

Kinematic Strategies for Upper Arm–Forearm Coordination in Three Dimensions

W. P. MEDENDORP,² J. D. CRAWFORD,¹ D.Y.P. HENRIQUES,¹ J.A.M. VAN GISBERGEN,²
AND C.C.A.M. GIELEN²

¹Medical Research Council Group for Action and Perception, Centre for Vision Research and Departments of Psychology and Biology, York University, Toronto, Ontario M3J 1P3, Canada; and ²Department of Medical Physics and Biophysics, University of Nijmegen, NL 6525 EZ Nijmegen, The Netherlands

Received 10 March 2000; accepted in final form 25 July 2000

Medendorp, W. P., J. D. Crawford, D.Y.P. Henriques, J.A.M. Van Gisbergen, and C.C.A.M. Gielen. Kinematic strategies for upper arm–forearm coordination in three dimensions. *J Neurophysiol* 84: 2302–2316, 2000. This study addressed the question of how the three-dimensional (3-D) control strategy for the upper arm depends on what the forearm is doing. Subjects were instructed to point a laser—attached in line with the upper arm—toward various visual targets, such that two-dimensional (2-D) pointing directions of the upper arm were held constant across different tasks. For each such task, subjects maintained one of several static upper arm–forearm configurations, i.e., each with a set elbow angle and forearm orientation. Upper arm, forearm, and eye orientations were measured with the use of 3-D search coils. The results confirmed that Donders’ law (a behavioral restriction of 3-D orientation vectors to a 2-D “surface”) does not hold across all pointing tasks, i.e., for a given pointing target, upper arm torsion varied widely. However, for any one static elbow configuration, torsional variance was considerably reduced and was independent of previous arm position, resulting in a thin, Donders-like surface of orientation vectors. More importantly, the *shape* of this surface (which describes upper arm torsion as a function of its 2-D pointing direction) depended on both elbow angle and forearm orientation. For pointing with the arm fully extended or with the elbow flexed in the horizontal plane, a Listing’s-law-like strategy was observed, minimizing shoulder rotations to and from center at the cost of position-dependent tilts in the forearm. In contrast, when the arm was bent in the vertical plane, the surface of best fit showed a *Fick*-like twist that increased continuously as a function of static elbow flexion, thereby reducing position-dependent tilts of the forearm with respect to gravity. In each case, the torsional variance from these surfaces remained constant, suggesting that Donders’ law was obeyed equally well for each task condition. Further experiments established that these kinematic rules were independent of gaze direction and eye orientation, suggesting that Donders’ law of the arm does not coordinate with Listing’s law for the eye. These results revive the idea that Donders’ law is an important governing principle for the control of arm movements but also suggest that its various forms may only be limited manifestations of a more general set of context-dependent kinematic rules. We propose that these rules are implemented by neural velocity commands arising as a function of initial arm orientation and desired pointing direction, calculated such that the torsional orientation of the upper arm is implicitly coordinated with desired forearm posture.

INTRODUCTION

The purpose of this study was to clarify the rules that govern the choice between various three-dimensional (3-D) arm configurations for different motor tasks. The human arm is provided with multiple degrees of freedom so that a given position of the hand in space can result from many different joint configurations (e.g., Buchanan et al. 1997). For example, one of these joints—the shoulder—is free to rotate about any axis in 3-D space, which allows a specific pointing direction of the upper arm to be obtained in different possible orientations. This poses a *degrees of freedom problem*, considered to be one of the most basic, yet hardest to unravel computational challenges encountered in the area of neural control (Bernstein 1967; Turvey 1990).

In this respect the shoulder is similar to the eye, a structure with 3 df—one more than necessary to specify its two-dimensional (2-D) gaze direction. It is well established that 3-D orientation of the eye is uniquely determined by gaze direction (at least when the head is stationary and the eye is looking far away), effectively reducing the number of controlled degrees of freedom from three to two (Donders 1848). This general principle is now known as *Donders’ law*. *Listing’s law* further specifies this constraint as follows: rotation vectors, which describe eye positions as a rotation relative to some reference position, are confined to a flat range called Listing’s plane (Ferman et al. 1987; Tweed and Vilis 1990). Considering the fact that both the eye and shoulder have three rotational degrees of freedom, it is perhaps not surprising that Donders’ law also applies to straight-arm pointing movements (Hore et al. 1992; Miller et al. 1992; Straumann et al. 1991; Theeuwes et al. 1993). In particular, during straight-arm pointing, the upper arm obeys a rule very similar to Listing’s law, leading some to suggest that the arm-control system might possess a Donders’ operator that takes in desired pointing direction and outputs a command for desired 3-D arm orientation (Crawford and Vilis 1995).

In contrast to these observations suggesting a consistent and reproducible reduction of the number of degrees of freedom, other authors have reported violations of Donders’ law for the arm (Desmurget et al. 1998; Gielen et al. 1997; Soechting et al.

Address for reprint requests: J. D. Crawford, Dept. of Psychology, York University, 4700 Keele St., Toronto, Ontario M3J 1P3, Canada (E-mail: jdc@yorku.ca).

The costs of publication of this article were defrayed in part by the payment of page charges. The article must therefore be hereby marked “advertisement” in accordance with 18 U.S.C. Section 1734 solely to indicate this fact.

1995). For example, Soechting et al. (1995) reported that the orientation of the upper arm for a given fingertip position in space depends on the starting position of the targeting arm movement. These results would seem to suggest that Donders' law has a much more limited application for understanding the neural control of arm movement, particularly for bent-arm configurations. Thus at this time the importance of Donders' law for limb motor control seems tenuous, or at best, controversial.

One possible clue for resolving this controversy comes from recent experiments that show how 3-D head orientation may depend on the contribution of the eye versus head position to a particular gaze direction (Ceylan et al. 2000; Crawford et al. 1999). During normal gaze shifts where the head acts as a platform for the eye, head orientations conform to a form of Donders' law called the Fick strategy (Glenn and Vilis 1992; Medendorp et al. 1998; Radau et al. 1994; Theeuwes et al. 1993). This entails that the orientations of the head behave qualitatively like those of a Fick gimbal, which has a horizontal axis nested within a space-fixed vertical axis. As a result, the rotation vectors representing 3-D head orientations define a twisted saddle-shaped surface with nonzero torsional components at the oblique facing directions. However, when the head was forced to act like a gaze-pointer (imposed by pin-hole goggles or a head-mounted laser), its twisted surface flattened out to become more Listing-like (Ceylan et al. 2000; Crawford et al. 1999). Moreover, when head movements were dissociated from gaze shifts, Donders' law for the head broke down in favor of a minimum-rotation strategy. Thus if one pooled the data from all of these conditions, it would appear as though Donders' law were not obeyed at all, whereas considered individually, different kinematic strategies (of which some obeyed Donders' law) were used to optimize various motor task constraints.

