metrics across all subjects … 16
Figure 4. Time series of direction and extent for sample subject … 18
Figure 5. Time series of direction and extent for all subjects … 20
Table 1. Mean extent errors and p values for all conditions … 21
Table 2. Standard deviation of extent errors and p values for all conditions … 22
Table 3. Mean direction errors and p values for all conditions … 23
Table 4. Standard deviation of extent errors and p values for all conditions … 24

CHAPTER 2

Figure 6. Experimental design for Chapter 2 … 32
Equations 1-5. Governing equations for the Next State Planner … 34
Equation 6. Governing equation for Stiff-Viscous controller … 36
Equation 7. Z-scoring system used to compare model predictions … 39
Figure 7. Raw trajectories for sample subject in response to perturbation … 40
Figure 8. Model fits of baseline trajectories … 42
Figure 9. Model predicted trajectories in response to perturbation … 43
Figure 10. Sample time series for all models and subject … 44
Figure 11. Sample comparison of feedback response metrics … 46
Figure 12. Z-scores for each feedback response metrics … 47
Figure 13. Composite Z-scores for each perturbation type and target location … 49
Figure 14. Composite Z-score for all models across experimental space … 51

CHAPTER 3

Figure 15. Baseline NSP fits to unperturbed trajectories … 58
Figure 16. Trajectories produced with a variable number of bases … 59
Figure 17. Error in fit as a function of the number of bases … 60
Figure 18. Timing differences between the most active bases … 61
Figure 19. Predicted trajectories for single target and all target fitting … 61
Figure 20. Numerical comparison of weights … 62
Figure 21. Sample time series of signals comprising NSP … 64
Figure 22. Comparison of feedback responses between NSP subtypes … 66
Humans interact with the world by reaching to and controlling various objects in the environment. In order for these reaches to be useful they must be accurate and precise. The accuracy and precision with which we reach is generally taken for granted despite the mathematics required to generate, execute, monitor, and continuously update a motor plan that controls a complex movement system. One of the key variables that the brain uses to perform these control functions is the difference in position between the current target and hand position. This is demonstrated by the significant errors that occur in reaches made without vision of either the target or hand (Gordon et al 1995, Sarlegna et al 2003, van Beers et al 2004). Therefore, in order to implement control of the hand, the brain must have some spatial representation of the relative difference in position between the hand and the target. Initial investigations of this representation asked in what coordinate system the brain calculates its motor plan by quantifying errors in movements made without concomitant vision of the hand. When the endpoints of these movements were circumscribed by an ellipse, a specific pattern of error emerged. The major axes of these ellipses aligned with the direction of motion indicating that error is larger for the extent of the hand than for direction (Prablanc et al 1986, Berkinblit et al 1995, Gordon et al 1995). This suggested that the direction and extent of hand position have independent sources of error and therefore are independently planned and controlled parameters of movement (Gordon et al 1995, Soechting and Flanders 1992). Further evidence for the parsing of movement space into separate direction and extent channels comes from learning studies. In these experiments, it was shown that adaptive mechanisms to perturbations of direction and extent are also independent because of distinct differences
in the learning rate for those two dimensions and differences in their patterns of generalization (Krakauer 2000, 2004).

In addition to human behavioral evidence, the parameterization of point to point reaching into hand direction and extent has been recorded from signals in the brain. Adaptation to directional or extent perturbations generate PET activations in separate and distinct regions of the brain (Krakauer 2004, Ogawa et al 2006, Shadmehr and Krakauer 2008, Filimon et al 2009). Furthermore, it has been known for quite some time that cells in motor cortex show clear movement direction and extent dependent firing modulation. It should be noted that there is such a strong correlation between tangential velocity and distance therefore cells which seemingly have extent modulation are possibly tuned to velocity (Kalaska et al 1983, Fu et al 1993). Regardless distance information is contained within cells of the primary motor cortex.

Previous work has demonstrated that it is highly likely that the brain plans and represents the direction and extent of a point to point reach in independent channels. With that in mind, we asked if the same was true about online visual feedback control, i.e. if the brain parses out the difference between current hand and target position into a direction and extent in order to implement closed loop control of the hand. Clearly the brain uses visual information about the position of the target and the hand to control ongoing movements, but whether or not this difference is calculated the same way as a motor plan is unclear. Some authors suggest that direction and extent are not independently processed parameters of movement during a reach (Sarlegna et al 2010) while others posit that the
coordinate system for trajectory control and endpoint position transitions throughout the course of movement (Ghez et al 2007).

With these conflicting view points in mind we decided to initially investigate whether there was behavioral evidence to suggest that positional control of the hand under various conditions of visual feedback manipulation was indicative of independent direction and extent control. In our first experiment we independently removed visual signals of the hand’s direction or extent and compared those time series to reaches made with both or neither of those dimensions removed. Our hypothesis was that if the brain independently processes the direction and extent of hand position during the course of a movement, then the average error and average variance of error throughout the reach duration should be equivalent in conditions in which feedback signals of the relevant dimension are matched regardless of the presence or absence of the orthogonal dimension. Therefore experimentally, if we only provide subjects direction information of the hand, the time series of hand direction in that condition should be identical in error and variance as the time series of hand direction when both direction and extent signals are present. Similarly if these two dimensions of position are processed separately than the presence or absence of the orthogonal component of position should have no influence on the dimension being examined. Therefore a condition, in which only extent information is provided, should have an identical hand direction time series to a condition in which neither direction nor extent information is available. Our first experiment demonstrated both of these trends. The standard deviation and mean error of the direction and extent of
movement were consistent with the hypothesis that they are independently controlled visual feedback parameters (Chapter 1).

After we found evidence for independent control of hand direction and extent during the course of a movement we became interested as to whether feedback responses to visuomotor perturbation also reflected independent polar control of position. To examine this issue we chose two model systems that utilized different control architectures and could be implemented in different coordinate systems. We then compared their predicted feedback responses to actual human behavior. Our hypothesis was that the model that most closely predicted human feedback responses uses a control scheme and coordinate system that approximates what is actually implemented in the brain to control visually guided reaching movements. Subjects were asked to making point to point reaches to visually displayed targets and on a very small subset of these trials, the visually displayed cursor position was abruptly offset from the actual hand position. During these trials subjects had to correct for this perturbation and bring the visually displayed cursor to the visually displayed target. The first model system which we decided to use was the Next State Planner (NSP) developed for robotic mimicry experiments (Ijspeert et al 2002, 2009). Among the many unique features of the NSP, it is capable of being embedded in various coordinate systems, and is designed to only use relative spatial differences between the hand and the target to implement linear feedback control. Using the NSP planner in various coordinate systems we were able to examine which coordinate system best described human feedback response. Since the NSP is a relatively new scheme in
terms of studying human motor control, we compared the NSP’s predictions to a long standing extant model of upper limb control, the Stiff-Viscous (SV) control model that compares actual position and velocity to a desired position and velocity and generates a corrective torque to compensate (Shadmehr et al 1994). In this manner the SV model implements closed loop control via an entirely different architecture than the NSP. The SV model to date, has done exceptionally well at modeling responses to haptic perturbations, however we became curious as to how its predicted responses to visuomotor perturbations compared to the NSP and human performance. When we modeled the perturbations and compared them to actual human responses several differences emerged. The SV model predicted some of the temporal components of human feedback responses quite well, however it did poorly overall especially when predicting spatial metrics. Among the different NSPs the controller based in a polar coordinate system was the one that most closely mimicked human behavior in response to visuomotor perturbation, also suggesting that the brain monitors and controls the direction and extent of hand position independently (Chapter 2).

Since we had demonstrated evidence for independent control of direction and extent in both unperturbed movements and in the responses to visuomotor perturbations, we wanted to further our investigation and determine why representing the same spatial information in different coordinate systems affects feedback control. Therefore in chapter 3 we did a numerical investigation of the NSP in Cartesian and polar coordinates to compare how the choice of coordinate system impacted closed loop control. The
NSP’s output is the sum of a nonlinear feedforward and a linear feedback signal both of which can be analyzed and compared to the output of the control system. We found several differences in how control was implemented. One of the primary differences that we discovered was that the parameters which are used to generate the feedforward signal were significantly more active in the beginning of movement for the control of hand direction than they were for any other dimension. This means that the control of direction in a polar coordinate space at the beginning of movement was primarily derived from feedforward control which tapers off as a movement unfolds. Furthermore, since the output of the NSP is the sum of feedforward and feedback signals this architecture naturally allows feedback control to dominate in response to perturbation. Indeed when we examined the control signals that comprise the NSP we saw that trend. Early in movement, the control of direction was completely under feedforward control, however subsequent to perturbation this switched and the control output signal was almost completely comprised of feedback. Because output of the polar based model was largely derived from feedback contribution and little feedforward contribution, this naturally led to more effective control, as evidenced by better feedback response metrics (Chapter 3).

Our investigation into the nature of visual feedback control of human reaching has led to some interesting conclusions. First we have extended previous assertions that the brain computes its motor plans in a polar like representation by demonstrating that reaches made with impoverished feedback behave in a manner consistent with the hypothesis that those two dimensions are independently controlled during the course of a movement.
Additionally, modeled feedback responses to visuomotor perturbations also suggest that control is implemented using a polar like graphical representation of space. Finally, we have demonstrated that the coordinate system in which spatial information is represented in a control system can affect how control is implemented, and that for controlling point to point reaching movements, a polar representation is ideal.
Abstract

Closed loop visual feedback control of the hand is essential for accurate and useful reaching movements. Without being able to see either the hand or target position, reaches are inaccurate and imprecise; therefore the brain must use these signals to control movements online. Previous studies from both neurophysiology and human psychophysics suggest that movements are planned or at least represented in a polar coordinate system prior to movement onset, and that direction and extent are independently specified and processed. To date it is unclear whether or not online visuomotor feedback control uses a similar representation of the movement space. Specifically we were interested to find out whether or not there was behavioral evidence for the independent control of hand direction and extent as a movement unfolded. In order to test this hypothesis we asked subjects to make a reaching movement in a virtual reality environment in which we singularly removed the visual presentation of direction and extent information of the moving hand. We found that errors in trajectory support the notion that direction and extent are processed independently during the course of a movement.
Introduction
In order to survive animals must necessarily interact with their environment. For human primates that interaction depends on accurate and controlled upper limb reaching. Previous research in motor planning has suggested that the brain uses a polar coordinate system by independently specifying a direction and distance to move the hand. Some of these studies have analyzed the errors made without vision of the hand and demonstrate that stereotyped patterns of error suggest independent parsing of direction and extent information (Favilla et al 1995, Lateiner et al 2003, Vindras et al 2005). Other 3D studies have shown that subjects are able to match target distance and elevation while ignoring target azimuth, yet are unable to match target elevation while ignoring target distance, implying that spatial information is parsed into separate channels (Flanders et al 1990).

