

Limb Stiffness Is Modulated With Spatial Accuracy Requirements During Movement in the Absence of Destabilizing Forces

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Wong J, Wilson ET, Malfait N, Gribble PL. Limb stiffness is modulated with spatial accuracy requirements during movement in the absence of destabilizing forces. *J Neurophysiol* 101: 1542–1549, 2009. First published January 14, 2009; doi:10.1152/jn.91188.2008. The motor system can use a number of mechanisms to increase movement accuracy and compensate for perturbing external forces, interaction torques, and neuromuscular noise. Empirical studies have shown that stiffness modulation is one adaptive mechanism used to control arm movements in the presence of destabilizing external force loads. Other work has shown that arm muscle activity is increased at movement end for reaching movements to small visual targets and that changes in stiffness at movement end are oriented to match changes in visual accuracy requirements such as target shape. In this study, we assess whether limb stiffness is modulated to match spatial accuracy requirements during movement, conveyed using visual stimuli, in the absence of external force loads. Limb stiffness was estimated in the middle of reaching movements to visual targets located at the end of a narrow (8 mm) or wide (8 cm) visual track. When greater movement accuracy was required, we observed modest but reliable increases in limb stiffness in a direction perpendicular to the track. These findings support the notion that the motor system uses stiffness control to augment movement accuracy during movement and does so in the absence of external unstable force loads, in response to changing accuracy requirements conveyed using visual cues.

INTRODUCTION

One of the most common problems the motor system must address is the control of movement accuracy. One way that movement variability may be reduced is by modulating limb stiffness. It has been suggested that limb stiffness stabilizes the limb against the perturbing effects of joint interaction torques (Debicki and Gribble 2004; Koshland et al. 2000) and neuromuscular noise (Selen et al. 2006a). A number of studies have investigated how the motor system modulates limb stiffness to achieve accurate movements in the presence of unstable force loads (Burdet and Osu et al. 2001; Franklin et al. 2007). In these environments any deviation from a specified hand trajectory (e.g., a straight line connecting the start and end targets) results in large forces (imposed by a robot arm) that further perturb the limb away from the desired hand path. These studies have shown that the motor system modulates limb stiffness to stabilize the limb and, in some cases, does so selectively in the direction of the mechanical instability. It is important to note, however, that the force environments used in studies such as these have a high positive feedback gain and are

thus highly unstable. Given the inherent variability in the motor system (Hamilton et al. 2004; van Beers et al. 2004) from a practical point of view it is infeasible that changes to the kinematic path of the hand or modified patterns of reciprocal muscle activations could fully counteract the perturbation. In the presence of highly unstable mechanical loads, the only functional solution available to the motor system is to produce an increase in limb stiffness.

It is thus important to address whether the nervous system uses stiffness control to facilitate movement accuracy in more naturalistic tasks that do not involve external destabilizing force loads. Previous studies have addressed this question to some extent by examining stiffness in statics. Arm stiffness is modulated at the end of reaching movements (and during very slow tracking tasks) to visual targets of different size (Selen et al. 2006a,b) and shape (Lametti et al. 2007). Similarly, arm muscle activation (estimated using surface electromyographic [EMG] recordings) increases at the end of arm movements to smaller targets (Gribble et al. 2003; Osu et al. 2004). Studies of jaw movements during speech have also described increases in stiffness associated with decreases in kinematic variability (Shiller et al. 2002). Importantly, these studies show that the motor system modulates limb stiffness in the absence of external unstable force loads, based only on accuracy requirements of the movement task (e.g., target size), and that increases in stiffness are associated with decreases in spatial variability.

However, the studies just described are largely based on measurements of limb stiffness in statics, at movement end, or based on single-joint movement tasks (Selen et al. 2007). Investigating stiffness modulation in multijoint tasks enables the estimation of stiffness in multiple directions and, in particular, allows one to assess whether the motor system modulates stiffness in a directionally selective manner. It is important to examine stiffness during movement because there is evidence that even for the same limb position, stiffness in statics may be significantly different from stiffness during movement (Darainy et al. 2007). Here we examine the extent to which stiffness is modulated during multijoint movements in tasks not involving destabilizing force loads. We assess limb stiffness during movement in response to changes in the visual accuracy requirements of a reaching task. Limb stiffness was estimated during reaching movements made to targets appearing at the end of a visual “track” that varied in width. Stiffness was measured midway through movements made in either an

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8-mm- or an 8-cm-wide visual track, using a position-servo-controlled method reported previously (Darainy et al. 2007; Wong et al. 2009). Limb stiffness in the lateral direction during movements made in the narrow track was modestly but reliably greater than that for movements made in the wide track and this was associated with reduced kinematic variability in the narrow track compared with that of the wide track. Moreover, for movements made in the narrow track, the orientation of maximum limb stiffness rotated perpendicular to the track. These findings support the idea that the neural control of limb stiffness is an important component of the ongoing control of movement accuracy.