These results further imply that Donders' law reflects a control principle for eye and head coordination since the control strategy of the head is dependent on what the eye is doing. In an attempt to derive general principles from their results, Ceylan et al. (2000) suggested that Listing's law is the optimal strategy for a system primarily concerned with pointing, whereas the Fick strategy was thought to be ideal for a weight-bearing inverted pendulum (to minimize torques resulting from gravity).

Just as the head acts as a platform for eye movements, the upper arm acts as a platform for the forearm during normal arm movements. The forearm is sometimes a pointer (like the eye) and sometimes an inverted pendulum with the potential for being used as a weight-bearing pillar, so it could make sense to incorporate elements of different Donders strategies into a control system that accounts for upper arm-forearm coordination. In other words, the choice of strategy for control of upper arm torsion would have to account for the way that it is coordinated with the forearm.

Thus whereas earlier reports suggested that a simple Donders' law is used in arm control (Hore et al. 1992), more recent studies (Nishikawa et al. 1999; Soechting et al. 1995) show that final arm postures are the result of a complex combination of kinematic and dynamic factors. The present study pursues these ideas further, wondering whether there could be a more general kinematic law that governs the range of arm positions in natural movement tasks, perhaps choosing

different Donders strategies to optimize different task conditions. In particular, the present study investigates whether task-dependencies related to coordination with the forearm could affect the manifestation of Donders' law for the upper arm. But before proceeding to METHODS, let us first consider the intimate kinematic linkage between upper arm orientation and forearm posture and how this might be influenced by different Donders strategies of the upper arm.

Arm kinematics and theory

Upper arm torsion—or rotation of the upper arm around its long axis—is often equated with the arm's redundant degree of freedom (Hore et al. 1992). However, this is only true when the arm is fully extended. In contrast, whenever the elbow is bent, upper arm torsion determines forearm orientation—and thus hand position (Soechting et al. 1995). Take for example the arm postures simulated in Fig. 1. This figure is set up to illustrate two of the main tasks used in the current study. But more importantly, it shows two different ways in which upper arm torsion could be used to determine forearm posture in a kinematically redundant task, and how these different strategies would be expressed in rotation vector space. Figure 1, *left* and *middle*, shows simulated “stick figures” of the upper arm and forearm, as viewed from the front of the “subject,” whereas Fig. 1, *right*, shows the surface of best fit to the corresponding orientation vectors of the upper arm. In each case, the task is to point the upper arm toward one of nine targets, with the elbow angle set at 90°.

Let us first consider the difference between the *left* and *middle* columns. If we just look at the central arm position of each of the Fig. 1, *left* (*A* and *D*), where the upper arm points at a target straight out of the page, one can see that the upper arm is bent upward by 90°. We called this the *V90* task. In contrast, for the same target direction and elbow angle (Fig. 1, *B* and *E*, *middle* column), the *H90* task aligned the forearm horizontally and pointing to the right (subject's left). Thus the upper arm has been rotating torsionally by 90° between the *V90* and *H90* tasks (*left* and *middle* columns). This is reminiscent of some of the arm movements described by Soechting et al. (1995); and there is no question that Donders' law must be violated to move the arm thus i.e., between these two configurations.

What is at issue here, is that once the baseline torsion is selected, i.e., within the *V90* or *H90* task, how it might further depend on the 2-D pointing direction of the upper arm? In other words, how would upper arm torsion be selected for the other pointing directions shown within each panel (Fig. 1, *A*, *B*, *D*, and *E*) and how would this further affect the posture of the forearm? Let us first suppose that the upper arm follows a Listing's law strategy (Fig. 1, *top* row). If the arm orientations shown in *A* and *B* are each allowed their own reference position—that is, they are each described relative to the central arm position of that panel—then the orientation vectors for the upper arm would have to align in a plane, as shown in Fig. 1C. (But note that if 1 common reference position were used, these 2 panels would give 2 different planes with a large torsional shift between them.) In contrast, if in these two tasks the upper arm followed a Fick strategy (Fig. 1, *bottom* row), then its orientation vectors would form a twisted surface (Fig. 1F), i.e., in Cartesian coordinates, its torsion would depend on pointing direction.