A common theme throughout this literature is that visual feedback is an indispensable part of controlled upper limb reaching. Repeatedly this has been noted by several experiments demonstrating that reaches become inaccurate and more variable without vision of the limb (Soechting et al 1992, Messier et al 1999). Some suggest that noise in central planning processes produce these errors, while others assert that execution noise is the main contributor to movement variability (Gordon et al 1995, van Beers et al 2002). Regardless of the source of error, the brain is using visual positional signals of the hand and the target to modify the ongoing motor command and compensate for errors generated in the movement process. Whether or not the position of the hand and target
are parsed into separate feedback channels for direction and extent during the course of a movement is unknown. Some studies suggest that they are not independently processed (Saunders et al 2003, Sarlegna et al 2010) while others suggest that there is a two distinct phases of control in which the coordinate frame changes (Ghez et al 2007).

With that in mind we became curious as to whether there was behavioral evidence for the independent control of hand direction and extent during the course of a reach. We developed a novel paradigm in which we selectively eliminated each dimension of visual feedback (either direction or extent) and compared the trajectories made in those conditions to conditions in which both or neither dimension of feedback was removed. Specifically, if direction is controlled independently from extent than the presence or absence of extent visual signals should not have any influence on the time series of direction. Similarly the control of extent should not be influenced by the presence or absence of visual direction signals. We reasoned that since visual feedback compensates for internally generated noise and for unexpected perturbations, that examining a time series of the mean and variability of dimensional error would quantify the effect of visual feedback control (Khan et al 2006).
Methods and Materials:

In order to test whether there was behavioral evidence for the independent control of direction and extent, we compared trajectories made in a virtual reality environment under conditions in which we selectively manipulated visual feedback of hand direction, extent, or both. Six neurologically normal, right handed subjects between the ages of 18 and 21 were used for this experiment.

Subjects came in and seated themselves in a chair facing a horizontally placed mirror that showed the reflection of a computer monitor used to conduct the study. An OPTOTRAK 3020 recorded the position of a LED at 100Hz that was mounted on a glove which the subjects wore during the experiment. Figure 1 shows a schematic of the experimental layout.

![Figure 1](image.png)

**Figure 1.** Overhead view of the workspace. Full hand and No hand conditions were positive and negative controls respectively. Arc hand gave the subject a visual extent signal without direction information while the Ray hand condition gave the subject direction information without extent. For clarity, only one of 6 potential target positions is shown.

The goal of the task was to bring the hand to a central starting position and when cued reach to a visually displayed target and hold that position until cued to return to the start circle and begin the next trial. *Importantly, no matter what visual feedback of the hand*
was given, the goal of the task was always to bring the hand to the 2D visually displayed target. We were interested in how the brain controlled both the direction and extent of hand position relative to the target under different visual feedback conditions. Therefore we always wanted subjects to reach for the target and not simply align either the arc or the ray with the target extent or direction respectively. There were 6 target positions (45°, 90°, 135°); (5cm and 10cm) and the target was pseudo-randomly selected on a trial by trial basis. After completing 10 movements to each target the block ended (60 trials total) and subjects rested before the commencement of the next block. Using the current, actual position of the hand, the visually displayed cursor on the reflected computer monitor was selectively manipulated. The experiment began for each subject with Full Hand (FH) trials where a 2D dot represented the veridical hand position under the mirror (far left of figure 1, hand position and visual cursor overlap). The Arc Hand (AH) condition was a block in which instead of receiving 2D feedback they only received the extent component of position which was represented as an expanding or contracting arc whose radius was equal to the distance traveled from the start circle (3rd schematic of figure 1). In contrast, the Ray Hand (RH) condition replaced the 2D dot representation of the hand with a ray whose direction was determined by the current hand position, but whose extent extended the entire workspace (far right, figure 1). In this way, subjects were provided veridical hand direction information but no extent signal. Finally, the No Hand (NH) was the negative control in which neither direction nor extent component of hand position was provided after the start hold time had been met (2nd schematic of figure
1). In all conditions, including FH, the beginning of the trial was indicated by a color change of the start circle and the end of the trial was determined by having traveled at least 4 cm away from the start location and keeping the hand velocity below 2 cm/s for 0.5s. In this way subjects were allowed to move freely and the impact of impoverished feedback could be ascertained without a presiding accuracy or speed constraint.

After the FH block, each subject received a unique order of experimental blocks (AH, NH, RH) so as to control for training effects across subjects. Since we are interested in feedback control and not adaptive effects it was paramount that we prevent as many adaptive influences as possible. Therefore we randomized the order of experimental blocks so that any adaptation would be averaged out across subjects. The design of this experiment was poised to determine what the average behavior was across subjects to interrogate questions about how the brain might control movement. In order to make comparisons across subjects some data reduction was necessary. Within subject analysis consisted of aligning trials to the start of movement (monotonic increase in velocity after 2cm/s) and then the time series of direction or extent were sampled according to percentage of completion since trials were of variable lengths, especially across conditions, e.g. Arc Hand reaches were consistently shorter than No Hand reaches. This permitted an examination across conditions and subjects despite differences in movement times.

For our purposes error was defined as the mean absolute difference between the target and the hand. This was done because at times people would over/undershoot the target
and sometimes make counterclockwise or clockwise errors in direction. When averaged, those errors would become zero. Since we were interested in the feedback corrective processes we were simply interested in the magnitude of error. To determine the standard deviation of error we used the unaltered distributions. Once we had determined the standard deviation and absolute value of error for these movements we compared those metrics at each time point across conditions using a permutation test.

Results

Data from these experiments were analyzed both within and across subjects. Trajectories were examined from the end of the start hold time (the time indicating when subjects

Figure 2. Raw trajectories for a sample subject. For clarity, 3/6 targets are shown. Note the dramatic overshoots in conditions without extent feedback (left column) and large angular errors in conditions without direction feedback (top row). These time series served as the basis for our subsequent analysis.
should leave the start circle) through the hold target time so as to maximize the number of
data points and to ensure that the portion of the movement under visual feedback control
was fully captured.

As can be seen for the sample subject in Figure 2, the experimental conditions produced
clearly different behavior from the subject. In the No Hand condition there were large
errors in both the direction and extent of hand position since no visual feedback was
available (figure 2, top left). In contrast, the bottom right plot shows trajectories in the
Full Hand condition in which reaches are accurate and precise (figure 2, bottom right).
In the Ray Hand condition (bottom left) the extent component of position was selectively
removed and as can be seen generated large errors in extent while preserving directional
accuracy. Finally, in the Arc Hand condition (top right) because there was no visual
direction signal, subjects made significant directional errors despite precise extent
control.

*Extent and direction errors and variance at endpoint*

Before we examined the time series data for all subjects, we first wanted to examine the
endpoint errors in each condition and verify previous results. Figure 3 plots the average
error and standard deviation for all the subjects in each of the experimental conditions.
Mean directional errors were large for the No Hand and Arc Hand conditions, ~5-6°, and
were not significantly different (p = 0.46) between the two conditions despite the large
tangential distance between the average endpoints (figure 2). There was little angular error for the Ray Hand and Full Hand conditions, in both conditions the error was <1°, and were not significantly different from each other (p = 0.15). There was a significant difference between conditions in which direction feedback was provided and those in which it was not, NH, AH vs. RH, FH, respectively each comparison p < 0.001. The standard deviation followed the same pattern as mean error; it was equal for No Hand and
Arc Hand conditions, ~3°, \( p = 0.77 \), and also equivalent for Full Hand and Ray Hand conditions, approximately 0.5° in magnitude, \( p = 0.2 \). When no extent information was provided for the task subjects made gross extent errors and were more variable than when this information was available. As figure 3 shows, the errors in extent for the Ray Hand and No Hand were equivalent between 11 and 12cm (\( p = 0.89 \)), while Full Hand and Arc Hand were had a significant difference of 0.6mm (\( p = 0.01 \)) yet were qualitatively very similar. Errors in extent were significantly different between conditions in which visual feedback of extent was provided (FH, AH) and conditions in which the extent component of position was absent (RH, NH) (all \( p < 0.001 \)). The standard deviation of extent errors in these conditions showed a similar pattern. Without visual signals of the hand’s current extent, errors were more variable. The standard deviation of extent error for the No Hand and Ray Hand conditions was between 1.5 and 2cm (\( p = 0.29 \)) while those for the Arc Hand and Full Hand were both much less than 0.5cm (\( p = 0.49 \)). The standard deviation of extent error was also significantly different between conditions in which visual feedback of extent and when those signals were absent (all \( p < 0.01 \)).

Without visual feedback there were gross errors in extent and direction as can be seen in the No Hand, Arc Hand, and Ray Hand conditions when compared to Full Hand (figure 2,3).

The pattern of error and standard deviation of error in figure 3 confirmed previous results that movements made without visual feedback of the hand reflect independent direction and extent processing. With that in mind we investigated the control of direction and
extent during the course of movement to begin interrogating whether there was evidence for independent direction and extent control in real time. For the same subject whose trajectories are plotted in figure 2, in figure 4 we plot the average error (thick lines) and the standard deviation around that error (shaded regions) for all conditions. For this subject there are apparent qualitative differences between the different experimental conditions that, as will be quantified in a subsequent section, were repeated by the other 5 subjects.

