Title: Stiffness, not inertial coupling, determines path curvature of wrist motions

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Running Head: Stiffness determines path curvature of wrist motions

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Abstract

When humans rotate their wrist in flexion-extension, radial-ulnar deviation, and combinations, the resulting paths (like the path of a laser pointer on a screen) exhibit a distinctive pattern of curvature. In this paper we show that the passive stiffness of the wrist is sufficient to account for this pattern. Simulating the dynamics of wrist rotations using a demonstrably realistic model under a variety of conditions, we show that wrist stiffness can explain all characteristics of the observed pattern of curvature. We also provide evidence against other possible causes. We further demonstrate that the phenomenon is robust against variations in human wrist parameters (inertia, damping, and stiffness) and choice of model inputs. Our findings explain two previously observed phenomena: why faster wrist rotations exhibit more curvature and why path curvature rotates with pronation-supination of the forearm. Our results imply that, as in reaching, path straightness is a goal in the planning and control of wrist rotations. That requires humans to predict and compensate for wrist dynamics but unlike reaching, nonlinear inertial coupling (e.g. Coriolis acceleration) is insignificant. The dominant term to be compensated is wrist stiffness.

Key words:

Wrist
Kinematics
Dynamics
Stiffness
Path
Introduction

Wrist rotations are essential for proper upper limb function but have received little attention, despite the fact that common disorders such as stroke often result in significant wrist impairment. To improve the assistance and rehabilitation of wrist function requires a more thorough understanding of wrist rotations, in terms of both biomechanics and neural control.

Wrist rotation paths exhibit a distinctive pattern of curvature (Charles and Hogan, 2010; Charles, 2008; Hoffman and Strick, 1999), but the origin of that curvature is unclear. This paper reveals the probable cause of this curvature pattern and what it implies about how the nervous system controls wrist rotations.

During wrist rotations, the hand draws paths on a roughly spherical surface surrounding the wrist joint. These spherical paths could \textit{a priori} be straight, like great arcs on a globe, or curved. We recently characterized the spatial characteristics of wrist paths between a central target (in neutral wrist position) and peripheral targets requiring flexion-extension (FE), radial-ulnar deviation (RUD), or a combination (Charles and Hogan, 2010). We found that while individual wrist rotations show substantial variability, \textit{on average} wrist rotation paths show an intriguing pattern of curvature: in general,

1. Outbound and inbound paths curve to opposite sides of a straight line (Figure 1).
2. Movements in the same direction but to opposite targets curve to the same side (for example, moves from an extended wrist position to neutral position, and moves from neutral position to a flexed position, both of which involve pure flexion, curve toward radial deviation—see Figure 1).
3. Fast movements are more curved than comfortably paced movements.

In addition, from a study by Kakei and colleagues (Kakei et al., 1999), we learn that:
4. The pattern of curvature rotates with pronation-supination (PS) of the forearm (Figure 1 of (Kakei et al., 1999)).

What is the origin of this pattern of path curvature? Is it intentional or unintentional? Is it neurally controlled or simply a consequence of wrist biomechanics? In this paper, we simulate various aspects of wrist dynamics and demonstrate that the observed pattern of curvature can be fully explained by the passive stiffness of the wrist joint. We also provide evidence against other possible causes, making stiffness the most likely candidate. Finally, we discuss what the observed pattern of curvature and its likely cause imply about how the nervous system controls wrist rotations.

**Methods**

To investigate the cause of the observed pattern of curvature, we simulated wrist dynamics under a variety of conditions, varying the contributions of inertia, damping, stiffness, gravity, and input torque to determine which of these parameters (if any) could cause path curvature. This section describes the model and parameters used to simulate wrist dynamics.

**Model of wrist rotation dynamics**

*Equations of Motion*

The pattern of curvature was observed in wrist rotations of moderate size (±15°). The dynamics of wrist rotations of this size are well-approximated by a set of two linear, coupled equations which can be written in matrix form as (Charles and Hogan, 2011):
\[ \begin{bmatrix} M_\beta & \gamma \\ M_\gamma & \beta \end{bmatrix} = \begin{bmatrix} I_\beta & 0 \\ 0 & I_\gamma \end{bmatrix} \begin{bmatrix} \ddot{\beta} \\ \ddot{\gamma} \end{bmatrix} + \begin{bmatrix} B_{\beta\beta} & B_{\beta\gamma} \\ B_{\gamma\beta} & B_{\gamma\gamma} \end{bmatrix} \begin{bmatrix} \dot{\beta} \\ \dot{\gamma} \end{bmatrix} + \begin{bmatrix} K_{\beta\beta} & K_{\beta\gamma} \\ K_{\gamma\beta} & K_{\gamma\gamma} \end{bmatrix} \begin{bmatrix} \beta \\ \gamma \end{bmatrix} - \begin{bmatrix} 0 \\ m g r \end{bmatrix} \]

where \( \beta \) represents wrist orientation in flexion-extension (FE; \( \beta \) is positive in flexion) and \( \gamma \) represents wrist orientation in radial-ulnar deviation (RUD; \( \gamma \) is positive in ulnar deviation). The matrices \( I, B, \) and \( K \) represent passive tissue properties: \( I \) is the inertia tensor of the hand about the wrist joint, and \( B \) and \( K \) are the passive damping and stiffness tensors of the wrist joint, respectively (due to the damping and stiffness of associated muscles and ligaments). \( M_\beta \) and \( M_\gamma \) represent the torque generated by active muscle contraction in FE and RUD, respectively (\( M_\beta \) is positive toward flexion, and \( M_\gamma \) is positive toward ulnar deviation). The last term accounts for the gravitational torque pulling the hand into ulnar deviation (\( m \) is the mass of the hand, \( g \) is the gravitational acceleration, and \( r \) is the distance from the wrist joint to the center of mass of the hand).

Because wrist inertia is well-approximated by a diagonal matrix, the equations of motion are coupled through the off-diagonal terms in damping and stiffness (\( B_{\beta\gamma} \) and \( K_{\beta\gamma} \)). In other words, the torque required to rotate the wrist in FE (\( M_\beta \)) depends not only on movement in FE (\( \beta, \dot{\beta} \) and \( \ddot{\beta} \)), but also on movement in RUD (\( \gamma \) and \( \dot{\gamma} \)), and vice versa (Charles and Hogan, 2011).