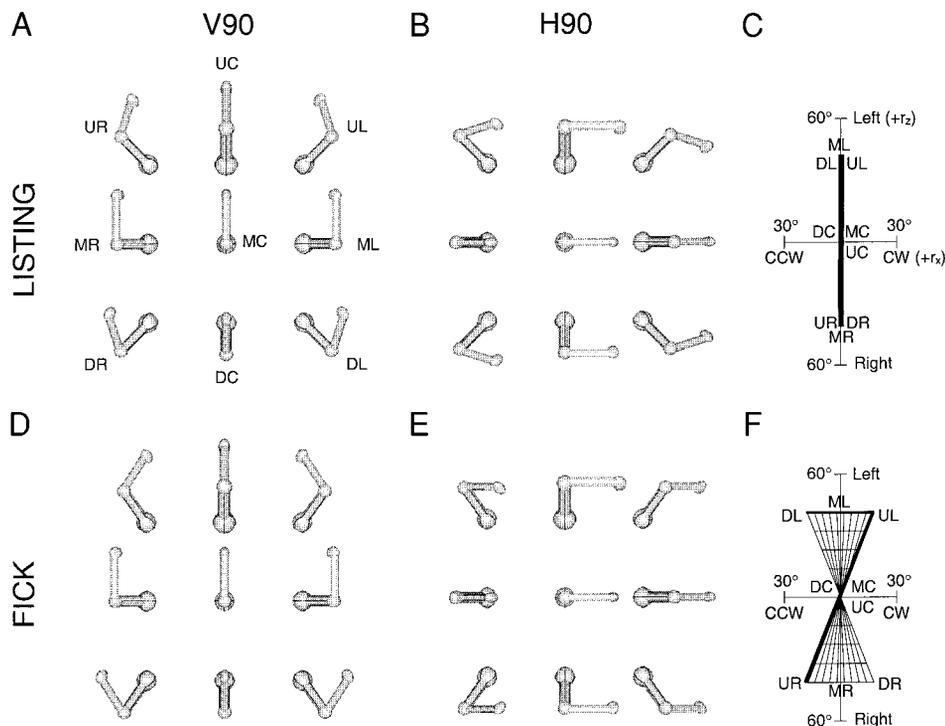


FIG. 1. Illustration of how using a Donders strategy in the upper arm—Listing (A–C) vs. Fick (D–F)—would affect forearm posture in 2 of the arm configurations used in this study (V90 and H90). *A*: vertically bent-arm postures (V90) resulting from upper arm rotation vectors in a flat plane (Listing strategy, twist score 0). The upper arm only shows those orientations that can be obtained by rotating the upper arm from the reference position (shown in the center of *A*, *B*, *D*, and *E*) about an axis in a flat plane. Shown are those orientations that would be used to point to the 9 targets used in this experiment. Pointing directions are labeled using the direction of the target as commanded to the subject (see METHODS), i.e., the 9 combinations of pointing upward (U), middle (M), downward (D), leftward (L), center (C), and rightward (R). *B*: horizontally bent-arm postures (H90) obeying Listings' law. Same conventions as in *A*. Note a clear violation of Donders' law between *B* and *A*. However, within *A* and *B*, the vertical components vs. the torsional components of the upper arm orientations fall within a flat range: Listing's plane (*C*). *D*: vertically bent-arm postures resulting from upper arm rotation vectors in a twisted plane (Fick strategy, twist score -1). Corresponding positions with *A* refer to identical pointing directions of the upper arm but with different upper arm orientations. Here the upper arm orientations in oblique directions differ from those in *A* by having an additional torsional component, resulting in different forearm configurations. *E*: horizontally bent-arm postures conform the Fick strategy. *F*: within *D* and *E*, the upper arm orientations fall within a twisted surface: arm postures in oblique directions (UR, UL, DR, DL) have non-zero torsion components. (C)CW, (counter)clockwise torsion.

The important thing to note here—relating this back to the stick figures in the *two left columns*—is that these different strategies produce different arm configurations as a function of upper arm pointing direction. In particular, they would produce different forearm tilts at the oblique arm positions, in the corners of each panel. For example, note that in the upward-oblique V90 positions the forearm tilts more inward—as projected onto the page—with the Fick strategy compared with the Listing strategy. More precisely, it can be easily shown that with the Fick strategy, the plane containing the upper arm and forearm remains fixed with respect to the horizon for every pointing target, whereas the Listing strategy causes this plane to tilt at the oblique positions. Therefore the choice of 3-D control strategy for the upper arm—Donders' or otherwise—will have real consequences for hand-arm posture, and one should bear in mind that whenever the elbow is bent the representations of upper arm torsion shown in RESULTS also correspond precisely to tilts in the forearm plane.

METHODS

Subjects

Experiments were performed on 19 human subjects, who were tested in nine different task conditions as described in the following

text. The main experiments (Figs. 2–7, RESULTS) were performed with naive subjects. In some additional control experiments (see Fig. 8, RESULTS), three subjects, who were familiar with the general purpose of the experiments (but not at that time with the hypotheses or results), also participated. Their basic results were not different from those of the other subjects. All subjects signed informed consent to participate in the experiment. All subjects but one were right-handed, and all were free of any sensory, perceptual, or motor disorders. All pointing movements were made using the right arm.

Experimental setup

Three-dimensional upper arm orientations were measured using custom-built 3-D magnetic search coils as described elsewhere (Glenn and Vilis 1992; Henriques et al. 1998; Tweed et al. 1990). In 12 subjects, we also monitored the orientation of the forearm. In addition, the orientation of the right eye was measured in six subjects using Skalar search coils. Subjects sat and were tested with the torso rotated 45° leftward with respect to a frontally placed stimulus array (see *Stimuli*) (see also Hore et al. 1992) so that the central pointing target was near the center of the arm's mechanical range. The limb and eye movements were measured using three mutually orthogonal magnetic fields (frequencies, 90, 124, and 250 kHz) generated by field coils 2 m across. After demodulation, the three voltages from each coil were

sampled at 100 Hz. Calibration and accuracy were as described previously (Henriques et al. 1998; Klier and Crawford 1998).

Stimuli

Experiments were either done in normal lighting conditions or with the background in complete darkness. The targets, either 1-cm-diam white dots (for experiments in the light) or green light-emitting diodes (LEDs; 0.17°; 2.0 cd/m²; for dark experiments), were mounted on a vertical screen oriented in parallel to the horizontal-vertical magnetic fields at a distance of 1.1 m before the subject's eyes. The target array contained a total of nine targets arranged in a square grid. The four cardinal targets were at 40° right, left, above, and below; the four oblique targets were 48° from the center of the right shoulder. Subjects pointed toward these targets either with the arm fully extended in the normal way (Henriques et al. 1998) or with the use of a laser pointer with the elbow at various configurations described in the next section. The laser pointer was attached to the distal part of the upper arm, about 5 cm from the elbow joint above the tendon from the triceps muscle, and secured in parallel to the upper arm. The central target was placed so that the upper arm was parallel to the frontal magnetic field (orthogonal to the target screen) on pointing at it.

Before the experiment began, the subject was familiarized with the positions of the targets on the screen. At the start of each task, the subject pointed the upper arm toward and visually fixated the center target for 3 s to define a reference position for the arm and right eye, respectively. Thereafter the subject was required to point toward each of the stimuli in the nine-target array at 2.5-s intervals. In the light, the stimulus order was determined by verbal commands to the subject, e.g., up-left, down-right, middle-center (see Ceylan et al. 2000) (see also Fig. 1), whereas in the dark, subjects pointed toward the LEDs as they came on (each for 2.5 s with no gap interval in between). In either case, the nine stimuli were repetitively "presented" in a random sequence of nine so that subjects pointed toward each target the same number of times from various initial positions. Experiments in the dark were used to control for potentially distracting visual feedback from the forearm, but the results revealed no significant differences for pointing with or without background lighting (see RESULTS). Sessions were divided into 50-s blocks, each block including two pointing movements to each of the nine targets. Each task consisted of three blocks unless otherwise stated. A brief rest was provided between blocks.

Experimental protocols

The main hypothesis tested in this study is that the control strategy of the upper arm is dependent on the orientation of the forearm relative to the upper arm. To this end, we introduced several task conditions in which we varied the orientation of the forearm relative to the upper arm. The arm-mounted laser paradigm was used to ensure that the upper arm used the same 2-D pointing direction for each target across tasks, without determining the third degree of freedom. Our basic hypothesis was that with straight arm pointing, the upper arm would use a more Listing-like Donders strategy, whereas with the elbow bent and held with the arm in a vertical plane, the upper arm would use the Fick strategy to minimize extraneous torsional torques on the arm resulting from gravity. To test this hypothesis, we used the following tasks.