METHODS

Subjects

Twenty right-handed subjects (16 females) between 17 and 35 yr of age were randomly assigned to three experimental groups. Subjects reported no history of visual, neurological, or musculoskeletal disorder. Written informed consent was obtained from each subject prior to participation. The UWO Research Ethics Board approved all procedures.

Apparatus

Subjects performed reaching movements while grasping the handle of an InMotion² robotic linkage (Interactive Motion Technologies, Cambridge, MA) in the right hand. A six-axis force transducer (ATI Industrial Automation, Apex, NC; resolution: 0.05 N), located inside the handle, measured forces at the hand. Movements were made in a horizontal plane along the surface of a desk, at shoulder height (see Fig. 1A). A custom-built airsled was used to support the subject's arm against gravity while maintaining minimal levels of friction between the airsled and desk. Shoulder straps were used to maintain the subject in a static seated position, keeping the shoulder in place and minimizing trunk movements. The wrist was braced as well, restricting movements to shoulder and elbow rotations. The subjects' view of their arm was occluded by a mirror placed just above the shoulder. Visual feedback of hand position was provided on the mirror in real time using a computer-controlled LCD projector.

Movement task

Subjects were asked to move their limb from a start target to an end target, both presented visually as filled circles (diameter = 25 mm; Fig. 1A). The start target was positioned 5 cm away from the subject's torso, along the subject's midline. The end target was located 35 cm away from the start target, also along the midline. Subjects were

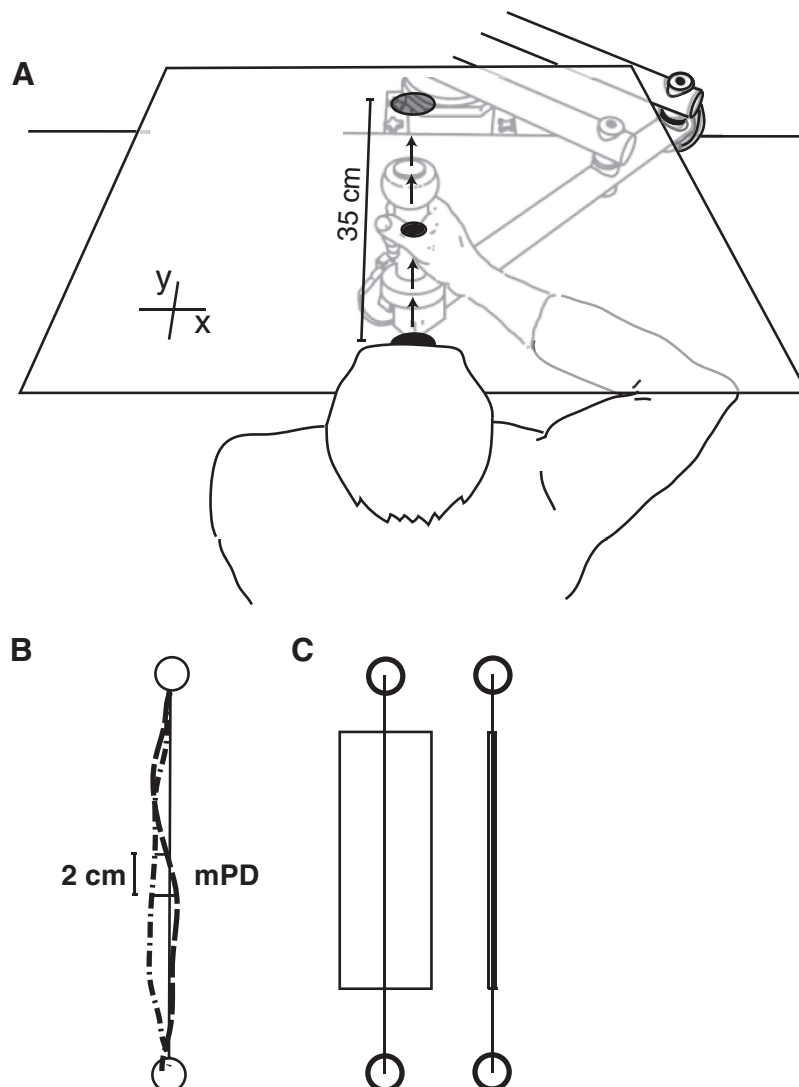


FIG. 1. Experimental apparatus. *A*: subjects performed seated reaching movements while grasping the handle of the robotic device. Vision of the limb was occluded. Movements of 35 cm were made along the subject's midline beginning 5 cm away from the body. *B*: movement accuracy was characterized by measuring the mean absolute deviation from a straight line in the middle 2 cm of movement. Two sample movements are shown. *C*: subjects performed movements within 2 different accuracy constraints: one high accuracy (± 4 -mm lateral deviations were permitted) and the other low accuracy (± 4 -cm lateral deviations).