\textbf{Solutions to equations of motion}

By choosing the torques applied to the wrist (\( M_\beta \) and \( M_\gamma \)) and solving Equation 1 for wrist orientation (\( \beta \) and \( \gamma \)), we determined the effect of inertia, damping, stiffness, gravity, and
input torque on path shape. We solved Equation 1 using a numerical solver (ode45 in MATLAB) for convenience.

Some of the observed pattern of curvature is observed in the step response of a simplified model of wrist rotation dynamics in which the degrees of freedom of the wrist are not coupled \((B_βγ = K_βγ = 0)\):

**Equation 2**

\[
\begin{bmatrix}
M_β \\
M_γ
\end{bmatrix}
\begin{bmatrix}
\ddot{θ} \\
\ddot{γ}
\end{bmatrix}
= \begin{bmatrix}
I_β & 0 \\
0 & I_γ
\end{bmatrix}
\begin{bmatrix}
\ddot{θ} \\
\ddot{γ}
\end{bmatrix}
+ \begin{bmatrix}
B_β & 0 \\
0 & B_γ
\end{bmatrix}
\begin{bmatrix}
\dot{θ} \\
\dot{γ}
\end{bmatrix}
+ \begin{bmatrix}
K_β & 0 \\
0 & K_γ
\end{bmatrix}
\begin{bmatrix}
θ \\
γ
\end{bmatrix}
- \begin{bmatrix}
mgr
da_β \\
da_γ
\end{bmatrix}
\]

**Model Parameters**

To investigate the cause of the path curvature, we first simulated wrist rotation paths using our best estimates of the actual values of the model parameters and then investigated how changing various parameters changed path shape. The parameter values described in this section represent our best estimates of the actual values. The parameter values used in subsequent simulations are described in the context of each simulation in the Results section and are summarized for convenience in Appendix 1.

**Inertia, mass, and moment arm**

The values for \(m\) (mass of the hand), \(r\) (the distance from the wrist joint to the center of mass of the hand), and \(I_β\) and \(I_γ\) (moments of inertia of the hand about the wrist joint) used in this paper represent average values from six young, healthy individuals (3 male, 3 female; age range 19-28) who participated in a prior study (Charles and Hogan, 2010). The values were calculated from measurements of link lengths and the regression equations of de Leva (de Leva, 1996).
The mean values for $m$ and $r$ among the six subjects were $m = 0.37$ kg (range 0.28-0.46 kg) and $r = 0.060$ m (range 0.047-0.071 m). For our simulations, we used $m = 0.37$ kg and $r = 0.06$ m. The mean inertial values were $I_\beta = 0.0020$ kgm$^2$ (range 0.0010-0.0033 kgm$^2$) and $I_\gamma = 0.0022$ kgm$^2$ (range 0.0011-0.0038 kgm$^2$), and the ratio $I_\gamma/I_\beta$ (discussed later) was on average 1.12 (range 1.10-1.15). For our simulations, we used $I_\beta = I_\gamma = 0.002$ kgm$^2$ (making the off-diagonal elements of the inertia tensor equal to zero).

Most of the analysis in this paper deals with wrist rotations of the hand alone (i.e. the hand is not grasping any objects). In one part of the Results section, however, we compare our simulations to data from an experiment by Hoffman and Strick in which subjects were asked to make wrist movements while grasping an apparatus which increased the inertia of the wrist rotations (Hoffman and Strick, 1999). The inertia of the apparatus in RUD is reported to be 0.0025 kgm$^2$, and we estimated the inertia in FE to be 0.005 kgm$^2$, so the total inertia (hand + apparatus) used in those simulations was $I_\beta = 0.007$ kgm$^2$ and $I_\gamma = 0.0045$ kgm$^2$.

Stiffness

Several past studies have measured the passive stiffness of the wrist in FE (Axelson and Hagbarth, 2001; De Serres and Milner, 1991; Gielen and Houk, 1984; Leger and Milner, 2000), with values generally ranging from approximately 0.5 Nm/rad (Gielen and Houk, 1984) to 3 Nm/rad (De Serres and Milner, 1991). The passive stiffness in RUD was recently measured to be 1.5 Nm/rad (Rijnveld and Krebs, 2007). However, Equation 1 models wrist rotations in combinations of FE and RUD and therefore requires the passive stiffness in combinations of FE and RUD (i.e. the complete stiffness tensor $K$). This passive stiffness tensor was recently measured by Domenico Formica in our lab (unpublished data) on ten young subjects (3 female)
using a wrist rehabilitation robot (Krebs et al., 2007). Subjects relaxed their upper limb while the robot slowly (less than 11°/sec) rotated the wrist in 24 equally-spaced directions involving flexion-extension, radial-ulnar deviation, and combinations (17° in each direction). For each direction, stiffness was calculated as the slope of the force-displacement relationship in that direction. The four elements of the stiffness tensor were computed from an ellipse fit to the stiffness values in each direction. For the ten subjects in that study, the mean stiffness tensor was (mean ± standard deviation):

\[
K = \begin{bmatrix}
1.28 & -0.178 \\
-0.178 & 1.74 \\
0.421 & 0.0829 \\
0.0829 & 0.342
\end{bmatrix} \text{Nm/ rad}
\]

It is convenient to represent stiffness (and damping and inertia) graphically as an ellipse, where the ellipse represents the torque produced by a unit displacement (unit velocity or acceleration for damping and inertia, respectively) rotated about the origin (Mussa-Ivaldi et al., 1985). Each ellipse is characterized by its size, shape, and orientation, which can be computed from its underlying tensor (Dolan et al., 1993). Considering the stiffness ellipse in Figure 2A, two important properties of passive wrist stiffness are immediately apparent. First, the stiffness of the wrist is anisotropic, with greater stiffness in RUD than in FE. This was true for all ten subjects; the ratio of the major to minor ellipse axes was 1.58 ± 0.385 (range from 1.14 to 2.43). Second, the directions of greatest and least stiffness are not aligned with the directions of RUD and FE. Instead, the major and minor axes are rotated (in the direction of pronation) by 21.2 ± 9.2° (range from 8.8 to 37°) with respect to the RUD and FE axes. It is this misalignment which makes \(K_{\beta\gamma}\) non-zero and couples the degrees of freedom through stiffness.