First, conditions in which the angular component of hand position was invisible (Arc Hand, No Hand) were divergent from the time series in which direction was visible (Ray Hand, Full Hand). Additionally for this subject when directional signals were present either singularly or in conjunction with extent visual signals, control of the

Figure 4. Individual time series for sample subject in Figure 2. Since we were interested in the control of direction and extent throughout the course of movement we wanted to examine how the error and variance of those dimension related through the duration of a reach. In these plots, the solid line demarcates the mean error while the shaded regions are the standard deviation of error.
angular component of hand position was similar as demonstrated by the significant overlap of the Ray Hand and Full Hand time series (figure 4, left bottom traces). Similarly, when visual feedback of hand direction is removed, the addition of extent visual signals does not influence the control of direction as evidenced by the significant overlap of the Arc Hand and No Hand time series (figure 4, left, top traces).

The overlap described for the control of direction also applied for the comparisons of extent. A similar, distinct divergence was observed between conditions in which this subject was deprived of extent signals (Ray Hand, No Hand) and those in which they were present (Arc Hand, Full Hand). Overlap between conditions in which extent information was visually available in the presence (Full Hand) or absence (Arc Hand) of direction was also quite clear in this subject (figure 4, right, bottom traces). Finally, when extent information was withheld, the presence (Ray Hand) or absence (No Hand) of direction information had no impact on the control of extent which can be seen again by the overlap of those two curves (figure 4, right, top traces).

*Extent error and variance throughout movement*

Figure 5 plots the average error and standard deviation for both direction and extent across all subjects. Conditions in which there was a visual signal of the extent the hand had traveled (Arc Hand/Full Hand) showed clear divergent behavior from conditions in which these signals were absent (No Hand/Ray Hand). The plots in Figure 5 (top row) show the time series for these 4 conditions and tables 1 – 4 contain the numeric differences.
Errors in extent depended upon having visual signals relaying that dimension of position. The top right plot of figure 5 shows the absolute error of extent for each of the four experimental conditions. From this plot it is clear that the NH and RH conditions had similar errors in extent throughout the course of movement that were dramatically different from AH and FH. Those differences are quantified in table 1. Extent errors in NH and RH conditions were quite large (~11 cm) however, not significantly different from one another for the duration of movement (p values range from 0.34 – 0.89). AH and FH had significant differences in extent error after 50% of movement completion but
this difference was 0.6 mm which we considered to be statistically but not biologically significant, since it has been previously demonstrated that 0.6mm is well below the precision of human proprioceptive control (van Beers et al 1998).

<table>
<thead>
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<th>Extent Error</th>
<th>Percent of movement completion</th>
<th>10%</th>
<th>30%</th>
<th>50%</th>
<th>70%</th>
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<th>100%</th>
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<tr>
<td>AHvRH</td>
<td></td>
<td>0.005</td>
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<td></td>
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<td>0.0251</td>
<td>5</td>
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<td></td>
<td></td>
<td>-0.46</td>
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<td>0.06</td>
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<tr>
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<td></td>
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<td>8.57</td>
<td>10.82</td>
<td>11.45</td>
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Table 1. Differences in extent error between each condition studied. P values were determined by permutation test and the effect size is the mean difference between the two conditions being compared. Conditions in which extent signals were available (AH,FH) had similar errors and were distinctly different from conditions in which extent signals were not available (NH, RH).
The standard deviation of extent error (figure 5, top left, table 2) throughout movement showed similar trends. There was no difference between the No Hand and Ray Hand conditions suggesting that additional direction information does not augment control of extent error (p values ranged from 0.29 to 0.87). Only at 50% of movement completion did the Full Hand and Arc Hand extent variability differ but this continued to be submillimeter (0.6mm) and when examined across the entire movement was 0.4mm.

<table>
<thead>
<tr>
<th>Extent STD</th>
<th>Percent of movement completion</th>
<th>10%</th>
<th>30%</th>
<th>50%</th>
<th>70%</th>
<th>90%</th>
<th>100%</th>
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<tr>
<td>NHvAH</td>
<td>P value</td>
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<td>0.0012</td>
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<td>Effect Size (cm)</td>
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<td></td>
<td></td>
<td>0.87</td>
<td>2.15</td>
<td>2.53</td>
<td>2.50</td>
<td>2.61</td>
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<tr>
<td>AHvRH</td>
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<td>0.0225</td>
<td>0.0003</td>
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<td></td>
<td>-0.75</td>
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<td>-1.91</td>
<td>-1.95</td>
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<tr>
<td>AHvFH</td>
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<td>0.0695</td>
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<td></td>
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<tr>
<td></td>
<td></td>
<td>0.73</td>
<td>2.06</td>
<td>2.17</td>
<td>1.93</td>
<td>1.96</td>
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</table>

Table 2. Differences in the standard deviation of extent error between each condition studied. The presence or absence of visual extent signals directly impacted the variability of error. Without vision of the hand’s extent reaches were more variable (NH, RH) than conditions in which they were present (AH, FH).
Angular error and variance throughout movement

Without vision of the hand’s current direction, errors in hand direction were large and more variable than conditions in which they were available. The bottom plots of figure 5 illustrate this point and table 3 quantifies those differences. The traces for NH and AH direction error (figure 5, bottom right) and standard deviation (figure 5, bottom left) overlap and diverge from the conditions in which visual direction was available (RH, FH).

Table 3. Differences in the angular error for all the conditions studied. The presence or absence of visual direction signals directly impacted direction error. Conditions that had no visual signals of direction (NH, AH) had similar errors and were dramatically different from conditions in which vision of the hand’s direction was available (RH, FH).
NH and AH had similar angular errors for the duration of the reach and were approximately 5° in magnitude on average across the whole movement (p values ranged from 0.1 to 0.67). The RH and FH conditions had similar error profiles however had a point of significant difference at 30% of movement that was 0.82°. Visual feedback of the hand’s direction also affected the standard deviation of angular error.  

**Angular STD**

<table>
<thead>
<tr>
<th>Percent of movement completion</th>
<th>10%</th>
<th>30%</th>
<th>50%</th>
<th>70%</th>
<th>90%</th>
<th>100%</th>
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<tr>
<td>NHvAH P value</td>
<td>0.6937</td>
<td>0.9315</td>
<td>0.9755</td>
<td>0.9787</td>
<td>0.8055</td>
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<tr>
<td>NHvRH Effect Size (degrees)</td>
<td>-0.28</td>
<td>-0.03</td>
<td>-0.01</td>
<td>0.01</td>
<td>0.09</td>
<td>0.11</td>
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<tr>
<td>NHvFH</td>
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</tr>
<tr>
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<tr>
<td>AHvFH</td>
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<tr>
<td>RHvFH</td>
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<td>0.0000</td>
<td>0.0000</td>
<td>0.0000</td>
<td>0.0000</td>
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</tbody>
</table>

Table 4. Differences in the standard deviation of extent error between each condition studied. The presence or absence of visual extent signals directly impacted the variability of error. Without vision of the hand’s extent reaches were more variable (NH, RH) than conditions in which they were present (AH, FH).

When subjects could not see the current direction of the hand (NH, AH) they had more variable errors than when they could (FH, RH). The bottom right of figure 5 shows that
the standard deviation of direction was significantly higher in the NH and AH conditions than in the FH and RH conditions. These differences were significant as quantified in table 4. Despite the large differences in extent, NH and AH had similar standard deviations of direction error (p values ranged from 0.69 to 0.98). RH and FH also had similar standard deviations of direction error despite the additional presence of visual extent signals in the FH condition (p values ranged from 0.04 to 0.22). There was one point of significant difference at 30% of movement completion that was 0.6°.

Discussion

Previous studies have examined endpoint errors in reaches made without visual feedback of the hand to interrogate questions of motor planning. These studies have found several lines of evidence suggesting that the brain generates movement plans in polar coordinates centered at the starting position of the hand. When reaches are made without vision of the hand over a number of trials a generalized pattern of error arises in that errors in direction are consistently less variable and smaller in magnitude than those in extent. To previous researchers this suggested that these two components of hand position are independently planned since one would expect equivalent errors if direction and extent shared the same planning mechanisms (Gordon et al 1994, Vindras and Viviani 2005). Furthermore, since the ellipses made by these errors are oriented such that their major axes are along the direction of movement suggesting that the brain uses a hand centered reference frame to orient its coordinate system (Gordon et al 1994, McIntyre et al 1998).
With this in mind, our study was designed to directly examine how direction and extent visual signals were processed and translated to the control hand position during the course of a movement. The hypothesis that direction and extent visual signals of the hand are processed independently to control hand position makes 2 distinct predictions confirmed by this experiment: 1) movements made without vision of the hand’s direction or extent should have identical time series of hand direction or extent to reaches made without vision of both, since we would predict there is no interaction between the two, and 2) reaches made with full, 2D vision of the hand should have identical times series of hand direction and extent compared to conditions in which visual feedback of only one dimension of movement was provided. If the brain parses direction and extent information into distinct channels to implement feedback control then the presence or absence of the orthogonal dimension should have no influence on the dimension under study. Therefore conditions where feedback dimensions are matched should have similar time courses for that dimension regardless of any other additional or missing component of feedback

Although similar in their ideals the combined tests of this experiment have some nuances. While examining how the control of direction varies with or without extent signals poses 2 slightly different questions. Comparing the No Hand direction time series to the Arc Hand angular time series is essentially asking how the control of direction varies with or without the presence of extent signals by essentially testing the feedforward control of a motor plan with respect to the direction of movement. In other words, since people
generally make point to point reaching movements that are roughly straight, is the motor plan for this direction fixed for the entirety of movement? Our experiment suggests that the direction of hand position is fixed throughout a trajectory no matter what distance is traveled (NH vs AH) and therefore is largely controlled via feedforward mechanisms. Consider that direction and extent are biomechanically coupled, thus to maintain a single direction as measured in movement space requires the precise timing of muscle contraction. Therefore, if direction is held constant even past the planned target position, then it suggests that a motor command is being issued to maintain the correct direction of movement regardless of distance traveled. Conversely, asking how the brain controls direction when only visual signals of direction are available, compared to a condition in which both direction and extent signals exist (RH vs FH) examines how visual feedback of hand direction is influenced by extent. In our experiment we demonstrated that the visual control of direction was the same with or without visual extent signals suggesting that feedback control of direction is processed in a separate channel than that of extent control. A similar pattern was observed for the control of extent in the presence (FH) or absence (AH) of visual direction signals.