instructed to move their limb in a straight, smooth fashion within a fixed duration of $1,200 \pm 75$ ms. A cursor (a small filled circle, diameter = 4 mm) was displayed in real time to represent the position of the hand. Feedback was given to the subject on a trial-by-trial basis about movement speed. Visual lines were also displayed to the subject that indicated a visual "track" and subjects were instructed to keep movements within this region. Figure 1C shows the two track widths used, one ± 4 cm (Wide condition) and the other ± 4 mm (Narrow condition). The experiment consisted of two blocks of 160 movements. In each block, subjects were given feedback when movements strayed laterally beyond the track width. Half of the subjects performed the first block in the Wide condition and the second block in the Narrow condition (Wide-Narrow), with the remaining subjects performing the opposite order (Narrow-Wide). In all cases adaptation was quantified by changes in movement accuracy over the course of training. To characterize movement accuracy we measured the mean perpendicular distance (mPD) over the middle portion of movement. The mPD was defined as the mean absolute perpendicular deviation made from a straight line connecting the start and end targets over the middle 2 cm of movement (see Fig. 1B). The location of this measure was selected to coincide with the location of stiffness measurement (see following text). Movement mPD was averaged across bins of 10 movements.

Stiffness estimation during movement

Stiffness was estimated during both the Wide and the Narrow conditions. Estimation of endpoint stiffness was made using position-servo-controlled perturbations using a method previously reported (Darainy et al. 2007; Wong et al. 2009). Briefly, stiffness was estimated by perturbing the hand a specified distance away from an on-line estimate of the trajectory the hand would have taken during an unperturbed movement and measuring the restoring forces at the robot handle (taking account of forces expected due to limb dynamics using inverse dynamics; see Wong et al. 2009).

Twelve millimeter (12.0 ± 0.1 mm) position-servo perturbations were applied in 8 directions spanning 360° (0, 45, 90, 135, . . . , 315°). Stiffness was estimated using a total of 24 measurements, 3 in each of the 8 directions. Perturbations occurred on randomly selected trials at a rate of 20% during the last 120 movements in each block. Visual feedback of the hand was removed during stiffness-measurement perturbations. Perturbations lasted 500 ms and force signals were estimated during a 50-ms time window that was selected on a per-trial basis about 250–300 ms after the perturbation onset, at which point the restoring forces were judged to be stable (e.g., see Fig. 2C). This delay between perturbation start and restoring force estimation was necessary to ensure that the hand was moved the full distance away and that force signals had stabilized. By subtracting estimated positions and forces from the positions and forces recorded during perturbation trials, we arrive at dPosition (dx and dy) and dForce (dFx, dFy). The stiffness matrix K is calculated by linear regression of

dForces on dPositions. Similar methods are reported in other recent studies of stiffness during movement (Darainy et al. 2007; Gomi and Kawato 1996, 1997). For a detailed description of the stiffness estimation procedure, including a number of tests of the sensitivity of the method to misestimation of the unperturbed trajectory and other sources of variability, see Darainy et al. (2007) and Wong et al. (2009).

Example stiffness measurement

Figure 2 shows an example of a typical perturbation, in this case one that perturbs the hand in a direction opposing movement. Gray vertical lines indicate the window over which restoring forces were measured. Figure 2A shows the major axis of movement; the perturbation is shown in red. The change in position from an estimated unperturbed path (dx and dy) is shown in Fig. 2B. Note that the positional perturbation is smooth and stable over the hold phase of the perturbation. Measured forces at the handle are shown in Fig. 2C, which illustrates the smooth and stable force signals we observed during the estimation window. Figure 2D shows a collection of 24 dx and dy measures, resulting from 3 perturbations in each of 8 directions. Note that the position servos are realized with very high accuracy and little variability. Figure 2E shows the measured dFs, which are defined as the mean restoring force over the estimation time window in both x and y axes. Note that dFs cluster according to the direction of the applied perturbation and the magnitudes are reciprocal to the positional perturbation. Leftward perturbations result in restoring forces (force applied by the hand on the robot) measured to the right and vice versa. This provides some additional confidence that the position servos and the estimates of (dx, dy) and (dFx, dFy) were reasonable. For a full description of sensitivity analyses, cross-validation tests, and a number of other controls to assess the sensitivity of the stiffness estimation procedure, see Wong et al. (2009).