The diagonal stiffness tensor \(K_p\) required for Equation 2 was obtained by rotating \(K\) to lie along the FE and RUD axes (Figure 2B):
Equation 1 also requires $B$, the tensor of passive damping coefficients in FE, RUD, and combinations. Unfortunately, measurements of passive damping throughout FE and RUD are not available in the literature. The only published measurement of passive damping in the wrist of which we are aware is for FE only: as part of their investigation of active damping in the wrist, Gielen and Houk measured passive damping in four subjects in FE alone and found values of 0.02-0.03 Nms/rad (Gielen and Houk, 1984). When combined with our estimates of inertia and stiffness above, this value of damping gives a low damping ratio (0.25 in FE) and much more overshoot than we observed in experiment. To match what we observed in experiment, we chose the damping coefficient in FE to be 0.064 Nms/rad (resulting in a damping ratio of 0.63).

To estimate the damping in combinations of FE and RUD (and not just in FE), we assumed that the damping ellipse has the same shape and orientation as the stiffness ellipse. We based this assumption on the facts that 1) passive stiffness and damping in this range of motion (i.e. away from the limits) are thought to be caused by the same phenomenon (stretching of relaxed muscles and tendons), and 2) several studies of the impedance of the shoulder and elbow have shown that, despite some minor differences, the stiffness and damping ellipses of the arm are similar, particularly in terms of orientation (Dolan et al., 1993; Perreault et al., 2004; Tsuji et al., 1995). Therefore, for this paper, we assumed a damping tensor proportional to the stiffness tensor, with $B = (0.05 \text{ sec}) \cdot K$:

$$B = \begin{bmatrix} 0.0640 & -0.0089 \\ -0.0089 & 0.0870 \end{bmatrix} \text{Nms/rad}$$
Importantly, we show in the Results section that the main features of the pattern of curvature are independent of damping. The diagonal damping tensor $B_p$ required for Equation 2 was obtained by rotating $B$ to lie along the FE and RUD axes (Figure 2B):

$$
B_p = \begin{bmatrix}
0.0610 & 0 \\
0 & 0.0900
\end{bmatrix} \text{Nms/rad}
$$

Results

Results are presented in the following order. First, we demonstrate that the model represented by Equation 1 reproduced the observed pattern of curvature. Second, we illustrate that it is the stiffness that causes the simulated paths to curve. Third, we show that the other model elements (inertia, damping, gravity, and input torques) are unlikely causes of the observed pattern.

A simple model recreates observed pattern of curvature

The simple mass-spring-damper model of the wrist (Equation 1) is able to recreate the pattern of curvature in all directions (compare Figure 1A and B). Outbound and inbound paths curve to opposite sides. Movements in the same direction curve to the same side as observed in experiment (for example, movements from ulnar deviation to the central target and movements from the central target to radial deviation, both of which involve pure radial deviation, curve toward flexion).

Effect of stiffness

The effect of stiffness is best illustrated in several steps (Figure 3):
Isotropic stiffness produces paths which are perfectly straight, with coincident outbound and inbound paths (Figure 3A).

Anisotropic (but uncoupled) stiffness produces paths which are straight in the cardinal directions (in pure FE or RUD) but curved in the diagonal directions (in combinations of FE and RUD), with outbound and inbound paths curving to opposite sides (Figure 3B). This phenomenon is explained in Figure 4.

Anisotropic and coupled stiffness produces paths which are curved in cardinal as well as diagonal directions (Figure 3C). The effect of tilting the stiffness ellipse is to couple the degrees of freedom, causing curved paths along all axes but two: the principal axes of the stiffness ellipse (Figure 5). When the orientation of the stiffness ellipse is aligned with a movement direction (i.e. at tilt angles of 0°, 45°, 90°, …), paths in that direction are straight (Figure 5B and F). At a tilt of 22.5°, the curvature is evenly distributed between the 8 movement directions (Figure 5D). The mean stiffness tilt measured in ten subjects was 21° (Methods), explaining why the magnitude of the observed curvature is similar in all four axes (Figure 1A). Note that the direction of curvature (i.e. the side to which the path deviates) in our simulations (Figure 5) matches the observed direction of curvature (Figure 1A) under certain conditions. If the stiffness ellipse is tilted by less than 45° in either direction (clockwise or counterclockwise), the simulation matches the observation in the diagonal directions. If the stiffness ellipse is tilted counterclockwise by more than 0° but less than 90°, the simulation matches the observation in the cardinal directions. It follows that simulation and observation match in all target directions as long as the stiffness ellipse is tilted counterclockwise by more than 0° and less than 45°. In the ten subjects measured for stiffness, the tilt ranged between 9° and 37° (counterclockwise), consistent with our simulations.
Because tilting the stiffness ellipse by less than 45° in either direction does not change the pattern of curvature in the diagonal directions (but simply modulates how much curvature is present), we can continue our analysis of path curvature by focusing on diagonal paths in the presence of un-rotated stiffness and damping (with zero tilt angle), resulting in uncoupled equations of motion (Equation 2) and greatly simplifying the analysis.

**Initial path direction**

The observed paths curve to one side of a straight line connecting start and end points and do not generally cross this straight line until the very end, if at all (Figure 1A). Therefore, the direction of curvature (i.e. the side to which the path veers) is largely determined by the path’s initial direction. As mentioned above, it is sufficient to investigate the diagonal paths in an uncoupled system (Equation 2). If the input torques are step inputs, the initial direction of the resulting diagonal paths can be shown to be (Appendix 2):  

\[
\frac{d\gamma}{d\beta} (t = 0) = \pm \frac{K_\gamma}{I_\gamma} \frac{K_\beta}{I_\beta}
\]

(positive for movements in ulnar deviation and flexion or radial deviation and extension; negative for movements in ulnar deviation and extension or radial deviation and flexion). Since stiffness is greater in RUD than in FE \((K_\gamma > K_\beta)\), stiffness causes the initial slope to lean more toward RUD than FE, as observed above.
Effect of inertia