During *the control task, C*, subjects made pointing movements (without laser) to the nine targets with the fully extended arm. During *the control laser task, CL*, the subject again adopted an outstretched arm but now pointed the laser to the target array. In some subjects, there was a slight dissociation of about a few degrees of the pointing direction of the laser and the natural pointing direction of the straight arm. However, by comparing both control tasks we were able to show that the laser pointer did not affect the control strategy of the upper arm (see RESULTS).

During the *vertically bent-arm laser tasks*, subjects were instructed to first stretch their arm straight out, bring their thumb up, and subsequently rotate their forearm vertically in the direction of the shoulder by three different angles: 45, 90, and 135°, while pointing with the upper arm laser toward the central target. In this way, the *initial* arm configuration was set with the upper and forearm contained in vertical plane, without providing the subject with any explicit verbal instructions about 3-D arm orientation that might influence their subsequent behavior. We will refer to these task conditions as: *the V45 task*, *the V90 task* (as in Fig. 1, *left*), and *the V135 task*, respectively. Subsequently, subjects were instructed to point the laser to each LED in the dark and to maintain their initial elbow angle, but no further specific instructions were given regarding the orientation of the forearm in space.

We also performed some additional control experiments. First, we tested whether the configuration, in which the forearm was bent, either horizontally or vertically (as in the preceding text), has implications for the pointing strategy. We examined this by the horizontally bent-arm laser task, *the H90 task*. During this task, the subjects were instructed to first stretch their arm, point with their thumb to the left, and subsequently rotate their forearm horizontally toward their body over an angle of 90°, meanwhile pointing with the upper arm to the central target (see Fig. 1, *middle*). Thereafter, subjects pointed the laser to the various targets while preserving the elbow joint angle at 90°.

The next control was designed to see how well subjects would follow a Fick rule when explicitly instructed to maintain the forearm vertically at all times. During this task, the subject initially took the same elbow configuration as during the V90 task but now was explicitly told to keep the forearm vertical with respect to gravity for all pointing directions (as demonstrated by the experimenter). To see his forearm in this task, the subject pointed in dim background lighting to the target array. By definition, this task did not involve a stable elbow angle, but because on average the elbow varied about 90°, depending on target elevation, we called it *the V90v task*.

Considering our hypothesis that the upper arm might use a Fick strategy to reduce torsional gravitational torques on the forearm, we also wondered whether loading the hand (and thereby increasing these potential torques) would further alter this strategy. Therefore in *the V90w task*, the subject carried a hand-held 1-kg weight (which was strapped across the hand with the weight nestled in the palm) starting in a 90° vertically rotated forearm position while pointing the laser toward the nine targets. This also acted as a control for inertial effects.

The final control experiment was inspired by the fact that head movements only obey Donders' law when they are part of a gaze shift (Ceylan et al. 2000). By using *the gaze-fixation task, GF135*, we tested whether there is a similar gaze dependency for arm movements. During the GF135 task, subjects were instructed to keep their head still and their eyes on the center target while pointing the laser to targets in the periphery using the same elbow configuration as in the V135 task (this angle was used because the subjects found it to be the least fatiguing). Subjects reported that gaze-fixation tasks were easy to perform. By measuring movements of the right eye, we checked whether subjects indeed fixated the center target throughout the task. Except for the gaze fixation task, all experiments took place under head-free conditions. As a variation on this concept and to test the hypotheses of Straumann et al. (1991) concerning 3-D eye-arm coordination (discussed later), we also tested four subjects in the C and V135 task with the head fixed (with the use of a bite bar) as opposed to moving freely (as in the other experiments).

Data analysis

From the 3-D coil signals, we computed rotation vectors that represent any instantaneous arm or eye position as the result of a virtual rotation from a fixed reference position to the current position.

In the space-fixed right-handed coordinate system, the rotation vector is defined by

$$\vec{r} = \tan(\theta/2) \cdot \vec{n} \quad (1)$$

where \vec{n} represents the direction of the rotation axis and $\tan(\theta/2)$ denotes the amount of rotation by an angle θ about that axis (Haustein 1989). The x component of the rotation vector describes the torsional orientation (clockwise/counterclockwise) of the arm or eye. The y and z components specify the vertical (up/down) and horizontal (right/left) orientation, respectively (see Fig. 1). For example, a rotation vector pointing in the positive z direction represents a position obtained by rotating the arm leftward from the reference position.

The rotation vector describing the orientation of the forearm with respect to the upper arm, \vec{r}_{FU} , was computed from the rotation vectors characterizing the orientation of both the upper arm and forearm in space, \vec{r}_{US} and \vec{r}_{FS} , respectively, using $\vec{r}_{\text{FU}} = \vec{r}_{\text{FS}} \circ \vec{r}_{\text{US}}$. In this way, we were able to check the ability of subjects maintaining a constant elbow angle, according to the instruction, when pointing for the different bent-arm configurations. Note that our experimental protocols and hypotheses were not dependent on a high degree of precision in maintaining the elbow angle, but we wished to check that subjects did not show any systematic drift in this angle. In all subjects, we found some trial-to-trial variation for all elbow angles with largest variation for the V45 task (about 10° SD). The standard deviations of the elbow angle for the C, CL, V45, V90, V135, and H90 task were 3.3, 4.3, 10.1, 7.2, 3.1, and 7.4°, respectively (averaged across subjects), which we deemed sufficiently small for the purpose of the present experiments.

The important analysis in this study concerned the 3-D orientation of the upper arm. Note that we did not analyze the trajectories of the ongoing movements but rather the range of orientations used during fixations, as in the previous study by Ceylan et al. (2000). Therefore onset and offset of each arm movement between targets were determined on the basis of an angular velocity criterion (velocity threshold 5°/s) (see Medendorp et al. 1999). All onset/offset markings were visually checked and corrected if necessary. The 3-D pattern of upper arm orientations at the offset positions were then computed by fitting a second-order surface to the rotation vector data (Hore et al. 1992; Miller et al. 1992; Straumann et al. 1991; Theeuwes et al. 1993) as follows

$$r_x = a + br_y + cr_z + dr_y^2 + er_yr_z + fr_z^2 \quad (2)$$

in which r_x , r_y , and r_z represent the torsional, vertical, and horizontal components of the rotation vectors relative to the reference position, as defined in the preceding text. Parameter e (denoted as the twist score) allows the surface to twist, whereas parameters d and f yield a parabolic curvature in the r_y and r_z direction, respectively.