Recent studies have suggested that direction and extent may not be completely independently controlled because relaxing extent control constraints amplifies directional corrections (Sarlegna et al 2010). However this study introduced errors to test this hypothesis while our task essentially had no perturbations but rather tested baseline performance. This may in fact contribute to the differences found in our two studies.
since it has been shown that task conditions influence direction and extent control (Messier et al, 1997). Furthermore, in Sarlegna et al 2010, reaches were quite rapid, on average, 334ms which if one assumes a feedback delay of 160ms, essentially reduces relevant feedback signals to the latter half of movement, 170ms (Barbur et al 1998, Saunders et al 2003). Our experiment had no temporal constraint such that we could maximize the portion of the movement under feedback control, which could also have contributed to the differences between the two studies.

Our experiment extends previous findings that the brain plans movements in separate channels of direction and extent by demonstrating that in unperturbed point to point reaching movements the online control of direction and extent are seemingly independent. The time series of mean error and the standard deviation of error were similar for conditions in which a single dimension of visual feedback was removed when compared to combined conditions of visual feedback. This explicitly tests the assertion that the presence or absence of the orthogonal dimension of movement does not contribute to the control of the other dimension. We furthered this finding by modeling a this type of control and demonstrating that human feedback responses to visuomotor perturbations are most closely mimicked by a model that implements this control in a polar based spatial representation.
Abstract

Online visual feedback is an integral part of accurate upper limb movement. Innumerable times during a given day we make reaches to objects in our environment that without visual feedback control would be non functional. The mathematics behind online visuomotor control are complex considering that relative positional signals of the hand and target of the reach are projected onto a 2D retina and then transformed through the brain into a descending motor command. Previous studies have suggested that the brain transforms visual positional signals of the hand and the target into motor plans that are centered at the starting position of the movement and based in a polar coordinate system. While we have previously confirmed these results, we sought to understand if responses to experimentally induced movement errors were indicative of a particular coordinate system or if perhaps as other models of movement suggest, planning and feedback control are implemented in different coordinate frames. Using a robotics based control model, the Next State Planner, and a long established model of feedback control, the Stiff-Viscous controller; we modeled feedback responses in different control architectures and coordinate systems to visual perturbations and compared their predicted responses to human behavior. Our findings suggest that feedback responses of human subjects to visuomotor perturbations are most closely described by a polar based control model suggesting that the brain independently processes error in direction and extent to implement closed loop control of the hand for point to point reaching.
Introduction

Humans rely on the use of their hands to interact with the world which in turn requires a relative visual position signal of the hand and the target. Reaches made without vision of the hand or target of the reach are inaccurate and highly variable over a number of repetitions further underscoring the importance of visual feedback (Prablanc et al 1986, Soechting et al 1989). In this study we used two very different high-level control models to investigate which control architecture and coordinate system best described human responses to visuomotor perturbation.

The first model system that we chose to investigate was the Stiff-Viscous controller developed by Shadmehr et al. The SV model is based off of studies in which haptic perturbations were applied to subjects holding a manipulandum (Shadmehr and Mussa-Ivaldi, 1994). By examining how humans responded in these altered movement environments, the stiff and viscous properties of the arm could be evaluated. In this system, a feedforward component is generated from a desired trajectory converted into torques by an inverse model. This feedforward signal is then combined with a feedback signal that utilizes the difference between actual and desired position and velocity to generate corrective torques in the face of perturbation. The SV model has very successfully described several experiments in which a perturbation is applied to the hand as a force, however it has not been examined in a visuomotor setting in which the kinematic signals of the hand may not be subject to the constraint of human dynamics.

The Next State Planner (NSP) was developed by Ijspeert et al, as control system for
humanoid robots that use cameras to imitate human movement (Ijspeert et al 2002). At its core, the NSP combines a nonlinear feedforward signal with a linear feedback signal that strictly uses the relative position of the target and hand to modify the ongoing motor command. One of the unique features of the NSP is that it can be modeled in different coordinate systems utilizing the same fundamental equations. Therefore we were able to not only compare the control architecture between the SV and NSP but were able to extend our previous study’s observation and investigate coordinate system influences on feedback control of the hand.

Human subjects were asked to make point to point reaching movements to visually presented targets in a virtual reality environment while only being able to see a visually presented cursor in lieu of their actual hand. On 16% of trials the cursor position representing their hand was offset from their actual hand position by either (-3 cm, 3cm) Cartesian perturbation, or a (-22.5°, 3 cm) rotation and extension polar perturbation. Responses to these perturbations were modeled using the Next State Planner (NSP) and Stiff-Viscous (SV) controllers and compared to actual human responses to determine which model and which coordinate system most closely mimicked human behavior.
Methods and Materials:

*Human experiment.* Figure 6 shows a schematic of the experimental conditions viewed from above. Subjects performed a simple point to point reaching movement to five visually presented targets which were located at (45°, 12.5cm), (67.5°, 10cm), (90°, 12.5cm), (112.5°, 10cm), and (135°, 12.5cm). The movement workspace was located below a half silvered mirror onto which were projected the targets, starting position, and a 2 dimensional cursor representing hand position. Hand position was determined by an OPTOTRAK 3020 sampling at 100Hz using custom MATLAB software.

When subjects first came in for the experiment they were seated comfortably in a chair facing the movement environment and placed their chins in a chinrest mounted to the experimental rig. The task itself was a modified version of the center-out reach task,
such that subjects first located the position of their hand indicated by the 2D cursor, brought their hand to the start circle, held it at the start for a variable amount of time between 300 and 500ms at which point the start circle turned green indicating “GO”. The subjects then reached toward the target circle and were required to hold it at the target for a variable amount of time between 300 and 500ms at which point the trial was concluded and the subject brought their hand back to the start to commence the next trial. The first experimental block consisted of 60 trials (12 to each target, presented in a pseudo random order) with an unperturbed cursor. This was the baseline condition to which the models were fit and used to generate predictions to visuomotor perturbations.

Subsequent blocks were perturbation blocks which consisted of intermittent trials with Cartesian or polar based visuomotor offsets imposed at a 6cm radial distance from the origin as a step input to hand position. The trial sequence was the same as above, however on pseudo random trials, the visual cursor was displaced from the actual position of the hand by either a rotation and extension (polar) or a lateral and vertical displacement (Cartesian). 4 blocks of both polar and Cartesian perturbations were given to each subject totaling to 8 perturbation trials out of 48 total trials ~16%. Target orders were randomly interleaved to prevent adaptive effects and perturbation trials were spaced by a minimum of five unperturbed trials.

Modeling. The Next State Planner (NSP) developed by Ijspeert et al was used to model used to fit the baseline trajectories in polar, Cartesian, or joint angle coordinate systems. Equations 1 – 5 describe the Next State Planner implementation that we used (Ijspeert et al 2002).
The output of the model is equation 2 in which \( \dot{y} \) (change in hand position in a single dimension and is integrated to generate actual position), is the sum of 2 terms: 1) \( z \), an internal signal derived from the actual feedback (target – hand position), and 2) the nonlinear forward term (the second term of equation 2). Equation 1 defines \( z \), within which there are 2 time constants, \( a_z \) and \( b_z \), these control the dampening of the system. In the original inception of the model \( a_z \) and \( b_z \) were set to 8 and 4 respectively. While this worked well for the robotic control necessary in Ijspeert et al, it was critically damped and therefore not very much like human behavior which typically shows some sort of over/under shoot. The \( (g-y) \) term relays the distance between the goal \( (g) \) and the current position of the hand \( (y) \) in whichever coordinate system is being examined. By design, this incorporates linear feedback control into the base equations. Importantly, \( y \) in equation 2 can be any dimension of position, i.e. direction, extent, \( x \), \( y \), \( q_1 \), or \( q_2 \).

The weights used to generate the nonlinear forward component \( (w_i) \) are fit using nonlinear least-squares fitting (lsqnonlin in Matlab) to the baseline reaches. These weights are multiplied by Gaussian basis functions (eqn 5) and then normalized as in

\[
(1) \dot{z} = a_z (b_z (g - y) - z)
\]

\[
(2) \dot{y} = z + \frac{\sum_{i=1}^{N} \Psi_i w_i}{\sum_{i=1}^{N} \Psi_i} y
\]

\[
(3) \dot{v} = a_v (b_v (g - x) - v)
\]

\[
(4) \dot{x} = v
\]

\[
(5) \Psi_i = \exp\left(-\frac{1}{2\sigma^2} (\tilde{x} - c_i)^2\right)
\]
equation 2. The basis functions are equally spaced throughout the movement duration and their widths are adjusted such that covered the movement workspace evenly, i.e. 1/25\textsuperscript{th} of the movement duration. The average reach for a given target for a subject’s first block (unperturbed movements) were fit independently for each dimension of the coordinate system being modeled, i.e., x and y individually, direction and extent individually, or q1 (shoulder angle) and q2 (elbow angle) individually. After determining weights for a given target and subject we were then able to model visuomotor perturbations by offsetting the hand position in the model and then observing the resulting hand trajectory prediction. Equations 3 and 4 generate the internal states necessary to time the feedforward signal that is combined with the nonlinear basis term in equation 2 to make the full nonlinear feedforward component. A full discussion of the model system is available in Ijspeert et al 2002.