The initial path direction—and therefore the direction to which the path veers—is inversely proportional to the ratio of inertias (Equation 3). A greater inertia in one direction will cause a relatively greater acceleration in the other direction, causing the path to accelerate initially more in the other direction. We calculated $I_\beta$ and $I_\gamma$ on six young, healthy individuals (3 male, 3 female; age range 19-28) using measurements of link lengths and the regression equations of (de Leva, 1996) (Methods). For these six subjects, the ratio $I_\gamma/I_\beta$ was on average 1.12 (range 1.10 to 1.15). The fact that $I_\gamma$ is slightly larger than $I_\beta$ would cause the path to start out toward FE, but this slight anisotropy in inertia is not large enough to overcome the greater anisotropy in stiffness (where the ratio of principal axes is 1.58 with a range from 1.14 to 2.43) (Methods), creating a mean initial slope which points toward RUD ($d\gamma/d\beta = 1.58/1.12 = 1.41$). Note that this phenomenon is quite robust: to neutralize the slope would require $I_\gamma/I_\beta$ to be 1.58, i.e. our estimate of $I_\gamma/I_\beta$ would have to be off by 41%. To reverse the phenomenon and cause paths that veer in the opposite direction (by the same amount) would require $I_\gamma/I_\beta$ to be 2.23, i.e. our estimate of $I_\gamma/I_\beta$ would have to be off by 100%.

Effect of damping

The pattern of path curvature can be reproduced by anisotropic and coupled stiffness, even if the damping is isotropic (Figure 3C). Therefore, anistropic damping is not necessary to reproduce the observed pattern. In fact, the initial slope of the path, which determines the side to which the path veers, is completely independent of damping (Equation 3). Although damping does not affect the direction of curvature, it does affect the amount of curvature, as demonstrated in Figure 3D and Figure 6.
Damping also affects the amount of overshoot by modifying the damping ratio, which is a function of inertia and stiffness as well. For an uncoupled system, the damping ratio in the FE direction is:

\[ \zeta_\beta = \frac{B_\beta}{2\sqrt{K_\beta I_\beta}} \]

(the damping ratio for the RUD direction is similar). The amount of overshoot in the step response of a second-order linear system depends only on the damping ratio and increases with decreasing damping ratio (Nise, 2000). Overshoot is increased when the inertia increases due to interaction with an object or manipulandum (if stiffness and damping remain constant). This phenomenon is simulated in Figure 7 and compared to data from an experiment by Hoffman and Strick (Hoffman and Strick, 1999) in which human subjects were asked to make wrist movements while grasping an apparatus which increased the inertia of wrist rotations. Our simulation (Figure 7B) shows that increasing the inertia to account for the apparatus (Methods) produces overshoot similar to that observed by Hoffman and Strick (Figure 7A).

**Effect of gravity**

The initial path direction (and therefore the side to which the path curves) is completely independent of gravity (Equation 3). The effect of gravity is simply to require a greater input torque in RUD (a constant torque) to overcome gravity. Ignoring gravity (and reducing the input torque in RUD accordingly) produces the exact same kinematics and path curvature, so gravity has no effect on the path curvature of our simulations.

**Effect of input torque**
For simplicity, the simulations up until this point have assumed that the torque inputs were step functions, but many other physiologically plausible torque inputs produce a similar pattern of curvature. In principle any trajectory, including a straight line, could be generated using an internal model of the dynamics equivalent to Equation 1; given any specification of $\beta(t)$ and $\gamma(t)$, differentiate and substitute to find $M_\beta(t)$ and $M_\gamma(t)$, the so-called inverse dynamics computations. The observations we are attempting to reproduce indicate that the biological controller does something much simpler, sending a similar time-course of activation to all muscles that produces the movement. A priori, the only constraint on the torque inputs is that their steady-state values be such that the path will end at the desired target. The final orientation produced by any input can be found by setting the derivatives in Equation 2 to zero:

**Equation 4**

$$
\beta_{ss} = \frac{M_{\beta,ss}}{K_\beta} \quad \text{and} \quad \gamma_{ss} = \frac{M_{\gamma,ss} + mgr}{K_\gamma}
$$

where the subscript ss denotes steady-state. For the path to end at any diagonal target requires that the absolute values of orientation be equal: $|\beta_{ss}| = |\gamma_{ss}|$. Combining with Equation 4 gives

**Equation 5**

$$
\left| \frac{M_{\beta,ss}}{M_{\gamma,ss} + mgr} \right| = \frac{K_\beta}{K_\gamma}
$$

In other words, for the path to end at a diagonal target requires that the ratio of input torques at steady-state (modified to account for gravity) match the stiffness ratio. If the time-course of variation of muscle activation is the same in all muscles, a similar ratio holds throughout the movement:
To satisfy Equation 6, $M_\beta(t)$ and $M_\gamma(t)$ are scaled and shifted versions of each other. Many such inputs cause path curvature remarkably similar to that produced by step inputs, as illustrated in Figure 8. Note that Equation 6 does not represent a necessary condition: many other, more complicated input torques (which do not satisfy Equation 6) will produce a similar pattern of curvature.

**Discussion**

When humans rotate the wrist in combinations of flexion-extension and radial-ulnar deviation, the resulting paths (like those produced on a screen while using a laser pointer) exhibit a distinctive systematic pattern of curvature. In this paper we showed that the stiffness of the wrist joint is sufficient to account for this pattern of curvature. We showed that with experimentally derived parameters a relatively simple model of wrist dynamics reproduces the observed pattern of curvature. Varying the model parameters, we showed that only the passive stiffness of the wrist, because it is anisotropic and misaligned with respect to the anatomical axes of the wrist, can fully account for the observation that paths curve to opposite sides of a straight line between targets, depending on the direction of movement.

Why are fast wrist rotations more curved than comfortably paced motions?
We propose that faster movements have greater path curvature because the neuromuscular system has insufficient time to straighten the path. To understand this hypothesis, consider the following two findings.

First, in an investigation of muscle activity associated with wrist rotations, Hoffman and Strick found that humans made wrist movements by modulating muscle activity in either of two spatiotemporal patterns, termed amplitude-graded and temporally shifted (Hoffman and Strick, 1999). Amplitude-graded muscle activity is very prevalent and consists of two bursts of muscle activity (an early agonist burst and a late antagonist burst). Because the wrist joint has many muscles acting on both DOF, adjusting the amplitude of the bursts changes the direction of the resulting movement. Temporally-shifted muscle activity is less prevalent and is characterized by a single burst of muscle activity occurring after the normal agonist burst but before the normal antagonist burst. Importantly, temporally-shifted muscle activity occurred in muscles which pulled in a direction perpendicular to the direction of the movement.