RESULTS

Movement accuracy

Figure 3, A and B shows movement accuracy (mPD) over all 320 movements for both Narrow-Wide (NW) and Wide-Narrow (WN) groups. A clear difference in movement accuracy can be observed between Narrow and Wide accuracy conditions. To test for differences in movement accuracy, a split-plot repeated-measures ANOVA was performed with one between-subjects factor (order, Narrow-Wide vs. Wide-Narrow) and one within-subjects factor (visual track width, Narrow vs. Wide). The dependent measure was mean mPD across all movement trials in each block. The main effect of order did not reach significance ($P > 0.05$) and no significant interaction effect of order by track width was found ($P > 0.05$); thus block

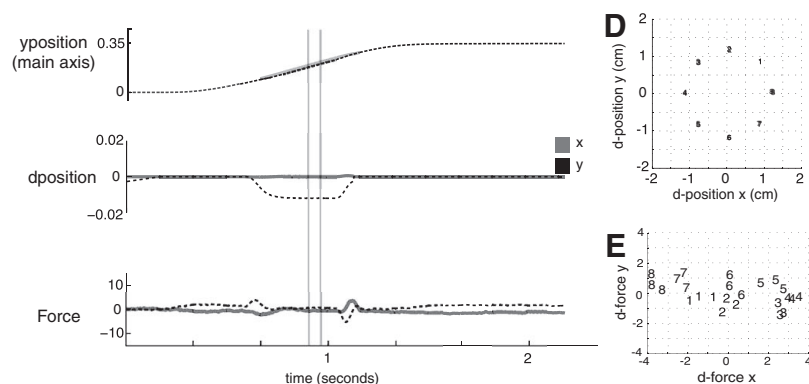


FIG. 2. Representative position servo. A: an example position servo, plotted as a dashed black line, made in the negative direction, opposite to movement direction. The estimated trajectory is shown in gray, in the middle of movement. B: changes in position during the perturbation. Note the change in y in the negative direction (black) and no change in x (gray). C: force signals during perturbation. D: a set of position displacements for 3 stiffness measurements; and the corresponding restoring forces, in E.