Although we were generally interested in the influence the choice of coordinate system had on the implementation of closed loop control, we also wanted to interrogate the ability of the NSP architecture to describe human behavior compared to extant control models. Therefore, we also compared the results of the NSP to trajectories predicted by a more established model in the literature, namely, the Stiff-Viscous (SV) control model (Shadmehr, Mussa-Ivaldi 1994). The SV model uses limb lengths and the weight of the subject as fit parameters for the model and thus these data were taken for each subject. The mathematical implementation of the model is fully described in (Shadmehr, Mussa-Ivaldi 1994). In equation 6 the controlled output torque, C, is the difference between a feedforward component that is generated by multiplying an inertia matrix of the arm (I)
by a desired joint accelerations summed with coriolis forces, G and 2 feedback terms that consider the stiffness (K) and viscosity (V) of the arm. We attempted to use 2 different types of desired joint accelerations; at first we used a minimum jerk based trajectory as was used in the original instantiation of the model (Shadmehr, Mussa-Ivaldi 1994). Although this works, it did not capture the baseline behavior well enough to make a straightforward comparison with the NSP controller. Therefore when we implemented the SV model to compare with the NSP we used the joint accelerations derived from baseline conditions, as calculated by a Savitsky-Golay filter. In this way the desired joint accelerations formed a 2 element vector for the elbow and joint angle accelerations. Feedback is implemented in this model by comparing desired and actual joint angle and joint angle velocities by multiplying them by stiff and viscous parameters of the arm respectively. The stiffness matrix is 2 x 2 and operates on the 2 element vector q, which contains the actual joint angles for q1 and q2. The torque generated by the stiff properties of the arm is then combined with a torque generated by the viscous component. The viscosity matrix (V) is also 2 x 2 so that it can be multiplied by the 2 x 1 vector that relays the difference between actual and desired joint angle velocity. In totality this controller works by generating a feedforward torque from which feedback, corrective torques are subtracted that compare desired position and velocities of the joint angles.

\[ (6) C(q, \dot{q}, t) = \dot{I} \ast \dot{q}^\star(t) + \dot{G} - K(q - q^\star(t)) - V(q - \dot{q}^\star(t)) \]

Since we are interrogating the feedback response predictions made by models compared
to those made by humans we used metrics from control systems engineering to quantify the differences between the model and human predicted trajectories. We used four in total, 2 temporal and 2 spatial. The time of corrective control initiation (Tc) was the time at which the difference between an unperturbed and perturbed trajectory differed by 10% and served as proxy to determine when the model or human responded to perturbation. The settling time (Ts) was determined by the first time at which the time series examined reached a 5% window of its final value and stayed within that window. Percent maximum overshoot (Mo) was determined by finding the maximum difference between the model response and the actual perturbation value which would give some indication as to the dampening of the system. Finally, the integrated square error (ISE) was the integrated area between the value of the time series examined and the ideal response (the step of perturbation).

Determining perturbation values. One of the objectives of this study was to examine the influence that the choice of coordinate system had on the subject’s feedback response to perturbation, therefore we first had to determine what values of perturbations would drive the largest divergence between model predictions. Using a pilot set of subjects we fit 3 NSPs (1 each based in polar, Cartesian, or joint angle coordinate systems) to unperturbed reaches. After determining their fits we then modeled responses to a variety of perturbations predicted by the 3 NSPs (Cartesian, polar, and joint angle) and used a systematic scoring system to determine the optimal perturbation values. We decided to
use a polar and Cartesian based perturbation so that we controlled for dynamic and static responses in the model. In a Cartesian based controller, a polar positional perturbation requires a dynamic response since a polar perturbation in Cartesian space itself is dynamic. In contrast a polar offset in position in polar space is effectively a step-perturbation. By imposing both Cartesian and polar based perturbations we were able to account for differences in the responses in the feedback control systems. The coordinate system of perturbation did have an asymmetric effect on the model responses (figure 13). In order to determine the appropriate polar and Cartesian based visuomotor perturbations we modeled perturbation responses across the movement and perturbation space. The boundaries of the perturbation space were determined by the limited area of the workspace that could be comfortably reached underneath the mirror (figure 1). Since we were considering movements in 2 dimensions and had four metrics to base these comparisons some amount of data reduction was necessary to compare model predictions. For each target and perturbation value tested, ISE, MO, Tc, and Ts were calculated for each model, normalized by the maximum value across all models and then combined across dimensions. This permitted an examination of the relative differences between the three model types. The values of perturbation that generated the largest difference between all of the models for Cartesian perturbations was (-3cm, 3cm) and polar perturbations was (-π/8, 3cm). This corresponded to a visual cursor displacement to the left and up and a counterclockwise rotation and extension of the visually displayed hand position in the Cartesian and polar perturbation conditions respectively.
Comparing models to human performance. Once the values of perturbations were chosen we then brought in 10 human subjects to perform the task with the perturbation values described above so that we could compare the actual, human responses to the model predictions. For each subject the baseline block (unperturbed trajectories) was used to fit the NSP weights and then the model predictions were determined by inputting the perturbation value as a step input to the current visual hand position. For the SV model these unperturbed trajectories were used as the desired trajectory input.

Since we were interested in determining which feedback response most closely mimicked human performance, we determined the Tc, Ts, ISE, and Mo for human subjects and compared them to the model predictions. In order to perform the necessary data reduction to investigate average model performance across all experimental dimensions (subject number (s), model type (m), target locations (t), perturbation type (p), spatial dimensions (d)) we converted differences between human and model performance into Z-scores according to equation 7. In this formalism a model’s difference from subject performance was standardized with respect to the average difference between a subject and all models for a particular perturbation (Cartesian, polar) and target (#1 -5) in a given dimension. In this manner, a given model’s prediction was in units of standard deviation away from the average model difference from subject performance.

\[
Z_{(s, m, t, p, d)}^{(7)} = \frac{|Model_{(t, p, d)} - Subject_{(t, p, d)}| - |Model_{(t, p, d)} - Subject_{(t, p, d)}|}{\sigma |Model_{(t, p, d)} - Subject_{(t, p, d)}|}
\]
After generating Z scores for each of the metrics, they could then be combined across all dimensions of the experiment by simply summing them for a given model type. Therefore with this scoring technique, the more negative the Z score the better because that means that that particular model’s performance is below that of the average model performance.

Results

Baseline, control reaches were performed when subjects first arrived for the experiment. The time series for these reaches were converted to joint angle (JA), Cartesian (Cart), or polar (Pol) coordinates and used to fit the 25 weights for each NSP and in the case of the SV model these reaches served as the desired trajectory for subsequent modeling of perturbation responses. Therefore the model responses by both the SV and NSP to perturbation are driven purely by baseline, unperturbed behavior since those parameters were derived solely from the initial blocks of unperturbed movement.

Figure 7. Responses to perturbation. Blue lines indicate individual trajectories while solid red lines are the mean trajectories for each target. Circles indicate visually displayed targets while asterisks represent the hand position required to achieve the visually displayed cursor after perturbation.
An individual subject’s trajectories in response to Cartesian (left) and polar (right) perturbation is plotted in Figure 7.

Despite only experiencing a given perturbation 8 times out 240 reaches (~3% of trials) subjects were able to respond appropriately and achieve the final target position reproducibly and with little difficulty. Model fits to the unperturbed trajectories were remarkably close as is evidenced by the significant overlap between the model trajectories and the sample subject trajectory in Figure 8. To us this indicated that the models initially captured the same information about a subject’s movement.

Plotted in Figure 9 are the model responses to Cartesian (left) and polar (right) perturbations to 3 out of the 5 targets used which demonstrate the distinct spatial predictions made by each model type.
Each of the models, 3 NSPs and the SV reached the perturbation target (the hand position necessary to bring the displayed cursor to the visually displayed target) although they arrived to that target by distinct trajectories. No model completely overlapped with the actual human trajectory although clearly some of the models were more closely aligned in space with the actual human response to visuomotor perturbations than others. The sample subject and corresponding models selected for this figure is typical for the responses across subjects and targets and therefore can be used to demonstrate some preliminary conclusions. First, the SV model despite arriving at the correct target location, takes a completely different trajectory compared to the NSPs and actual human

Figure 8. Baseline fits to the unperturbed trajectories. The significant overlap of all the trajectories indicates excellent model fits to the baseline trajectories. Cart – Cartesian based NSP; Pol – polar based NSP; JA – joint angle based NSP; Human – subject; SV – Stiff -Viscous controller. These conventions are used throughout chapter 3.

42
response. This spatial discrepancy was present throughout all the different subjects and will be discussed in a subsequent section. Among the NSPs the polar model was more spatially aligned to actual human trajectories than either the joint angle or Cartesian based models.

To further examine the differences in model performance compared to human movement we investigated the predicted time series for each dimension of movement across subjects and spatial locations (targets).

**Time Series Analysis.** Perturbations were modeled as inputs to the control system as they were programmed into the task, i.e. as step functions. Perturbations were “turned on” once a subject had reached a tangential distance of 6cm away from the origin of movement and was an observable shift of the 2D cursor representing the hand position and thus was modeled an input perturbation to the brain’s visuomotor controller.

![Figure 9. Predicted model responses to visuomotor perturbation plotted along with actual human trajectories.](Image)
Previous work has suggested that motor planning is done in a polar coordinate system centered at the starting point of the reach. We hypothesized that since planning was done in this coordinate representation then it is possible that feedback control is calculated in a similar space. To interrogate this question we modeled responses to experimentally imposed visuomotor perturbations in different coordinate systems and with different control system architectures. Using control system engineering metrics we compared model and human responses and reasoned that the model which most closely predicted
human responses was most closely related to what is actually instantiated in the brain. A sample time series for a polar and Cartesian perturbation to a single target is plotted in Figure 10. The black lines are the reference positions that the subjects hand had to obtain to complete the trial based on the visually displayed target and cursor. The large step in the reference line is the effect of the perturbation that was imposed when the subject had reached a tangential distance of 6cm. Actual time series for a movement in a given dimension of position (direction – top left, extent – top right; x – bottom left, y – bottom right) are the colored traces. Subject data is cyan while the other colors represent model predictions. The metrics that we used, ISE, MO, Tc, and Ts were derived from these traces for all subjects and models. From this perspective it is evident that the temporal considerations of movement indicate a more complicated feedback response than can be seen in simply the overhead spatial plots. And as these sample time series demonstrate, feedback responses predicted by the various models are qualitatively different. In our subsequent analyses we quantify this difference and determine which model on average performs most like human subjects.

To present a more generalized picture of how our analysis evolved figure 11 plots model metrics against subject metrics for all 10 subjects the x component of position in response to a Cartesian perturbation for a single target.
the polar based NSP predicted smaller overshoots than the other models based in Cartesian and joint angle coordinates. Among the NSP model types, the polar based If the models were 100% accurate in predicting subject responses they would fall on the black line ($y = x$). From these sample plots it is clear that the different models make distinct predictions for feedback responses. Spatially, the SV model was very far off from actual human performance, as evidenced by an ISE approximately 6-7cm$^2$ larger.
than human performance (figure 11, top left). This is somewhat expected given the counterintuitive trajectories seen in figure 9.