Second, Hoffman and Strick found that monkeys’ wrist movements displayed amplitude-graded muscle activity but not temporally-shifted muscle activity, and that monkeys’ wrist paths were much more curved than humans’ wrist paths, leading them to hypothesize that temporally-shifted muscle activity functions to reduce the amount of path curvature (Hoffman and Strick, 1999). However, the questions of why and how temporally-shifted muscle activity functions to straighten paths remained unanswered. If, as the work reported here indicates, stiffness is the origin of path curvature, it can explain why and how temporally-shifted muscle activity could reduce path curvature. In an anisotropic stiffness field, a path which starts out toward its intended target will veer off-target (Figure 4) unless an appropriate force is applied perpendicular to the direction of travel and toward the higher stiffness to “keep the hand on track” toward the target.
Such a force could be supplied by temporally shifted muscle activity, which Hoffman and Strick found to occur 1) not at the beginning or end but during the movement and 2) in directions perpendicular to the movement direction. In essence, temporally shifted muscle activity would act to keep the path from “slipping down” the stiffness gradient perpendicular to the movement direction (Charles, 2008). Thus, the current finding that path curvature is likely caused by stiffness also provides a reasonable mechanism by which temporally shifted muscle activity could serve to reduce path curvature, as hypothesized by Hoffman and Strick.

We therefore propose that faster movements have greater path curvature because the neuromuscular system has insufficient time to straighten the path. As movement duration decreases, the gap between the agonist and antagonist bursts of amplitude-graded muscle activity decreases, limiting the opportunity to insert a burst of temporally-shifted muscle activity and thereby reducing the ability of temporally-shifted muscle activity to straighten the path. With limited temporally-shifted muscle activity, fast movements must rely almost entirely on the agonist and antagonist bursts of amplitude-graded muscle activity. In the presence of stiffness anisotropy, the only way for amplitude-graded muscle activity to produce a path which ends on-target is to aim off-target (toward the stiffer direction) and rely on the stiffness gradient to curve the path toward the target.

Why does the pattern of curvature rotate with pronation-supination of the forearm?

Wrist stiffness reflects the combined elastic properties of the muscles and ligaments of the radiocarpal and intercarpal joints. Because the wrist resides distal to the forearm, its ligamentous structure rotates with pronation-supination of the forearm. Wrist muscles rotate with pronation-supination of the forearm as well (though not as much as the wrist joint itself (Kakei et
Therefore, as the forearm rotates in pronation-supination, the stiffness ellipse of the wrist (anisotropic and misaligned) rotates as well and can explain why the pattern of curvature changes with rotation of the forearm.

**Robust simulation**

The inertial and stiffness parameters used in our simulations (Methods section) represent our best estimates of the actual physical parameters. For mass, moment arm, and inertia, we used the average values from six young, healthy individuals who participated in a prior study. For stiffness, we used average values measured on 10 young, healthy subjects. Damping was chosen to match the amount of overshoot between our simulations and our observed data (Methods).

More importantly, the results presented in this paper are insensitive to modest inaccuracies in model parameters. For example, we showed that the direction of curvature (i.e. the side to which a path deviates) is independent of damping (Equation 3) and therefore unaffected by inaccuracies in the value of damping used in our simulations. While inertia and stiffness vary greatly between subjects (due to variations in body size), the direction of curvature depends on ratios (of inertia and stiffness in the two DOF) which remain quite similar between subjects of different body size. For example, while subjects’ inertia in RUD and FE ranged between 0.001 kgm² and 0.0038 kgm² (380% variation) the ratio of inertias only ranged between 1.10 and 1.15 (less than 5% variation).

The direction of curvature depends on the orientation of the stiffness ellipse but remains the same as long as the orientation of the stiffness ellipse is within a relatively large range (45°).

Furthermore, the mean orientation measured on ten subjects (Methods) was right in the middle of
this range (21°), i.e. far from where the direction of curvature would change, and the orientation of all ten subjects was within the range (9-37°).

Interestingly, according to Equation 3, inertial anisotropy affects intial path direction as much as stiffness anistropy, even though inertial effects are small compared to stiffness effects in wrist rotation dynamics in general (Charles and Hogan, 2011). Equation 3 is not specific to the wrist but holds for any 2-DOF joint whose dynamics can be approximated as linear and uncoupled (we decoupled the dynamics of the wrist by rotating to the principal axes of the stiffness and damping ellipses—the inertia ellipse is a circle and unaffected by rotation because the inertia tensor is symmetric). Thus, while proximal joints rotate larger inertias and are generally dominated by inertial effects, and distal joints rotate smaller inertias and are generally dominated by stiffness effects, the initial path direction would be the same if the ratio of anisotropies were the same and if the dynamics were linear and uncoupled. However, the dynamics of proximal joints are generally highly coupled through inertial interaction torques (Hollerbach and Flash, 1982), so Equation 3 does not generally apply to proximal joints.

**Active stiffness**

A limitation of this study is that it relies on measurements of passive wrist stiffness (stiffness measured in the nominal absence of muscle activation) even though the stiffness present during movements is a combination of passive stiffness and active stiffness—muscle activation is always accompanied by an increase in net stiffness which may be due to intrinsic muscle mechanics and/or local spinal reflex pathways (Hu et al., 2011). Unfortunately, measurements of wrist stiffness during movement are not available. However, this paper demonstrates the passive dynamics that the neuromuscular controller must deal with (through the
production of muscle force and active stiffness), and that the passive dynamics themselves (i.e. in the absence of correcting control) predispose paths to curve. In addition, there is evidence from studies of shoulder-elbow movements indicating that while the size of the stiffness ellipse increases during movement (due to the contribution of active stiffness), the shape and orientation of the stiffness ellipse tend to stay relatively unchanged (Mussa-Ivaldi et al., 1985). In this paper we showed that it is the shape and orientation (i.e. the anisotropy and misalignment) of the stiffness ellipse—not its size—that can explain the observed pattern of curvature.

Other candidate causes of path curvature

We showed that wrist passive stiffness is sufficient to explain the pattern of path curvature observed in wrist rotations. We have also shown quantitatively that inertia, damping, and gravity are unable to account for the curvature pattern. However, there remain other factors which might, in principle, cause path curvature: kinematic, neuromuscular, and feedback-related effects.