If parameters d , e , and f are zero, the surface is planar, which means that Listing's law holds perfectly. A negative twist score (parameter e) indicates that orientations of the arm are similar to those produced by a Fick gimbal system, which has a horizontal rotation axis nested within a vertical rotation axis. A perfect Fick gimbal has a twist score of -1 . In contrast, for a system that behaves like a perfect Helmholtz gimbal system, for which the order of nesting in the rotation axes is reversed compared with the Fick-system, the twist score would be $+1$ (Theeuwes et al. 1993). But in practice, each of these parameters can fall anywhere in the continuum from Fick, to Listing, to Helmholtz, and beyond (Ceylan et al. 2000).

The scatter of the data relative to the fitted surface (commonly denoted as the thickness of the surface) is defined by the standard deviation of the distances of all samples in the r_x direction to the fitted surface (in degrees). The smaller the thickness, the closer the rotation vectors stay to their surface, and therefore the better Donders' law is obeyed. Unless otherwise specified, an ANOVA was used to determine whether differences in the results between various task conditions were statistically significant ($P < 0.05$).

RESULTS

Task-dependent manifestations of 3-D constraints

To test the hypothesis that the control strategy of the upper arm can be manipulated by changes in arm kinematics, six subjects performed the following pointing tasks: C (control), CL (straight arm laser), and the three vertically bent-arm laser tasks V45, V90, and V135 (see METHODS). The question to be addressed is whether these various kinematics of the arm affect the way in which the control system of the upper arm deals with its three rotational degrees of freedom. To this end, we analyzed the upper arm data by using rotation vectors, which represent any instantaneous arm position as the result of a virtual rotation from the reference position to the current position. We will start by describing the results within a general framework before presenting each of the various findings in more detail.

Figure 2 presents the data of *subject HH* for each of the tasks. Figure 2, *left*, shows the horizontal and vertical components of the rotation vectors for the upper arm in magnetic field coordinates. During the laser tasks (CL, V45, V90, and V135), the 2-D arm trajectories were generally more curved than those in the control task (C), but the end points where the arm is pointing at the targets—the subject of this study—remained about the same. These end points are shown as squares (\square) in the “side view” and the “top view” panels (*middle* and *right*), which show their torsional components as a function of their horizontal and vertical components, respectively. These plots show that, for all tasks, the subject keeps the torsional components limited to a restricted range for all movement directions.

To quantify and visualize the shape of the 2-D surface defined by these arm orientations, we fitted *Eq. 2* to the data for the movement end points (\square). In Fig. 2, the side view and top view of the fitted 2-D surfaces (represented as vertical-horizontal grids) are superimposed on the data. At first glance, these surfaces seem to fit the data. We will provide more detailed quantitative analysis to check the actual adherence of the data to these surfaces in subsequent sections (see Figs. 4 and 5, and Table 1). But for the time being, we will focus on the shape of these surfaces.

These surface plots immediately revealed several noteworthy differences between the straight-arm pointing tasks (C and CL) and the bent-arm laser tasks. For pointing with the fully extended arm (C and CL), the surface of rotation vectors was relatively flat (i.e., Listing-like, see Fig. 1C), meaning that upper arm “torsion” remains approximately the same, independent of the target/pointing direction. However, in the bent-arm laser tasks (V45, V90, V135), the surfaces of best fit were more twisted (as in Fig. 1F), meaning that now arm torsion depended on pointing direction. Specifically, for upward-leftward and downward-rightward pointing directions, the upper arm now took on a clockwise torsion (in space-fixed coordinates), whereas the opposite corners took on a counterclockwise torsion. In other words, the *direction* of this twist was consistent with the twist observed with the Fick strategy (Hore et al. 1992; Medendorp et al. 1998).

The observation that the fitted surface becomes more twisted during vertically bent-arm laser pointing was a general finding in all six subjects tested with this experimental protocol. In Fig. 3 we have depicted the side views of the fitted surfaces for each

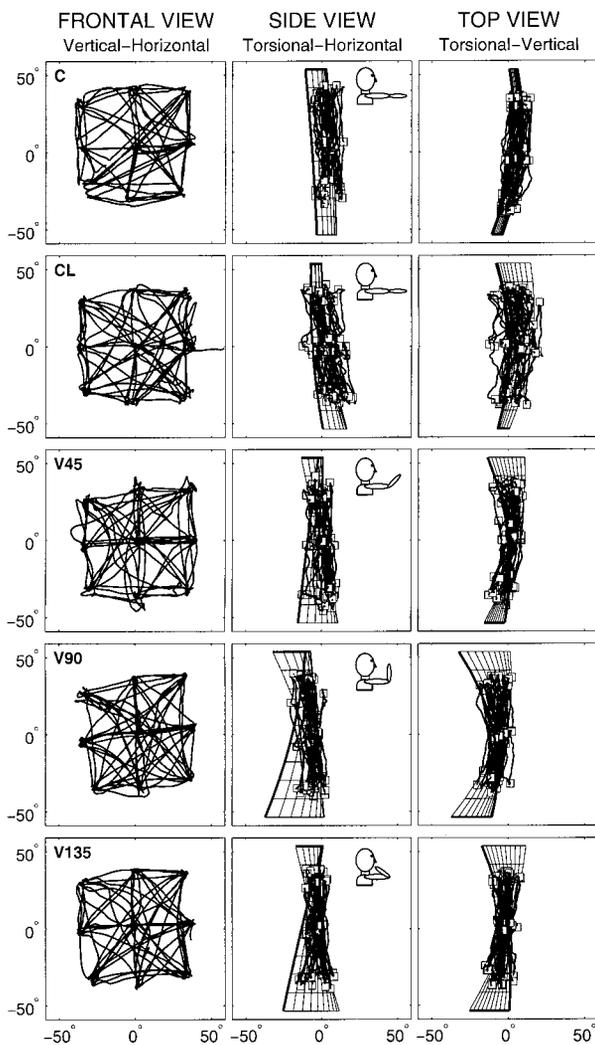


FIG. 2. Three-dimensional arm trajectories during movement with a fully extended arm (C and CL) or a vertically bent-arm configuration (V45, V90, and V135) from subject HH. C, control task; CL, control laser task; V45, 45° vertically bent-arm task; V90, 90° vertically bent-arm task; V135, 135° vertically bent-arm task. The small icons in the side view panels provide a side view of the initial arm configuration. Frontal, top, and side views show a projection of the rotation vectors of all movements performed for each task. Axes are calibrated in degrees. Two-dimensional surfaces were fitted to the movement end points (speed <math>< 5\%/s</math>, see □) and superimposed on the data in the side and top view panels. Note that the 2-dimensional (2-D) surfaces of the data in bent-arm conditions (V45, V90, and V135) are more twisted compared with those in the extended arm conditions (C and CL).

subject during the course of the experiment. As can be seen, the surface was fairly flat across most subjects during the control tasks (C and CL). However, all subjects showed a consistent magnitude and direction of twist during the bent-arm laser tasks (V45, V90, and V135), always in the Fick-like pattern. Moreover, there appeared to be a tendency for the surfaces to become progressively more twisted for larger elbow angles.