The responses of the NSPs were much closer to human performance and as can be seen in this particular example the polar based NSP (green) was the closest among them. Interestingly, the SV model predicted a critically damped response in this example as its MO was 0 for every subject (figure 11, bottom left). The NSPs had varied MO depending on the coordinate system in which they operated.

Figure 12. In order to reduce the high dimensionality of this experiment we converted metrics for each model into Z-scores and then summed them. As can be seen the SV model did well at predicting the Ts, however for other metrics the polar NSP model was the closest to human behavior.
For this particular example version was closer to its prediction of Ts than the others and this trend held up generally across the other dimensions and spatial locations. Temporally, the SV was surprisingly a much better predictor of the settling time than any of the NSPs as exemplified by the proximity of the SV line of best fit to the black line of subject equivalence. Finally, in this example the SV controller predicted a 30ms faster Tc than human performance, while the NSPs predicted a 30-40ms slower Tc.

Since it was clear that the models made distinct predictions in their feedback responses, we wanted to know which model was closest to human performance (black lines in figure 11). In Figure 12 we have plotted for each metric across spatial locations, dimensions of movement, perturbation types, and subjects the composite Z score for each of the metrics. By representing each metric as the difference between model and human into Z space (eqn. 7) we were able to combine across the high dimensional experimental space and get a global picture of how well the models compared to each other in terms of predicting human responses.
As expected from the time series and spatial plots (Figures 9, 10) the SV controller was a very poor predictor of ISE and Mo. SV predictions for ISE and Mo were +15 and +3 standard deviations away from the mean difference between models and human responses respectively and were significantly greater than all the other NSP models $p$ values all < 0.001 for one tailed t test (figure 12). Among the 3 NSPs the polar based NSP had the lowest composite $Z$ score for both ISE and Mo, -5.2 and -1.3 standard deviations respectively which was significantly lower than all other model types, $p$ values < 0.01. The Cartesian based NSP had ISEs that were on average -4.8 standard deviations away from the mean while the joint angle based NSPs was -4.9 standard deviations, there was no significant difference between these two models, $p$ value = 0.46. Among the NSP model types, the most dramatic differences arose when examining the composite
scores across perturbation types. As shown in Figure 13 after combining all the metrics across subjects, the Cartesian and joint angle based models do quite well at predicting the feedback response for Cartesian perturbations. However in the face of polar perturbation the Cartesian and joint angle based NSPs do quite poorly and therefore when examined across perturbation types, the polar model ends up being the most human like controller. This is interesting as it suggests that the polar based model is better at a dynamic response than are the Cartesian and joint based controllers since when there is a mismatch between coordinate system of control and that of the perturbation it is essentially a test of dynamic response. In other words a Cartesian perturbation is a dynamic polar perturbation and a polar perturbation is can be viewed as a dynamic Cartesian perturbation.

The final summary figure 14 shows the average Z score for the composite metrics across all dimensions of the experiment. As shown by this figure the NSP controllers do a much better job of describing human feedback responses than the SV controller. The SV controller is 4.43 standard deviations above the average difference between human and model performance.

This difference was significantly larger than all the other NSP controllers with p values < 0.001. Within the subtypes of NSP, the polar model was -1.235 standard deviations below the average model difference whereas the Cartesian and joint angle models were – 0.73 and -0.74 standard deviations below, respectively. The polar model was significantly less than the other 2 model types, p values < 0.001. The Cartesian and joint
angle models were not significantly different.

Discussion.

Generally, the NSP was a much better predictor of human feedback responses than the SV controller. When we modeled the response to perturbation using the actual kinematics that were experimentally given to the subjects, the spatial aspects of the SV response predicted Ts quite well, however for the other metrics, it did not. The Ts that the SV model predicted was much closer than the other models, and may be in part due to the fact that the SV implements control based on actual dynamics of the arm and not an estimate derived from the baseline trajectory unlike the NSP model. Therefore, it is entirely reasonable to consider that perhaps part of visual feedback control implemented by the brain takes into account this internal model and adjust corrections accordingly. In

![Composite Z-Score](image)  

*Figure 14. Summed across all the metrics the polar model has the most negative Z-score indicating that is closest to human performance.*
fact, the use of an internal model may in fact be of use in the NSP to make it a more functional model of human motor control. Behaviorally there is certainly evidence that the brain uses an internal model both for its feedforward and feedback control (Mehta et al 2002, Wagner et al 2008).

Despite the exemplary prediction of Ts by the SV model, the trajectories that the SV model predicted were often dramatically different from those predicted by the other models and actual human behavior, see figure 9. When we examined why this might happen we noted that at the time of perturbation, the velocity of the hand is essentially infinite since there is a step perturbation. When this occurs, the viscous component of feedback torque spikes to quite a large value since it is comparing apparent velocity (near infinite at the time of perturbation) to a desired velocity. To investigate this issue we low pass filtered the perturbation to determine whether or not that rapidness of the step perturbation caused the counterintuitive trajectories and responses seen in figures 9, 10, and 11. After low pass filtering the input perturbation and multiplying the given stiff and viscous values by a free parameter we were able to generate more human-like trajectory. Without these adjustments however, the SV model was not a good model system for online feedback control. To us this suggests that the brain likely does not use a model of the arm’s stiffness and viscosity to generate a corrective command to visual perturbations.

The NSP models were reasonably accurate in predicting the timing of feedback control, as well as the spatial components of the response. By using the baseline trajectory to fit
the basis functions, the model was able to capture the spatial dynamics of each movement and then when perturbed and to use the incorporated feedback term to naturally implement control. Among the NSP’s the polar based model was the best performing across all metrics, spatial locations (targets), and dimensions of movement. In conjunction with our previous study then it seems likely that the brain parses the position of the hand into direction and extent channels when comparing its position to the target and uses that relative position signal to control the hand. Previous work with the NSP as a robotics controller allude to this choice of coordinate system by demonstrating that when at least one dimension of movement is along the line of the target value, generalization to other spatial locations is much better (Ijspeert et al in press). The reasoning behind this phenomenon could be that the interplay between feedforward and feedback signals in this type of coordinate system naturally establishes a more efficient controller. That idea is in part supported by the observation that the polar based model does a relatively better job at handling Cartesian perturbations than the Cartesian or joint angle based controller do at compensating for polar perturbations (figure 13). In each case the controllers are dealing with dynamic perturbations unlike the step perturbations for a native coordinate system (e.g. a Cartesian model correcting a Cartesian perturbation). Since the polar model does a better job correcting Cartesian perturbations this implies that it is better at responding to dynamic perturbations which suggests that it perhaps is a more efficient controller. The idea that a polar representation naturally leads to more efficient control for point to point reaches is discussed in chapter 3.
In this study, the NSP and SV feedback signal were not temporally delayed. Feedback control is necessarily delayed in that it takes processing time to determine the relative position, pass that signal, and subsequently allow that signal to be processed and implemented. Most studies cite this delay between 100 and 160ms (Desmurget et al, 2000, Saunders et al, 2003, 2004). When we first worked with the model we attempted to put this feedback delay into the model however the trajectories that were produced were unstable. In retrospect this was probably because of the manner in which we fit the model, because recently when we refit the trajectories with the delay in place, it worked. Those results will be examined more completely and used for subsequent studies. At the time of this study however we chose to change the gain on the feedback signal so that responses were more like human behavior. We justified this because modeling studies have demonstrated that the temporal lag of feedback is a considerable issue in the brain and have suggested that the visual feedback component of movement is weighted significantly less heavily than the feedforward component (Sabes, 2000). In our preliminary investigations it was quite apparent that underdamping the feedback signals made trajectories much more like those of the subjects. Critically, under weighting the feedback signal works well in a polar based system compared to other coordinate frames because the control signal is essentially just transforming error into movement (see chapter 3), so dampening does not affect it as significantly if it were being combined with a real valued, dynamic feedforward component.

Although the brain has no explicit notion of coordinate system, its spatial representation
during point to point (straight-line) has properties like a polar coordinate system. This may not be true for all tasks involving the upper limb, in that they would not be optimally described in a polar based system, e.g. stirring a pot. Indeed, previous work has demonstrated the flexibility of motor control by demonstrating the seeming ability to change coordinate systems given task demands (Heuer et al 1998).

At the highest level of control, the brain must continuously subtract the current hand position from the position of the target in order to update and pass that value to a visuomotor controller in order to generate a corrective command. Our data from this experiment suggests that this subtraction is done in a polar coordinate system. Furthermore, the direction and extent of the hand position are independently processed and controlled during the course of a reach to correct for unanticipated perturbation.
Introduction

Our previous behavioral studies have extended previous observations by suggesting that online feedback responses to visual perturbations suggest the use of a polar coordinate representation of movement space. In this particular study we sought to understand how the nature of the spatial representation affects the visual control of the hand. We used the Next State Planner (NSP) developed by Ijspeert et al for robotic mimicry to examine the contributions of feedforward and feedback control of the hand in different coordinate systems. We found significant differences in how a controller might putatively implement closed loop control of the hand depending strictly on the coordinate system used to represent the position of the hand and target.

At its core the NSP generates a change in hand position as an integrated combination of a nonlinear feedforward component (2\textsuperscript{nd} term of eqn 2) and a linear feedback component (1\textsuperscript{st} term of eqn 2) that relays the relative position between the current position of the hand and the goal of the reach. This is an appealing system of equations because it implements control in the same way that one generally considers motor control in the brain by initially forming a motor plan (nonlinear feedforward signal) which is constantly modified by an ongoing visual feedback signal (Gritensko et al 2009, Sabes 2000). In this manner, the equations that define the NSP form a closed model system of visuomotor control and permit the interrogation of signals that comprise this model to develop hypotheses about how the brain’s representation of space might influences its control.
signals and ultimately the trajectory of the hand. The feedforward signal is comprised of base model dynamics and a normalized, nonlinear sum of Gaussian basis functions the weights of which are fit for each model and target position multiplied by internal state $v$, the second term in equation 2. Importantly the bases are centered at equally spaced intervals throughout movement completion, thus they can make different contributions through time. The feedforward signal is summed with a feedback signal that is captured by equation 1 where the relative position of the hand and target are used to generate a linear feedback response whose dampening is controlled by the $a_z, b_z$ time constants. A complete discussion of the model is available in Ijspeert et al 2002.