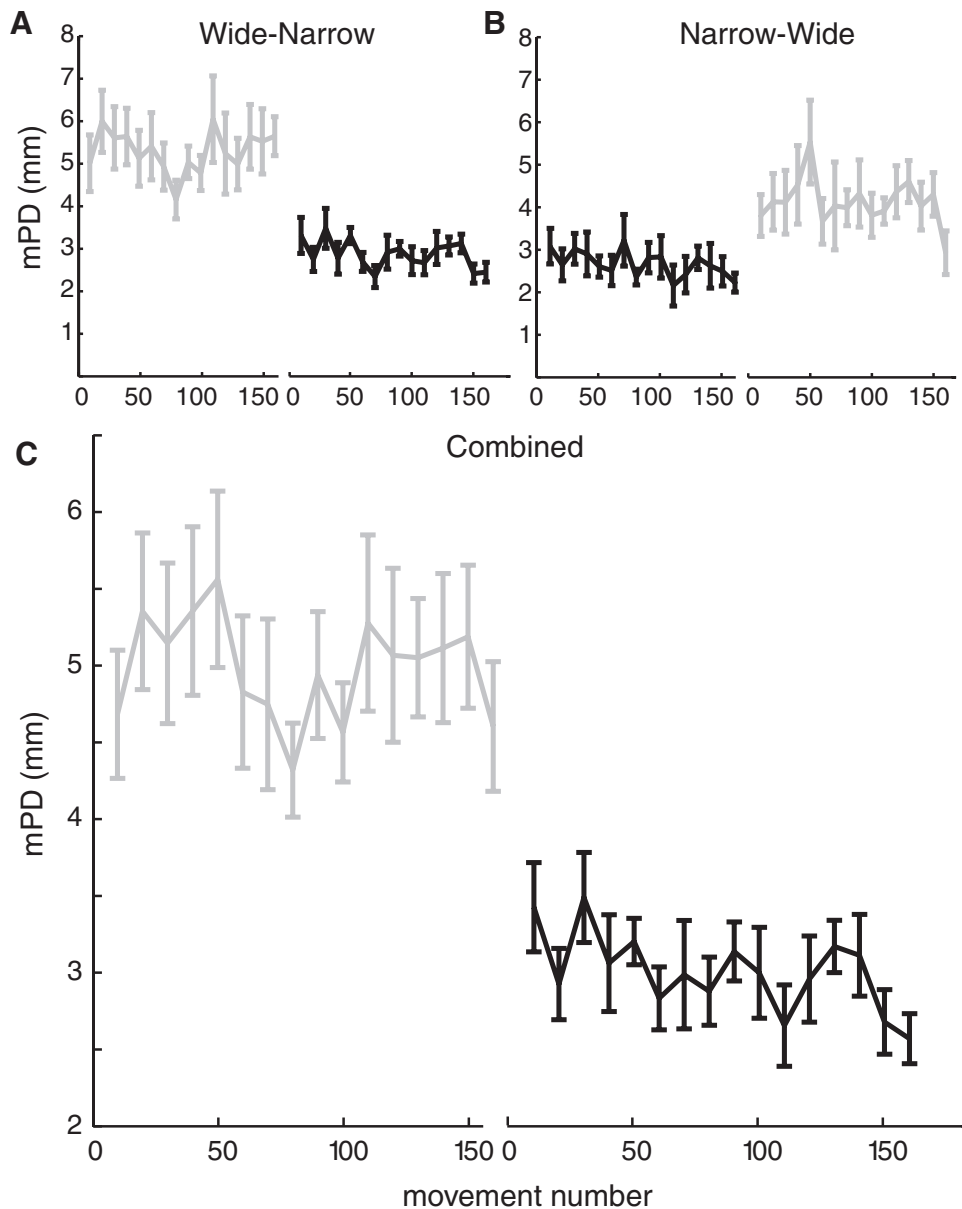


FIG. 3. Performance across training. Mean absolute deviation in the middle of movements (mean perpendicular distance [mPD]), as a function of movement number, for all subjects. Vertical bars represent 1 SE. Gray represents Wide track movements; black represents narrow track movements. *A*: Wide-Narrow order ($n = 10$). *B*: Narrow-Wide subjects ($n = 10$). *C*: combined data ($n = 20$).

order did not affect overall movement accuracy. In contrast, the main effect of visual track width did reach significance ($P < 0.001$). Subjects increased movement accuracy during movements in the Narrow condition. For subsequent analyses, the data were collapsed across the Narrow-Wide versus Wide-Narrow orders. Figure 3C shows combined movement accuracy data. Mean mPD over each block was 4.99 ± 1.3 mm in the Wide condition and 3.0 ± 0.6 mm in the Narrow condition.

Stiffness

To assess whether stiffness was modulated in response to different visual accuracy demands, endpoint stiffness was estimated in both Wide and Narrow visual track conditions in 20% of movements during the last 120 movements of each condition. Figure 4A shows the mean stiffness ellipses that graphically represent the stiffness matrices (following Mussa-Ivaldi et al. 1985) across all subjects. The black and gray ellipses represent stiffness during the Narrow and Wide con-

ditions, respectively. Singular-value decomposition of the stiffness ellipses was performed to characterize the orientation, eccentricity, and ellipse area. No statistically significant differences were found in either ellipse eccentricity or area between the two conditions ($P > 0.5$). A significant difference was found between ellipse orientation in the two conditions ($P < 0.001$). Orientation of the primary stiffness axis was rotated about 7° toward the horizontal in the Narrow condition compared with the Wide condition: thus the direction of greatest stiffness became oriented toward the axis requiring greatest accuracy.

We also assessed changes to individual components of the stiffness matrix. A MANOVA was performed to test for statistically reliable changes to elements of the stiffness matrix between the two accuracy conditions. A main effect of visual track width (Narrow vs. Wide) did reach significance ($P < 0.001$). Post hoc tests showed statistically reliable differences in stiffness component K_{xx} , which represents stiffness in the