To substantiate this observation, we averaged the quantitative results of all subjects, and summarized them in Fig. 4. Graphic depictions of the average surface fits (i.e., based on fit parameters averaged across subjects) are shown in A, whereas B plots the average (\pm SE) twist score for each task. The difference between CL and C was not statistically significant [$F(1,5) = 3.1, P = 0.14$], indicating that laser pointing does not affect the control strategy of the upper arm. However, there

was a systematic relationship between the upper-arm twist score and elbow angle (see Fig. 4B).

Although the average twist scores for all tasks were intermediate between the ideal Listing value (0) and the ideal Fick value (-1), the degree of elbow flexion changed the value of the score along this continuum. On average the 2-D surface of the upper arm was rather flat (small twist score) for both the standard control task (C) and the laser control task (CL), whereas it became progressively more twisted (more negative twist score) in the Fick direction for pointing with larger elbow angles (V tasks). A pair-wise comparison among the different laser tasks revealed the following statistical analyses: CL-V45 significant [$F(1,5) = 11.3, P = 0.02$]; V45-V90, significant [$F(1,5) = 7.12, P = 0.04$]; V90-V135 significant [$F(1,5) = 7.60, P = 0.04$]. Moreover, an ANOVA revealed significant interactions between elbow angle and twist score [$F(4,20) = 31.0; P \ll 0.001$], suggesting that the elbow configuration is an important constraint on the control strategy of the upper arm across the vertical-arm laser tasks.

Figure 4C shows the average (\pm SE) torsional thicknesses (SD) of the orientation ranges relative to their fitted surfaces, which quantifies the goodness of fit of our surfaces. In all tasks, the average (across subjects) thickness of the fitted planes was close to 4° , and the differences in thickness for different task conditions were not significant [$F(4,20) = 0.47, P = 0.76$]. This suggests that, despite the changes in the shape of the fitted surfaces for different elbow angles, adherence of the arm orientations to the fitted planes was equally as good in each of our vertical-arm laser tasks as the controls.

Dependence of arm orientation on previous movement history

So far the results indicate that a 2-D surface can describe the upper arm orientations adopted during each task reasonably well. The torsional thickness of the fitted surfaces was about 4° , which is small considering the large torsional range of shoulder movements. However, this is still large compared with the thickness of Listing's plane of the eye ($\sim 1^\circ$) (Straumann et al. 1991; Tweed and Vilis 1990) and comparable to other ranges that were said to *not* obey Donders' law (Ceylan et al. 2000; Soechting et al. 1995). So where do we draw the line between a system that obeys Donders' law and one that does not?

One possible way is to rely not on torsional thickness per se but rather on another part of the original definition of Donders' law—that eye orientation is independent of the previous saccade path (Donders 1848). This is not always true for certain movements of the eyes (Crawford and Vilis 1991), head (Ceylan et al. 2000), and arm (Soechting et al. 1995). But if it held true here, we could claim that these movements still obeyed a form of Donders' law, just not as precisely as the oculomotor system.

To test this, we calculated for each final position the torsional distance to the fitted surface when starting in one of the eight other positions. When this distance does not significantly deviate from zero, there is no dependence on starting position. Figure 5, showing the results for both the control task and the V90 task, indicates that the torsional distance to the surface is not significantly different from zero with only a few minor exceptions (t -test, $P > 0.05$ for ○ and $P < 0.05$ for ●). This

TABLE 1. Mean coefficients of the fitted 2-D surfaces for the various task conditions

Task	a	b	c	d	e	f	σ , deg	n
C	0.00 ± 0.04	0.10 ± 0.06*	-0.04 ± 0.07	-0.19 ± 0.12*	-0.20 ± 0.19*	-0.01 ± 0.15	3.4 ± 0.6	12
CL	0.03 ± 0.07	0.14 ± 0.10*	-0.05 ± 0.12	-0.30 ± 0.22*	-0.19 ± 0.17*	-0.05 ± 0.20	3.8 ± 1.1	18
V45	0.01 ± 0.01	0.05 ± 0.06	-0.03 ± 0.04	-0.27 ± 0.19*	-0.41 ± 0.12*	-0.10 ± 0.10	3.5 ± 1.1	6
V90	-0.01 ± 0.03	0.06 ± 0.06*	0.00 ± 0.05	-0.27 ± 0.20*	-0.46 ± 0.13*	-0.12 ± 0.12	3.6 ± 0.6	12
V90v	0.01 ± 0.04	0.07 ± 0.05*	-0.08 ± 0.02*	-0.27 ± 0.14*	-0.49 ± 0.10*	-0.04 ± 0.15	2.6 ± 0.7	6
V90w	-0.01 ± 0.04	0.05 ± 0.08	0.00 ± 0.04	-0.24 ± 0.31	-0.44 ± 0.11*	-0.11 ± 0.16	3.8 ± 1.2	6
V135	0.01 ± 0.05	-0.01 ± 0.10	0.02 ± 0.07	-0.16 ± 0.22*	-0.57 ± 0.11*	0.01 ± 0.14	4.3 ± 1.2	12
GF135	0.07 ± 0.09	-0.01 ± 0.12	0.14 ± 0.14	-0.17 ± 0.43	-0.53 ± 0.11*	0.08 ± 0.22	4.8 ± 1.8	6
H90	0.03 ± 0.03	0.24 ± 0.09*	0.02 ± 0.05	-0.20 ± 0.16	-0.12 ± 0.22	-0.03 ± 0.13	4.0 ± 0.7	6
P	0.12	<0.0001	<0.001	0.38	<<0.0001	0.59	0.08	

Values are means ± SD. Rotation vector data of the upper arm were fitted using the equation $r_x = a + br_y + cr_z + dr_x^2 + er_y r_z + fr_z^2$. The SD of the distance of the rotation vectors in the r_x direction to the fitted surface is given by σ (in degrees). The number of subjects who participated in each task is given by n . An ANOVA [$F(8,75)$] tested whether there are differences in the values of the coefficients among tasks, as given by the P value in the lower row. The fact that the coefficients b and c , characterizing the orientation of the plane, are near zero indicates that the plane is nearly aligned with the yz plane of our coordinate system. Further, from the coefficients d , e , and f , describing the curvature of the surface, only the twist score (parameter e) varied significantly among tasks ($P \ll 0.0001$). C, control; CL, control laser task; V45, V90, and V135, 45, 90, and 135° vertically bent-arm tasks, respectively; V90v, 90° keeping forearm vertical task; V90w, 90° vertically bent-arm with load task; GF135, gaze-fixed task; H90, 90° horizontally bent-arm task. * Significantly deviate from zero (t -test, $P < 0.05$).

indicates that there are no systematic trends, producing starting position dependencies in the scatter of the surfaces. Similar results were found for the CL, V45, and the V135 task, suggesting that—by the definition outlined in the preceding text—Donders' law was obeyed within each of the tasks, albeit with a considerable amount of random scatter.