One of the appealing features of the NSP is its ability to be implemented in different coordinate systems utilizing the same base equations (Ijspeert et al 2002). In chapter 2, we embedded the NSP in different coordinate systems and modeled its responses to perturbation. To our surprise the polar based NSP most closely mimicked human responses to imposed visuomotor perturbations. To get a better understanding of how this difference arose we decided to investigate how the choice of coordinate system might influence the implementation of positional control. Specifically, we examined the feedforward and feedback control signals in the different coordinate systems to see if we could determine what differences in control were manifested from differences in spatial representation.
NSP implementation

**Fitting.** We fit the 25 weights for the Gaussian basis functions using a nonlinear least squared error fitting (lsqnonlin in Matlab) to human trajectories to a specific target in either Cartesian or polar coordinates. Therefore for each coordinate system we had 2 sets of 25 weights (x and y, direction and extent). As Figure 1 shows, no matter what coordinate system the movement was represented in, the NSP was able to completely describe the baseline movement.

![Model Fits](image)

Figure 15. Baseline model fits, using the original 25 weights described in Ijspeert et al. Both models were able to fully capture human movements as demonstrated by the significant overlap of the model trajectories with human reaches (blue)

In the original development of the model, the NSP uses 25 bases to describe a trajectory; however we became interested in how the number of bases contributed to the overall fit
of the models in each coordinate system. To do this we refit the trajectories with a variable number of bases ranging from 2 – 25 and examined the amount of error in the fits as a function of the number of bases. Interestingly when performing this analysis the number of bases is highly dependent on the coordinate system used to model the reach. It takes fewer bases in a Cartesian representation than it does a polar representation of the same reach. The trajectories in Figure 16 show how the number of bases had a dramatic impact on the baseline reaches. As evidenced by these trajectories, the number of bases need to accurately describe a movement is coordinate system dependent. Figure 17 shows the amount of error as a function of the number of bases. It shows that representing the reach in a Cartesian system requires fewer bases for a given amount of error than does a polar representation. This is interesting because it suggests that there is a resolution requirement necessary to control a trajectory in a polar coordinate system.
that is not present in a Cartesian based representation. To investigate this point further we began to examine which bases were most active, i.e. 1-25, in the different coordinate systems. The most active bases were those with that had the highest absolute value of weight meaning they dramatically influenced the nonlinear component of the feedforward signal. Since each dimension, x and y, direction and extent, were independently fit to their respective time series we were able to examine which bases were most active for each dimension of movement the results are summarized in figure 18. For the x component of position in the Cartesian based NSP the most active bases were the ones centered near the latter part of movement (bases 18-22).

![Figure 17](image.png)

*Figure 17. The amount of error to fit a trajectory as a function of the number of bases used to fit. The Cartesian model requires fewer bases but the two types of models quickly become equivalent as the number of bases*

When performing the same analysis on the directional component of position in the polar based NSP the most heavily weighted bases were those near the very beginning of
movement bases (2-5). This difference was significant p value < 0.01 using a permutation test.

Figure 18. Bases are equally spaced in movement completion. 1 is the earliest and 25 is the latest. As is shown by this figure the major difference between these coordinate system implementations is the timing of bases in the first dimension. Clearly the bases controlling direction are active far earlier than those controlling the x component of position. 2nd dimension timing is equivalent between the two coordinate systems.

Figure 19. The Cartesian based NSP (left) could be fit to all target locations using a single set of weights, while the polar based model (right) could not. In each subplot the blue line represents the trajectory made with weights fit to the straight ahead target, magenta is the actual human reach that was fit, and the red line is the trajectory based on a single set of weights for all target locations.
When examining the orthogonal dimension of movement, y or rho, there was no significant difference in terms of the base timing reflecting the dynamic nature of these dimensions of movement. Given these interesting differences between the number and timing of bases depending on coordinate system, we decided to investigate how specific to spatial location were the weights governing the basis functions. In our instantiation of the NSP we fit a set of weights for each target individually. When we tried to fit all the trajectories at once and generate a single set of weights we found an interesting coordinate system dependency. The Cartesian based models were better at generalizing to other spatial locations than the polar model. In other words, one set of Cartesian weights could perform movements to a number of spatial targets well, while this was not the case for polar. This can be explained when considering the time series for each of these dimensions of movement.

Figure 20. Weights for an all target fit versus weights for a single target fit (x-axis) in polar and Cartesian coordinates. Note the wide range of single target fits in the polar system versus those in the Cartesian system. The black line in each plot is y = x and thus would indicate individual and all target fits being equal.
For a Cartesian based system the initial starting conditions are generally similar in that X and Y are always close to 0 for a given reach. This is not true for polar in that the direction can take on an infinite number of values at movement initiation, therefore when fitting a particular polar trajectory the base selection becomes specific to an initial start and target combination. This problem can be alleviated by foreshortening the actual time series of direction. The polar model required weights specific for each target it was reaching toward to be accurate. Figure 19 shows trajectories for a single target comparing weights that were fit for that particular target to those fit for all targets at once. For the Cartesian model it was clear that the single target fits (blue) generated comparable trajectories to the all target fits (red). This was not the case for the polar model where single target fits were clearly much better at producing trajectories than the all target fits. Since there was clearly a significant difference in the ability of the NSP to generalize depending on the coordinate system in which it operated we compared the numerical differences between the individually fit weights and the all target fit weights. As figure 20 shows, there is a much larger range for polar weights (x-axis range vs. y-axis range) than there is for Cartesian which contributes to the ability of the NSP based in Cartesian coordinates to fit a wide range of target locations. We reasoned this occurs because of the nature of the coordinate system. When considering the time series for theta, at the time of movement there is often times a numerically large error signal (imagine you need to go 90° but are at 45°) that is quickly reduced as time progresses. This is possible because the onset of movement, extent = 0 and therefore the hand can be
at an essentially infinite number of non-zero directions and still be at the origin. This generates a wide range of initial error that is specific to a given starting position. Conversely, in a Cartesian coordinate system, by definition the beginning of movement will always be close to 0 at the origin for both x and y. Thus in a polar coordinate system, the initial error changes drastically with each change in target location and starting position and therefore require highly active bases early in movement to make accurate reaches.

Figure 21. Signals underlying the two NSPs in their respective coordinate systems Cartesian (top row, x-left, y-right), polar (bottom row, direction-left, extent-right). Perturbations were applied by 15% of movement completion. Note how the output signal more closely follows the polar feedback signal than does the Cartesian based model. These differences are quantified in Figure
From our initial investigations into the general working of the unperturbed NSP in polar and Cartesian coordinates we observed: 1) more bases were required to fit a polar trajectory than Cartesian, 2) that the range of weight values for polar was much larger across different targets than Cartesian, and 3) that the most active weights in the polar system were those in the beginning as compared to the Cartesian which were more active in the latter part of movement.

It seemed likely then that the control signals under perturbation would reflect these differences. Specifically we reasoned that since there was an earlier activation of weights in the beginning of the polar based NSP feedforward signal that post perturbation it was likely that the polar model would be largely feedback driven.

In other words, since in eqn 2 the output of the model is the sum of feedback and feedforward terms, and maximum activation of the feedforward signal occurs early in movement control in the latter portion of movement has a greater contribution from feedback. To first examine this issue we looked at the component signals in the NSP in response to a perturbation applied at 6cm radial distance from the origin (as was done in our previous study). Since movement times were variable, we sampled the signals at various percentages of completion in figure 21. As can be seen by these traces there are interesting dynamics between the signals. Dimensions of movement which are dynamic show significant contributions from both feedforward and feedback control signals.
For example, the top left plot shows that the X position of the hand is equivalently comprised of feedforward and feedback components early in movement and eventually becomes more feedback dominated. In contrast, in the bottom left plot, hand direction is completely feedforward driven until after the perturbation when the feedback and output signals essentially overlap, suggesting that the vast majority of control output is derived from feedback signaling.

Figure 22. A comparison between the Cartesian and polar NSP using the feedback control metrics we used to quantify model responses. ISE was normalized the maximum ISE across both model types to allow us to combine across spatial dimensions. Otherwise the metrics are averaged across perturbation types and target locations. For each metric compared the polar based model was smaller indicating more efficient control (see text).
If the model output in a polar coordinate system has a greater contribution from feedback than a Cartesian based model then feedback responses in the polar based NSP should be more effective than those in a Cartesian NSP. To address this issue we quantified the feedback responses to imposed perturbations. Specifically we used the ISE, MO, Tc, and Ts from chapter 2 to compare the performance of the Cartesian NSP to the polar NSP.

We reasoned that a more effective controller would have: 1) less integrated square error, meaning that it ran closer to the ideal response, 2) smaller MO, less overshoot, 3) a faster time of corrective control initiation, and 4) a faster settling time. When we averaged these metrics across the experimental space we found those differences.

It was necessary to normalize the ISE by the maximum value across both model types so that we could combine ISE values over spatial dimensions. As can be seen by the top right plot in figure 22, the polar model had a smaller normalized ISE than the Cartesian model (0.64 vs 0.68 respectively). The settling time was 15 ms faster for the polar model than the Cartesian model, while the time of corrective control initiation was only 2.4ms faster. The largest difference was in MO where the polar model had a 10% smaller maximum overshoot compared to the Cartesian based NSP.

Discussion

Using the NSP as a model control system for the brain’s visual closed loop control of the hand has demonstrated some key features of that control that are dependent on coordinate
system representation. Several empirical studies of human psychophysics and direct neurophysiologic recordings have suggested that the brain may use a polar-like representation to compute point to point reaching movements. Our mathematical description of control in various coordinate systems points out features that would be necessary to enact that type of control.