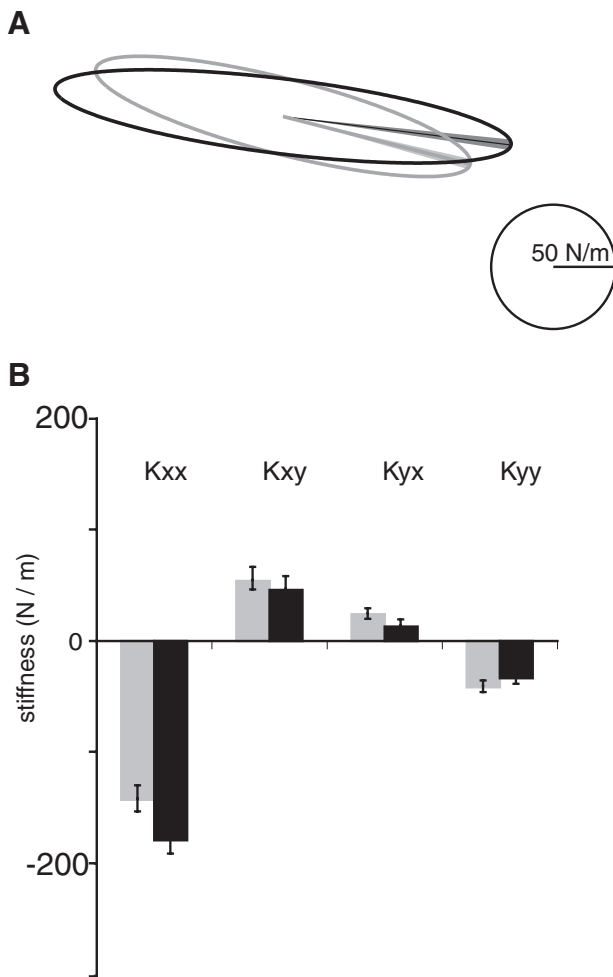


FIG. 4. Stiffness ellipses. *A*: mean stiffness ellipses for subjects. Gray represents Wide movements and black represents Narrow movements; shaded regions around the major axes of the ellipses represent 1 SE of ellipse orientation. *B*: stiffness matrices. Stiffness components are shown averaged for all subjects. Gray bars indicate stiffness measures during the Wide task; black bars indicate the Narrow task. Vertical bars represent 1 SE.

lateral (x) direction due to a perturbation in the same direction ($P < 0.01$), and K_{yx} , stiffness in y due to a perturbation in the left–right (x) direction ($P < 0.05$), in Narrow versus Wide visual track conditions. The mean increase in stiffness in the Narrow condition over the Wide condition was 29.39 N/m for K_{xx} (a roughly 20% increase over K_{xx} in the Wide track condition) and 11.34 N/m for K_{yx} .

Figure 4*B* shows mean values across subjects of the four elements of the stiffness matrix. In particular, a clear change in K_{xx} is observed. Table 1 shows stiffness matrices for individual subjects. The left column shows stiffness matrices for movements in the Wide condition and the right column shows stiffness matrices for movements in the Narrow condition.

Control tests

It has been reported that tonic levels of EMG activity in limb muscles following reaching movements increase as peak joint velocity increases (Suzuki et al. 2001) and that stiffness increases with the velocity of single-joint elbow movements (Bennett 1993). It is thus important to rule out the possibility that the observed differences in limb stiffness in narrow versus

wide visual tracks could be due to higher movement speed (and thus higher stiffness) in the narrow track compared with the wide track. We compared peak hand tangential velocity for movements in the narrow and wide tracks and, in fact, found the opposite pattern. Peak hand tangential velocity of movements in the narrow track (mean = 0.354 m/s, SD = 0.012 m/s) was reliably lower ($P < 0.01$) than that for movements in the wide track (mean = 0.380 m/s, SD = 0.014 m/s).

The presence of voluntary or involuntary responses to the perturbations required for measuring stiffness could result in biased measures of restoring force and thus biases in estimated stiffness. We monitored the possibility of voluntary or involuntary reactions to the force perturbations in a number of ways. First, we examined the time-varying pattern of restoring forces that, if contaminated by sudden voluntary responses to the measurement perturbation, may show increased variability over time. Specifically, we compared the variability of the force signal over time during stiffness perturbation trials (during a window 250–300 ms after perturbation onset). No statistically reliable differences in the SD of restoring force in the lateral (x) direction were observed between movements in the narrow (mean = 0.37 N, SD = 0.54 N) versus wide (mean = 0.39 N, SD = 0.07 N) track conditions ($P = 0.54$). Similarly no statistically reliable differences were observed for the SD of force in the y direction between narrow (mean = 0.32 N, SD = 0.05 N) versus wide (mean = 0.29 N, SD = 0.07 N) tracks ($P = 0.18$). In addition, we repeated stiffness estimates by shifting the time window used to estimate restoring force ± 50 ms and compared the results. Force signals over this time period were relatively stable, resulting in consistent estimates of stiffness (see Wong et al. 2009). Finally, based on control experiments in which subjects were explicitly instructed to attempt to intervene after a perturbation (see Wong et al. 2009), we rejected measurement trials in which the SD of the force signal over the measurement window exceeded a predetermined threshold; this resulted in $<2\%$ of trials being rejected.