Candidate kinematic causes

The 2-DOF motion of the wrist can be approximated as a universal joint, resulting in non-linear equations of motion which could potentially cause path curvature. However, the pattern of path curvature was observed for moderately-sized wrist rotations (±15°), and we have previously shown that for wrist rotations of this size, the difference between the non-linear equations of motion of a universal joint and the linear equations used in this paper (Equation 1 and Equation 2) is negligible (Charles and Hogan, 2011).
Wrist paths lie on a roughly spherical surface surrounding the wrist joint, but the pattern of path curvature discussed in this paper is generally illustrated on paths which have been projected onto a plane (as in Figure 1), and this non-linear projection could, in principle, cause paths to appear curved. However, we have previously shown that the difference between the curvature of the actual, spherical paths and the curvature of their planar projections is negligible for the moderately-sized wrist rotations ($\pm 15^\circ$) in which the pattern of path curvature was observed (Charles and Hogan, 2010).

Finally, the kinematics of the individual carpal bones, which produce wrist motion, are complex and could, a priori, cause path curvature. However, such kinematic constraints are unlikely to cause different path curvature in outbound and inbound directions. Furthermore, it is very unlikely that the complex interaction of carpal bones would produce a pattern of path curvature which varies with movement direction as regularly and smoothly as the experimentally observed pattern (Figure 1).

_Candidate neuromuscular causes_

Path curvature could also result if muscles pulling in different directions pulled at slightly different times or rates. For example, if the muscles pulling in radial-ulnar deviation acted more quickly than the muscles pulling in flexion-extension (either because of a difference in the timing of neural signals or because of a difference in muscular dynamics), a movement to a target in radial deviation and flexion might start out toward radial deviation and then curve toward flexion. The inbound path would start out toward ulnar deviation and then curve toward extension, producing an oppositely curved path, as observed. While this example makes it appear
that differences in the timing of muscle activity might be the cause of the observed pattern of
curvature, there are at least two pieces of evidence against this hypothesis.

First, while Hoffman and Strick did observe differences in the timing of muscle activity,
the “temporally shifted” (i.e. delayed) muscle activity did not act in the right direction, but rather
acted perpendicular to the intended movement direction (see above). For example, for
movements involving flexion and some radial deviation, which curved first toward radial
deviation and then toward flexion, the temporally shifted muscle activity occurred in extensor
carpi radialis longus, an extensor muscle that acts perpendicular to the intended movement
direction (and even contributes to radial deviation).

Second, the strongest evidence comes from a study by Hoffman and Strick in which they
recorded the path produced by individual stimulation of five wrist muscles (Hoffman and Strick,
1999). Upon stimulating each muscle separately, the hand traced a path which was initially
straight but which invariably ended up curving toward flexion or extension. In other words,
while it is possible that the path curvature could be caused by differences in muscular or neural
timing between muscles, stimulation of individual muscles alone produces marked path curvature
which matches the experimental observation. Veering toward flexion or extension is fully
consistent with stiffness anisotropy: as the hand increases its deviation from neutral position, the
stiffness gradient perpendicular to the movement direction will cause it to turn away from the
stiffer direction (roughly radial-ulnar deviation) and toward the less stiff direction (roughly
flexion-extension), which is the “path of least resistance.”

The second argument also indicates that the observed pattern is not caused by differences
in strength between muscles acting in different directions. In summary, the available evidence
indicates that the observed pattern of path curvature is not due to differences in timing or strength between muscles acting in different directions but due to passive wrist stiffness.

Candidate feedback-related cause

Does visual feedback play a role in the generation or modification of path curvature? In our experiments, the pattern of path curvature was most prominent when movements were performed as fast as possible. Such movements were often composed of an initial, high-speed, high-amplitude movement, which placed the hand close to the target, followed by one or several later, low-speed, low-amplitude movements, which brought the hand to rest within the target boundary. Importantly, the observed pattern of curvature stems from the initial, high-speed, high-amplitude movements, not the later, low-speed, low-amplitude movements. For fast wrist movements, where path curvature was observed most prominently, these initial, high-speed, high-amplitude movements were often completed within 200 msec, making it very unlikely that visual feedback played any role in the generation or modification of the path curvature. Interestingly, none of the subjects who participated in the observations of path shape (Charles and Hogan, 2010) were aware of the curvature in their wrist movements.

Implications

The findings in this paper have four important implications. First, the fact that humans can make on-target movements in the presence of anistropic and misaligned stiffness implies that the neuromuscular system can predict and compensate for this stiffness. Both strategies discussed above—using temporally-shifted muscle activity (for slow movements) and the strategy of aiming off-target and relying on the stiffness to curve the
path toward the target (for fast movements)—rely on the ability to predict the dynamic behavior of the system. The strategy for fast movements (aiming off-target), in particular, relies on prediction (rather than feedback correction) because the aiming occurs before movement onset. This ability to predict and compensate for stiffness during wrist rotations is similar to the demonstrated ability to compensate for inertial interaction torques during reaching movements (Hollerbach and Flash, 1982). However, the dynamics are completely different. In reaching, inertial coupling torques are prominent; the terms depending on velocity are comparable to those depending on acceleration. Unimpaired humans learn to compensate for them, but patients with cerebellar damage exhibit incomplete compensation (Bastian et al., 1996). In contrast, in wrist rotations inertial coupling is irreducibly small. Instead, the coupling to be compensated arises from wrist stiffness. Whether patients with neurological disorders are unable to compensate for wrist stiffness is not known.

Second, Hoffman and Strick’s hypothesis that temporally-shifted muscle activity functions to straighten paths, strengthened by our explanation of why and how temporally-shifted muscle activity could straighten paths, implies that humans care (at least to some degree) that wrist paths be straight. This is consistent with many past studies of reaching movements which demonstrated that path straightness is a predominant factor (among others) in planning and controlling discrete movements.