Does Donders' law hold globally

Up until now our analysis revealed that Donders' law for the upper arm holds in good approximation for any particular elbow configuration. The question to be faced now is whether it is also obeyed *across* different tasks. Soechting et al. (1995) emphasized that Donders' law for the arm does not hold for movements under more general testing conditions. Is there a discrepancy with their results and the results of the present experiment?

To explore this issue, we recomputed the arm orientations for each elbow configuration by taking one common reference position, which is the particular position when the subject is pointing to the center target in the control task (C). (Note that the previous section focused on the shape of the best-fit surface with a separate reference position in each task, so that torsional shifts between tasks would not be evident). The results for *subject HH* are shown in Fig. 6A, where each panel illustrates the torsional range of upper arm orientations across all tasks (gray patch) together with the specific set of arm rotation vectors for the indicated task (black subspace). As the figure demonstrates, each specific elbow configuration introduced a mean torsional shift (in addition to the twist effect described in the preceding text), and this shift was different for different elbow angles.

Accordingly, the corresponding arm orientations cover a sub-range of the overall range of rotation vectors. The torsional thickness for each particular task condition, ranging from 2.1 and 5.4° in this subject, was much smaller than the thickness of a 2-D surface fitted to all movement endpoints, which was 12.5°. Across all subjects tested, the average scatter of the total set of rotation vectors was $11.9 \pm 3.4^\circ$ (mean ± SD), ranging from 6.5° to 16.1°. This suggests that upper arm orientations do not obey Donders' law globally.

As shown by Fig. 6B, each sub-range of rotation vectors can

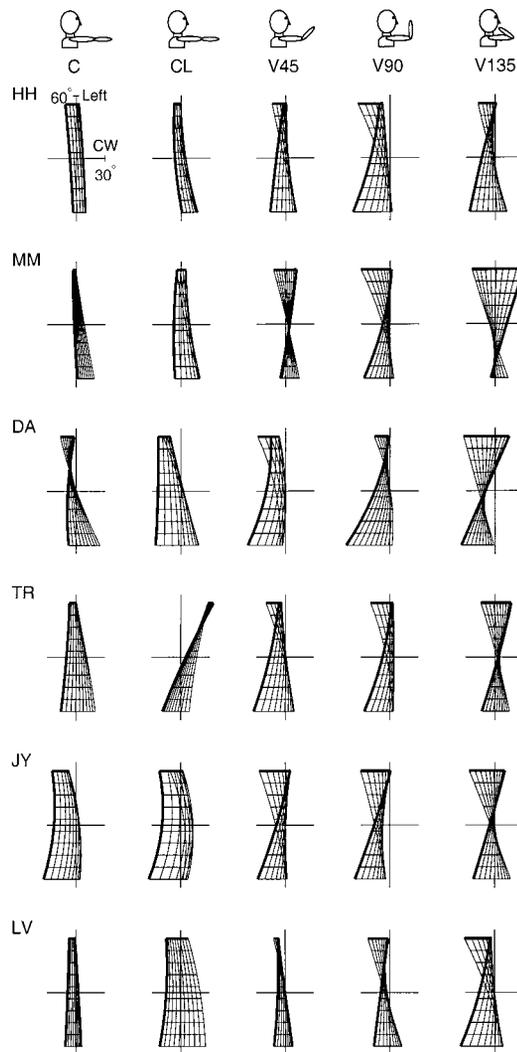


FIG. 3. Side views of the fitted planes in 6 subjects during the various paradigms: the standard control task (C), the control laser task (CL), and the vertically bent-arm tasks (V45, V90, and V135). CW, clockwise torsion. For all subjects, the rotation surface is rather flat during the straight-arm pointing tasks but twisted when pointing with a bent-arm configuration. *Top*: the small icons provide a side view of the initial arm configuration.

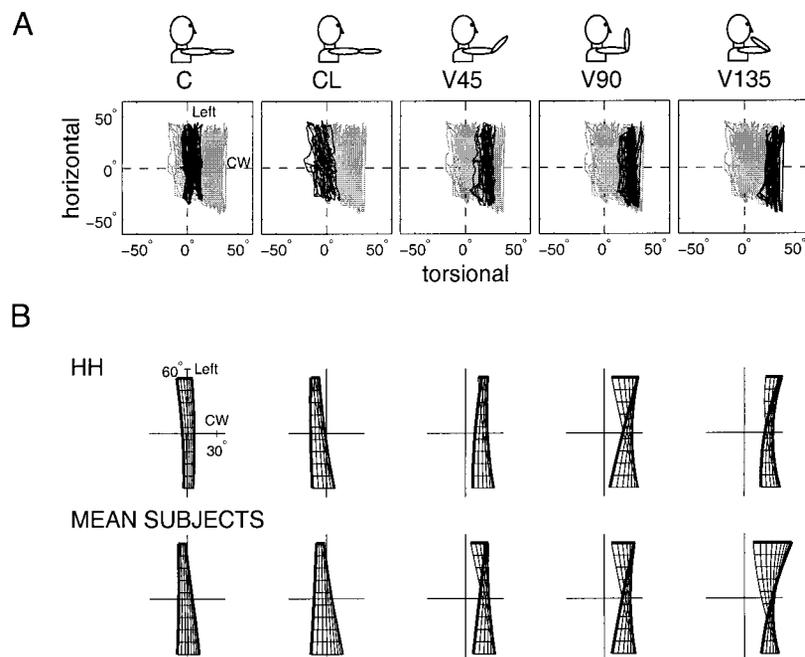


FIG. 6. All arm rotation vectors for various task-constrained pointing paradigms relative to 1 common reference position. The reference position was taken when the subject pointed to the center target in the beginning of the control task (C). A: each panel illustrates the range of arm orientations across all tasks (gray patch) together with the specific set of arm rotation vectors for the indicated task (black subspace). Subject: *HH*. B: the fitted 2-D surface is shifted in torsional direction for larger elbow angles for *subject HH* (top). The average 2-D surfaces across all subjects are depicted in the lower panel. C = control task. CL = control laser task. V45, V90, and V135 = 45°, 90°, and 135° vertically bent-arm tasks.

orientation of the forearm will remain constant with respect to both the horizon and the line of the pointing arm, like an earth-fixed telescope (Hore et al. 1992).