DISCUSSION

We investigated the hypothesis that the motor system modulates limb stiffness during movement to decrease variability in response to spatial accuracy constraints imposed by visual stimuli and does so in the absence of external destabilizing forces. Indeed, we found statistically reliable changes to limb stiffness midway through movement for movements in a narrow visual track compared with a wide track. Although the observed increases in limb stiffness are relatively modest compared with changes observed for movements in unstable force loads (Franklin et al. 2007; Wong et al. 2009), the observed effects are nevertheless consistent with previous reports of changes to muscle cocontraction during naturalistic reaching tasks involving different accuracy constraints based on visual target size (Gribble et al. 2003; Osu et al. 2004).

The present finding that the orientation of maximum stiffness aligns with the direction requiring greatest spatial accuracy is also consistent with a previous report by Lametti et al. (2007) demonstrating modulation of stiffness orientation at movement end, in response to changes in visual target shape. Lametti et al. observed that maximal endpoint stiffness was consistently oriented in the direction of greatest required movement accuracy. These authors measured stiffness modulation in

TABLE 1. *Stiffness matrices in the Wide and Narrow conditions*

Subject	Wide				Narrow			
	$K_{x,x}$, N/M	SD	$K_{x,y}$, N/M	SD	$K_{y,x}$, N/M	SD	$K_{y,y}$, N/M	SD
NW								
1	-161.7	15.5	76.0	19.8	-239.9	18.3	7.5	13.3
	5.9	14.2	-26.3	18.3	13.9	16.0	-36.6	18.7
2	-154.4	15.8	70.4	31.7	-186.7	20.4	65.0	28.2
	7.9	21.8	-23.1	38.9	18.8	19.9	-29.0	33.5
3	-158.2	15.6	69.3	22.2	-214.9	17.9	50.4	20.6
	3.0	15.2	-31.8	26.8	-4.6	17.2	-26.3	33.5
4	-156.2	23.1	27.7	13.8	-177.5	21.3	71.6	20.3
	27.5	16.4	-35.8	22.2	16.0	22.0	-27.1	14.5
5	-105.7	15.9	30.2	21.7	-128.4	14.6	-0.3	33.3
	18.6	19.5	-61.1	13.0	29.8	15.0	-55.6	26.0
6	-119.5	17.9	68.8	21.7	-136.6	15.5	50.0	27.0
	23.0	22.0	-45.0	22.4	37.9	14.7	-35.7	21.7
7	-93.4	9.8	61.1	7.9	-148.5	13.2	59.0	10.1
	14.9	9.8	-24.7	13.5	7.7	10.3	-12.9	9.2
8	-84.1	14.7	49.8	26.1	-160.9	19.2	63.2	27.9
	13.5	13.5	-26.0	28.7	2.0	15.0	-57.9	23.0
9	-141.0	29.2	22.7	20.8	-185.0	23.5	-8.9	24.5
	27.6	20.1	-28.0	22.9	11.5	20.5	-40.8	14.0
10	-135.5	19.1	37.5	21.4	-131.3	18.8	59.9	14.2
	24.2	12.9	-44.9	21.8	-15.3	18.5	-9.6	18.1
WN								
11	-170.5	19.3	7.4	24.1	-197.0	28.3	5.2	24.6
	47.7	27.3	-60.8	26.8	45.4	43.1	-16.0	24.4
12	-163.0	18.2	54.7	14.0	-213.4	33.1	11.5	15.0
	17.7	20.0	-59.2	19.0	22.0	28.3	-78.1	11.0
13	-165.5	18.5	87.4	17.2	-244.8	18.1	109.0	14.0
	39.5	12.1	-48.0	17.3	-2.0	15.4	-21.4	18.8
14	-122.0	15.1	57.6	21.0	-162.4	12.6	82.1	9.4
	48.1	14.8	-61.3	20.4	28.3	13.4	-24.0	13.5
15	-114.0	10.7	79.9	15.5	-117.6	14.3	30.3	18.6
	30.7	27.7	-49.9	28.8	-5.5	14.8	-51.4	22.4
16	-121.9	15.6	44.3	7.5	-139.1	27.3	49.6	23.3
	16.5	16.5	-64.4	15.9	-15.0	26.7	-9.1	20.7
17	-235.1	17.0	110.2	23.2	-220.7	15.9	111.5	30.6
	33.0	16.3	-38.0	20.9	40.8	15.1	-40.7	24.5
18	-200.2	17.3	56.9	23.7	-231.6	23.7	73.7	16.4
	20.4	21.5	-44.0	19.9	-5.1	29.7	-27.7	24.7
19	-112.8	25.8	-22.1	17.1	-103.1	21.5	-16.6	37.3
	33.9	23.1	-46.0	21.1	20.7	19.1	-28.1	30.8
20	-131.6	24.4	3.3	33.2	-206.4	30.7	10.0	35.9
	49.7	16.5	-54.4	27.7	29.5	32.0	-54.0	28.0

statics during the 200 ms following movement end; thus our findings complement the previous report by showing stiffness modulation during movement itself.