Third, if temporally-shifted muscle activity acts to straighten paths, then the fact that paths are not perfectly straight implies that the observed curvature is either not perceived or not worth reducing. Wrist rotations, especially fast ones, exhibit a relatively large amount of variability in path shape (Charles and Hogan, 2010), and it is possible that the path curvature is not perceived amid the noise in path shape. In addition, the path of the hand during wrist
rotations (and therefore the path curvature) spans a relatively small angle in the visual field (e.g.
compared to arm movements) and may simply go unnoticed. Indeed, of the subjects who
participated in the observations of path shape (Charles and Hogan, 2010), none were aware of
the curvature in their wrist movements. If the curvature is perceived, it is possible that further
reduction (beyond what is accomplished through temporally-shifted muscle activity) is not worth
the effort. After all, if straightness of path is a factor in the control of wrist rotations, it is
certainly not the only factor.

Fourth, because passive stiffness plays a substantial role in wrist rotations, one might
expect a pattern of muscle activity slightly different from the usual tri-phasic burst pattern; in
movements from the neutral position outward, stiffness could (at least partially) replace the role
of antagonist muscles in braking movement and maintaining posture. In (Hoffman and Strick,
1999), antagonist activity does indeed appear smaller than agonist activity, as expected. Also as
expected, agonist activity is present during the third phase of the tri-phasic pattern (to counteract
the restoring effect of stiffness), while antagonist activity is small or absent during that phase
(since stiffness can fulfill that role). This is different from normal arm movements, which
generally occur far away from the limit of their range of motion, where passive stiffness is
relatively low. However, similar behavior has been observed when arm movements are made to
the end of their range of motion (Berardelli et al., 1996), where passive stiffness increases in
relative importance.

We have illustrated the effects of stiffness on path curvature for movements from or to
neutral position, and seen that the stiffness gradient causes curvature in all directions except
along the principal axes of the stiffness ellipse. However, we would expect wrist stiffness to have
a path-curving effect for movements between any two points within the range of motion of the
wrist, as long as the points do not both lie on the same principal axis (in which case we would
expect a straight path).

Conclusion

We have shown that a simple mass-spring-damper model of the wrist can recreate the
distinctive pattern of path curvature observed during wrist rotations, and that it is the stiffness of
the wrist—because of its anisotropic and rotated nature—that causes this pattern. Other possible
causes (including kinematic, neuromuscular, and feedback-related causes as well as other
mechanical causes) were unable to account fully for the observed pattern. Our results imply that
in wrist rotations as in reaching humans attempt to make straight paths; and that they predict and
compensate for anisotropic wrist stiffness, not inertial coupling, to do so.
1. Modeling wrist dynamics as a set of linear, coupled equations of motion approximates a more anatomically accurate model of the wrist as a universal joint with non-intersecting axes. For wrist rotations of ±15°, the approximation error is extremely small, only 0.80 ± 0.60% (mean ± std) of the maximum torque (averaged over wrist rotations of various speeds and directions).

2. These active torques are functions of displacement and its derivatives (as well as being functions of neural activation) because they include (in addition to pure torque) torques due to changes in stiffness and damping associated with muscle contraction.

3. The pattern of curvature described in the Introduction and depicted in Figure 1A was observed with the forearm in the horizontal plane, midway between pronation and supination, with gravity acting in the direction of ulnar deviation.
Acknowledgements

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References


Figure 1 A: Mean paths observed during fast wrist rotations involving flexion-extension, radial-ulnar deviation, and combinations (Charles and Hogan, 2010). Outbound paths (from the central target to a peripheral target) are in black, and inbound targets in gray. Paths which differed significantly from a straight line ($p < 0.10$) are designated by an arrow. The curvature of the arrow specifies the side to which the paths deviated. B: Paths simulated by Equation 1.

Figure 2: Ellipses representing the stiffness, damping, and inertia tensors used in the simulations with Equation 1 (A) and Equation 2 (B). The units are Nm/rad, (Nms/rad)/15, and (Nms$^2$/rad)/400 for stiffness, damping, and inertia, respectively (i.e. the damping and inertia ellipses were multiplied by 15 and 400 to be comparable in size to the stiffness ellipse).

Figure 3: Effect of stiffness and damping. A: Isotropic stiffness, damping and inertia (represented by circular impedance ellipses) produce equal outbound and inbound paths (the black outbound paths are underneath the gray inbound paths). B: Anisotropic (but uncoupled) stiffness causes curved paths in the diagonal directions. C: Anisotropic and coupled stiffness causes curved paths in all directions. D: Changing the damping changes the amount of curvature, but the pattern of curvature (i.e. the side to which paths deviate) remains unchanged. The paths and impedance ellipses in D are the same as in Figure 1B and Figure 2A, respectively. The scale of length 1 (for the impedance ellipses) has units of Nm/rad, (Nms/rad)/15, and (Nms$^2$/rad)/400 for stiffness, damping, and inertia, respectively (i.e. the damping and inertia ellipses were multiplied by 15 and 400 to be of comparable size as the stiffness ellipse).
Figure 4: Outbound and inbound paths between the central target (CT) and the peripheral target (PT) requiring extension and radial deviation. Outbound path OB1 starts out with an equal torque in extension and radial deviation, so its initial direction points directly from CT toward PT (because the stiffness torque is zero at CT). However, once the path has left CT, the stiffness is greater in radial deviation than in extension, and path OB1 soon veers toward the direction of lower stiffness (extension). To end up on target, the initial direction of outbound path OB2 points more toward radial deviation than extension, as illustrated. At PT, the restoring force due to stiffness (represented by the arrow) is greater toward ulnar deviation than toward flexion, so the initial direction of the inbound path (IB) points more toward ulnar deviation than toward flexion, causing the inbound path to curve to the opposite side of the outbound path (OB2). The dashed line indicates a straight line from CT to PT.

Figure 5: Effect of the orientation of the stiffness ellipse for seven orientations (represented by the angle between the major axis of the stiffness ellipse and the RUD axis). A: -11.25°, B: 0°, C: 11.25°, D: 22.5°, E: 33.75°, F: 45°, and G: 56.25°.

Figure 6: Five different damping ellipses (A) with corresponding outbound paths (B) between the central target (CT) and the peripheral target (PT) requiring extension and radial deviation. In all five cases, the stiffness and inertia ellipses (not shown) were kept the same as in Figure 2B. Note that damping affects the amount of curvature and overshoot, but the initial path direction—and therefore the side to which the path veers—is independent of damping.
Figure 7: Increased inertia decreases the damping ratio, resulting in increased overshoot. A: Data from an experiment by Hoffman and Strick (Hoffman and Strick, 1999) in which human subjects were asked to make wrist movements while grasping an apparatus which increased the inertia of wrist rotations. B: Simulated paths with stiffness and damping equal to that shown in Figure 2A, but with increased inertia to account for the apparatus used in the experiment by Hoffman and Strick.