If one accepts the NSP as a model system for high level control, the coordinate system in which movement is represented makes specific implications for how control is implemented. In a polar based coordinate system, the directional component of position is controlled and fixed very early in movement, as would be expected for controlling an object that moves in straight lines. In order to accomplish this, a feedforward signal would have to be generated very early in movement to bring the hand to the reference value and then subsequent feedback responses could fine tune and bring the hand directly to the target. This is supported by the significant difference in the timing of the most active bases in the different coordinate systems. For the polar based controller the most active bases are near 5 meaning that they are the ones most closely centered to the onset of movement. The Cartesian based controller has its most active bases much later. When we interrogated the nature of the feedforward and feedback signals in their respective coordinate systems we discovered that after perturbation, the output of the polar based NSP is primarily comprised of the feedback control signal. This allows for more feedback driven control as a natural consequence of the representation in space and may
explain why this polar model was closer to human performance than the Cartesian based NSP.

Additionally, we investigated the proposition that if a polar based representation leads to naturally more effective feedback control, then that should be reflected in metrics of feedback response. Using the metrics described in chapter 2, we discovered that in fact, a polar based NSP outperforms the Cartesian based NSP (figure 11). The differences were quite small, however this is because we combined metric scores across dimensions and therefore when we averaged the extent and direction feedback control metrics, the advantage of a static dimension of movement (direction) was effectively washed out by combining its control with that of a dynamic dimension of movement, extent. Despite this averaging however, the polar based controller still demonstrated less error and overshoot and also corrected and settled on the target value more quickly.

Although generally this NSP implementation uncovered some interesting findings there were a few problems with the interaction between feedforward and feedback signals. For some simulations we independently removed X, Y, direction, and extent feedback signals, the first term of eqn 2, by essentially setting z to 0. When we examined the trajectories produced by those simulations the movements were somewhat unnatural. For example, without rho feedback reaches were consistently undershot by as much as 60%.

This suggests that the model fit then depended on visual feedback of extent from the very beginning of movement which can be seen in figure 21. There is a significant non-zero
contribution of feedback from the very beginning of movement. This was a constant feature of dimensions that were dynamic throughout movement, (X,Y, and extent). Therefore when modeling these reaches without feedback contributions, odd trajectories were formed since they did not have the feedback necessary to generate the appropriate output. Interestingly, model simulations with no feedback of hand direction were very much like those from our empirical study (chapter 1, AH), however, this is derived from the fact that the majority of hand direction is controlled via feedforward signal in a polar representation (figure 21). In future applications of this model, fitting the weights of the feedforward signal to reaches made without visual feedback and then refitting trajectories would solve this issue and make the model simulations more realistic (discussed further in the general discussion).

Although the Cartesian and polar coordinate systems contain the same spatial information, their representation through time makes a difference in the way feedback control is implemented. This study suggests that if one considers high-level control of the hand to be the sum of feedforward and feedback signaling then the optimal way to describe space for point to point reaching is in a polar coordinate system.
General Discussion

The experiments described in the previous chapters were focused on examining how the spatial representation the brain uses to control upper limb reaching influences the control that it imparts in real time. The common theme through the first two chapters is that humans seemingly behave as if the coordinates in which they process point to point reaching movements is in a polar coordinate space centered at the origin of the hand. In the first study when we provided visual feedback of either direction or extent, people controlled those components of hand position in the same manner as when both dimensions of feedback were available. To us this suggests that the brain parses the direction and extent components of visual relative position between the hand and target and independently uses those values to implement control. This was a robust finding given that at times the differences between trajectories were quite large. For example, when comparing the time series of direction they were similar for the RH and FH hand conditions, suggesting that the presence (FH) or absence (RH) of extent information did not influence the control of direction. The same was true for the control of extent when comparing the AH and FH conditions. The negative controls in that experiment also supported the separation of direction and extent information as the time series of direction in the AH and NH conditions were equivalent despite the presence (AH) or absence (NH) of visual extent signals. While several previous experiments have documented an independence of direction and extent specification with respect to motor planning and sensory transformation (Gordon et al 1994, Soechting and Flanders
1989, 1992, Bagesteiro et al 2006) to our knowledge this is the first time differential control of a 2D movement system in polar coordinates has been explicitly tested.

When we modeled high level control of the hand using the NSP in different coordinate systems, people responded to perturbations most like a controller based in polar space. Conversely the SV model made feedback predictions that were completely different than human responses, suggesting that the control architecture in the SV model was not analogous to the control implemented in the brain. With that in mind we decided to dissect the signals that comprise the NSP and examine what might be contributing to the differences in feedback responses since the only difference between the models was the coordinate representation of space. Although Cartesian and polar coordinate systems contain the exact same spatial information (i.e. every point in space can be described by both coordinate systems), their graphical and numerical representations vary. Cartesian coordinate systems have dynamic dimensions throughout their duration of movement, i.e. x,y are constantly changing throughout the course of a point to point reach. This is not true of a polar representation in which the first dimension, direction, is static for the duration of the reach. If one is reaching at a 45° angle in a straight line, that angle becomes fixed for the entirety of movement, while the orthogonal dimension, extent is dynamic. The advantage of a coordinate system representation in which at least one dimension of movement is static arises when one considers the control system as a whole. Control of the moving hand is likely a combination of a feedforward, motor plan combined with an ongoing feedback signal (Desmurget et al 2000, Sabes, 2000,
Gritsenko et al 2009). If one accepts that to be true then it follows that feedforward control of direction must be established very early to get the hand traveling along the correct direction very early in the movement. This was supported by findings in chapter 3 that showed significant activation of bases very early in movement for direction whereas they were much later for other dimensions (figure 18). After feedforward control of direction has been established then the forward signal becomes static and quiescent since the reference value has been achieved. Therefore, in the face of perturbation, any change in feedback gets combined with a static, non contributory forward signal, which then is transmitted to downstream actuators. Therefore in the face of perturbation, the output of the control system is largely dominated by feedback signals since the feedforward component is essentially 0. This means that the generation of the change in hand position in the NSP is almost solely derived from feedback control as opposed to another coordinate system in which a dynamic feedforward and feedback signal are combined. In a Cartesian based system the underlying change in hand position has contributions from feedforward and feedback signaling throughout movement, and therefore by necessity is less efficient. Indeed a qualitative examination of the feedforward and feedback signals suggest that in a polar coordinate space, the output of the control system after perturbation is largely comprised of feedback contributions. When we quantified what this meant in terms of feedback responses we demonstrated that the polar based model exhibited better feedback responses than the Cartesian controller. This is very interesting because it would suggest that the brain establishes a
coordinate system for point to point reaching in which it takes advantage of the representation of spatial information to impart control.

Although generally our experiments were a success there are a few places that could use improvements. In chapter 1, we removed visual feedback of direction and extent. This essentially uncovers the motor plan for those dimensions. In the NSP framework this would ostensibly represent the nonlinear feedforward signal. Ideally one would separate out the components of the NSP and fit the basis functions for the forward signal to the trajectory from these experiments. Using the weights from that fit then, one could then fit a nonlinear feedback term to a control movement and get a better estimate of a dynamic, nonlinear feedback term. Previous studies suggest that there is nonlinearity in visual feedback control (Desmurget et al 2000). This would provide a more accurate assessment of the control being implemented and may make the model predictions closer to human performance.

Additional improvements could be also be made by introducing terms that would weight the contribution of hand and target information. Some studies have shown that people respond differently to perturbation when there is a change in the visual hand position from when there is a change in target position (Sarlegna et al 2003). This perhaps could be due to proprioceptive information contributing to the determination of hand position which is absent for the target, or because the target is generally foveated during a reach with the hand remaining in peripheral vision (Bedard et al 2004, Lawrence et al 2006).
We consider the latter possibility more likely since the loss of proprioceptive feedback can almost be completely compensated for by utilizing visual feedback (Ghez et al 1995). The NSP assumes an equal contribution of the target and hand position to determine its feedback response, which could be adjusted by introducing weighting terms to both and performing an experiment where each is removed independently to select the appropriate weighting scheme.

Our studies assume that feedback control and motor planning are both based in hand-centered reference frames. This assumption stems from the studies cited in which errors generated in reaches made without concomitant vision of the hand show alignment with a coordinate space centered at the starting location of the movement (Gordon et al 1994). Other studies have suggested that the brain may use an eye-centered or shoulder-centered reference frame and that specific regions of the brain have the capacity to perform reference frame transformations (Carrozzo et al 1999, McIntyre et al 1998, Buneo et al 2006). Our experiments were not sensitive to differences in reference frame. In chapter 1, we fixed the reference frame for visual feedback by centering the ray and the arc based on the starting location of the reach. Therefore, the mean error and the distribution of error were in some way fixed. Even if the brain used a different reference frame for online control versus planning, it would not be evident from that experiment because subjects would necessarily generate responses along the dimensions of feedback provided in the RH and AH conditions. However, since the time courses of the FH and NH conditions seemingly matched the single dimension feedback conditions, we are justified
in this assumption. Indeed if the brain were using another reference frame to impart visual feedback control the time series of direction and extent in the FH condition compared to the RH and AH conditions respectively would not match. This is because in the FH condition the control of direction and extent during the course of movement would be aligned with the native reference frame used for control and necessarily not match those in the experimental conditions. While we did see some significant differences between positive control condition and the experimental conditions, they were remarkably small and below the threshold of human detection, and therefore we consider them to be biologically insignificant and not evidence for a transitioning reference frame (Ghez et al 2007, van Beers 2002). In chapter 2 the control models operationally used the same definition of position (i.e. the origin of all coordinate systems being the starting point of movement). However the conclusion of that experiment was that visual feedback control of the hand was most closely imitated by a controller that operated in a polar coordinate system. This conclusion is resistant to differences in reference frame. The polar based model as discovered in chapter 3 operates more efficiently because of the definition of the coordinate system. Even if closed loop control of the hand utilizes a different reference frame, the coordinate system that is used likely has similar properties to that of the polar based representation. In other words point to point reaches even as defined by another reference frame, likely have some dimension of position that is static throughout the course of movement to take advantage of that representation when implementing feedback control.
For normal point to point reaching behavior and to compensate for unanticipated perturbation, the brain has to use some representation of space to compute the distance of the hand from the target. This signal is used to implement visual feedback control of the hand and ensure that the reaches are accurate and precise. Our research suggests that the brain represents the spatial difference between the hand and the target in a polar-like coordinate space, and furthermore, independently controls the direction and extent of the hand. In this manner, the brain naturally optimizes a feedback strategy that takes advantage of the representation of movement space.
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