Stiffness values estimated in the current study are comparable to those reported in the literature for human planar arm movements. Stiffness estimates are slightly lower here than those in our previous study (Wong et al. 2009): average values of the four elements of the hand stiffness matrix [K_{xx} , K_{xy} , K_{yx} , K_{yy}] were [-141.1, 50.5; 24.1, -41.6], compared with [-208.2, 60.0; 39.2, -47.2], and this may be reflected in a difference in the ratio of male to female participants between studies: 33% of subjects were female in the previous study, compared with 80% female in the current study. The magnitude of our two-dimensional limb stiffness estimates falls above that reported by Frolov et al. (2006) and Mah (2001), is very similar to that reported by Darainy et al. (2007), and slightly below that reported by Burdet et al. (2001) and Franklin et al. (2003, 2007). For a more detailed comparison of stiffness estimates using our procedure to those in previous reports, see Wong et al. (2009).

In a recent study we investigated whether two-joint limb stiffness is modulated in response to a visual perturbation designed to mimic changes in visual feedback associated with movements in unstable force loads (Wong et al. 2009). We compared stiffness modulation in unstable force environments to that in a purely visual perturbation that magnified (by a factor of 2) the apparent deviation of the hand from a straight-line path connecting start and end targets. This manipulation of visual feedback provided subjects with a new visuomotor mapping that effectively doubled the amount of visual information about movement variability. We found that limb stiffness was not modulated to adapt to the visual perturbation, but rather the nervous system made changes to feedforward movement planning, resulting in straighter movement trajectories. If the motor system was able to effectively use enhanced visual feedback to plan more accurate movements, perhaps limb stiffness change in the context of this visual magnification was simply an energetically inefficient solution when compared with changes to movement planning. In contrast to our previ-

ous study, the visual task in the current study afforded no such increase in the information regarding movement curvature and an increase in limb stiffness was observed. The results of the previous study and those of the current study may be reflective of a heuristic that the motor system uses when implementing stiffness change. Perhaps sensory signals above a certain perceptual threshold carry sufficient information to inform the motor system about errors in movement planning, whereas signals below this threshold do not, in which case stiffness modulation is the only reliable adaptation.

Another possibility is that the visual channels used in the present experiment may have provided a more specific goal regarding allowable trajectories. Such explicit goals may better induce changes in stiffness, which are likely to be energetically costly and may be restricted to situations in which clear performance advantages are seen despite the increase in energetic cost.

It is worth noting that the procedure used in the current study to estimate limb stiffness is based on position and restoring force measurements at the level of the whole limb. Presumably the stiffness modulation reported here and in other similar studies (Burdet et al. 2001; Darainy et al. 2007; Franklin et al. 2007; Perreault et al. 2002, 2004) is based on some combination of the modulation of neural control signals for muscle cocontraction (e.g., Gribble et al. 2003; Milner 2002; Osu and Gomi 1999) and modulation of segmental and long-loop reflexes (e.g., Lacquaniti and Maioli 1989; Perreault et al. 2008). Nevertheless, at the behavioral level the current results indicate that limb stiffness as a whole is modulated during movement in response to the accuracy requirements of the reaching task.

Data such as those presented here should be of interest to researchers working on computational models of the neural control of movement. There is a growing literature documenting how limb stiffness and muscle cocontraction are modulated in response to a wide variety of movement task characteristics such as movement speed (Bennett 1993; Suzuki et al. 2001) and spatial accuracy (Gribble et al. 2003; Shiller et al. 2002). These data should be important for constraining computational models of movement control, in particular those that postulate distinct central commands for movement and stiffness control through muscle cocontraction and/or reflex modulation (Bhusan and Shadmehr 1999; Feldman et al. 1995; Gribble and Ostry 2000; Gribble et al. 1998; Todorov 2000).

In summary, we have shown that stiffness is modulated during movement in the absence of destabilizing forces, in response to visual stimuli indicating the midmovement accuracy requirements of a reaching task. These results in combination with previous reports of how stiffness is modulated in naturalistic reaching tasks support the idea that the neural control of limb stiffness is an integral part of the voluntary control of movement.

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