Figure 8: Different time courses of input torques produce similar path curvature. A: Input torque $M_\beta$ (solid) and $M_\gamma$ (dashed) for step input (thin black), ramp input (thick black), and sigmoidal input (gray). B: Resulting displacement in $\beta$ (solid) and $\gamma$ (dashed) for the three input types (same colors as in A). C: Paths for the three input types (also same colors as in A). All three paths curve to the same side and exhibit similar amounts of curvature. A straight line is shown for reference.
Appendix 1

Simulation Parameters

Stiffness, damping, and inertia tensors used in the simulations, listed by figure number. All tensors were symmetric, so only one off-diagonal term is provided here. The tensor units are Nm/rad (stiffness), Nms/rad (damping), and Nms²/rad (inertia). Ratio (tensor ellipse major axis divided by minor axis) and tilt (the counterclockwise angle in degrees between the radial-ulnar deviation axis and tensor ellipse major axis) were calculated from each tensor.

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Appendix 2

Derivation of Initial Path Direction

The step response of the decoupled set of equations (Equation 2) has a well-known analytical solution (Nise, 2000). In general, the step response of a second-order system can take on different forms depending on the level of damping in the system. Wrist rotations are underdamped (Lakie et al., 1984; Sinkjaer and Hayashi, 1989), so the step response in FE is

\[
\beta(t) = \frac{A_\beta}{K_\beta} \left[ 1 - e^{-\zeta_\beta \omega_\beta t} \left( \cos \left( \omega_\beta \sqrt{1 - \zeta_\beta^2} t \right) + \frac{\zeta_\beta}{\sqrt{1 - \zeta_\beta^2}} \sin \left( \omega_\beta \sqrt{1 - \zeta_\beta^2} t \right) \right) \right]
\]

where \( A_\beta \) is the magnitude of the step input in \( M_\beta \), \( \omega_\beta = \frac{K_\beta}{I_\beta} \) is the natural frequency, and \( \zeta_\beta = \frac{B_\beta}{2\sqrt{K_\beta I_\beta}} \) is the damping ratio. The equation for RUD is similar except that it also includes a term for gravity:

\[
\gamma(t) = \frac{A_\gamma + mgr}{K_\gamma} \left[ 1 - e^{-\zeta_\gamma \omega_\gamma t} \left( \cos \left( \omega_\gamma \sqrt{1 - \zeta_\gamma^2} t \right) + \frac{\zeta_\gamma}{\sqrt{1 - \zeta_\gamma^2}} \sin \left( \omega_\gamma \sqrt{1 - \zeta_\gamma^2} t \right) \right) \right]
\]

with variables \( \omega_\gamma \) and \( \zeta_\gamma \) defined the same as for \( \beta(t) \).

The initial path slope is given by:

\[
\frac{dy}{d\beta}(t = 0) = \lim_{t \to 0} \frac{dy}{d\beta} = \lim_{t \to 0} \frac{dy}{dt} \frac{dt}{d\beta} = \lim_{t \to 0} \frac{dy}{d\beta} \frac{d\beta}{dt}
\]

Because the modeled movements start from rest, the initial velocity in each direction is zero, and the limit is undefined. However, by L'Hopital's Rule,

\[
\frac{dy}{d\beta}(t = 0) = \lim_{t \to 0} \frac{dy}{dt} \frac{dt}{d\beta} = \lim_{t \to 0} \frac{d^2y}{dt^2} \frac{d\beta}{dt} = \lim_{t \to 0} \frac{d^2y}{d\beta dt^2}
\]

The second time derivative in each direction can be calculated from the step response above:

\[
\frac{d^2\beta}{dt^2} = \frac{A_\beta}{K_\beta} \cdot \omega_\beta \sqrt{1 - \zeta_\beta^2} e^{-\zeta_\beta \omega_\beta t} \left[ \omega_\beta \sqrt{1 - \zeta_\beta^2} \cos \left( \omega_\beta \sqrt{1 - \zeta_\beta^2} t \right) - \zeta_\beta \omega_\beta \sin \left( \omega_\beta \sqrt{1 - \zeta_\beta^2} t \right) \right]
\]

At time \( t = 0 \),

\[
\frac{d^2\beta}{dt^2} (t = 0) = \frac{A_\beta}{K_\beta} \omega_\beta^2
\]

The initial acceleration in \( \gamma \) is similar except for the gravity term:
\[ \frac{d^2\gamma}{dt^2} (t = 0) = \frac{A_y + mgr}{K_y} \omega_y^2 \]

778

The initial path slope therefore becomes

\[ \frac{dy}{d\beta} (t = 0) = \frac{A_y + mgr}{\frac{A_\beta}{K_\beta}} \cdot \frac{\omega_y^2}{\omega_\beta^2} \]

779

In order for the path to end up at a diagonal target, the steady-state response in the two DOF must be equal:

\[ \lim_{t \to \infty} \beta(t) = \frac{A_\beta}{K_\beta} = \lim_{t \to \infty} \gamma(t) = \frac{A_y + mgr}{K_y} \]

780

Therefore,

\[ \frac{dy}{d\beta} (t = 0) = \frac{\omega_y^2}{\omega_\beta^2} \]

781

Since \( \omega_\beta = \sqrt{\frac{K_\beta}{I_\beta}} \) and \( \omega_y = \sqrt{\frac{K_y}{I_y}} \), the initial path slope depends only on the ratios of stiffness and inertia between the two directions:

\[ \frac{dy}{d\beta} (t = 0) = \frac{K_y}{K_\beta} \cdot \frac{I_\beta}{I_y} \]
A. Experiment

B. Simulation

[Diagram showing radial, flexion, and ulnar directions]
Rad Ext Flex Uln
AC BD E F G
A. Input Torque

B. Orientation

C. Path

- **A. Input Torque**: Graph showing the absolute input torques (Nm/rad) over time (sec) with step, ramp, and sigmoidal functions.
- **B. Orientation**: Graph showing the absolute orientation (rad) over time (sec) with step, ramp, and sigmoidal functions.
- **C. Path**: Graph showing a straight line path.