Based on this argument, for vertically bent-arm pointing where the forearm is an inverted pendulum, it might be advantageous to use a Fick-like strategy because it minimizes torques in torsional direction due to gravity. Note that Nishikawa et al. (1999) showed that the plane of the arm did *not* remain invariant with respect to gravity during a reaching task. However, with the static elbow angles used in the current study, our subjects could have been tapping into a *postural* control strategy where minimization of torsional torques with respect to gravity might be expected to be more important. If so, then 1) one might expect an even stronger Fick strategy when carrying a load during vertically bent-arm pointing, whereas 2) by contrast, one might expect the advantages of Listing's law to prevail for *horizontal* bent-arm pointing, where joint torques due to gravity are unavoidable, and thus there is less incentive to optimize movement kinematics according to the Fick strategy.

We tested these hypotheses on the basis of the following task conditions: control task (C), 90° horizontally bent-arm laser pointing (H90), the standard 90° vertically bent-arm laser pointing (V90), and 90° vertically bent-arm laser pointing by carrying a hand-held 1 kg weight (V90w). For comparison, in a fifth task (V90v), we explicitly instructed subjects to maintain their forearm vertical with respect to gravity during pointing to see if this would produce an even more extreme Fick-like constraint. The mean results of all subjects are given in Fig. 7. Figure 7A illustrates the average shape of the fitted surface for the various task conditions in the same format as Fig. 4. The corresponding twist scores and thickness values of the fitted surfaces (averaged over all subjects) are given in Fig. 7, B and C, respectively.

As hypothesized, the plane remained flat during horizontally bent-arm pointing (H90). The twist score, at a value of -0.12 , was even less negative, although not significantly different

from the control task [$F(1,16) = 0.6$, $P = 0.90$]. Thus the arm configurations observed in the H90 task resembled the Listing configurations shown in Fig. 1B rather than the Fick configurations shown in Fig. 1E.

In contrast, for vertically bent-arm pointing tasks (V90, V90v, and V90w), the twist score became more negative, reaching a value of about -0.46 (average) as it did in the previous experiments. In comparison with the control task (C), the increase in twist score was highly significant [$F(3,32) = 8.6$, $P < 0.001$]. However, the load task (V90w) did not have any further effect on the shape of the surface and neither did the V90v task. An ANOVA indeed revealed no significant differences between the twist scores for all three V90 task conditions [$F(2,21) = 0.31$, $P = 0.52$]. So, both the specific instruction task (V90v) and the loading task (V90w) failed to change the shape of the surface compared with natural bent-arm pointing (V90). To summarize, *all* of the vertical bent-arm tasks produced a more twisted surface than the H90 and straight-arm controls, and each by the same amount, tending to show the more Fick-like configurations illustrated in Fig. 1D rather than the Listing configurations shown in Fig. 1A.

Finally, in all tasks except the V90v task, the thickness of the fitted planes was about 4° , as can be seen in Fig. 7C. The differences in thickness values across the C, H90, V90, and V90w task conditions were not significant [$F(3,32) = 0.86$, $P = 0.94$]. However, statistical analysis suggested that Donders' law was much better obeyed in the V90v task compared with the normal V90 task [$F(1,16) = 9.3$, $P = 0.02$]. Thus although the shape of the best-fit surface remained fairly constant in this task (see preceding text), the accuracy of how Donders' law was obeyed could be manipulated by instruction and voluntary intent.

Gaze dependency of arm orientations

Ceylan et al. (2000) showed that head movements violated Donders' law when they were dissociated from gaze shifts. We

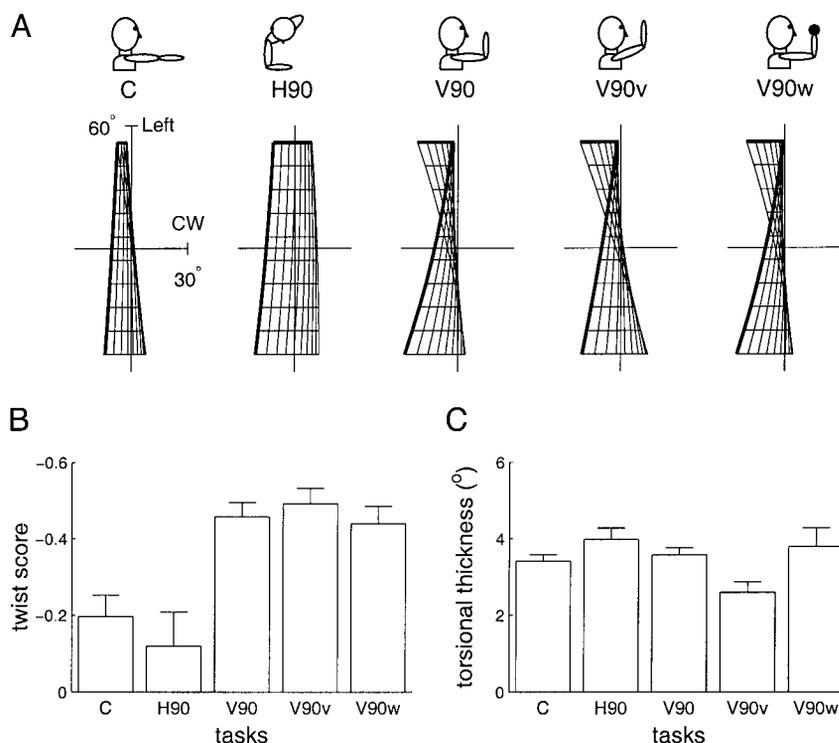


FIG. 7. Mean results of 6 subjects performing various task-constrained pointing paradigms. A: side view of the average 2-D surfaces during the experiment. Note that each task has its own reference position, as in Figs. 2–4. B: average twist scores of the fitted planes with standard error. C: average torsional variability with standard error. V90v, 90° keeping forearm vertical task; V90w, 90° vertically bent-arm with load task. The H90 icon provides a top view of the initial H90 arm configuration. The other icons provide a side view of the initial arm configuration.

wanted to test whether there is a similar gaze dependency for arm movements, which are also strongly linked to gaze during pointing tasks (e.g., Henriques et al. 1998). To check this idea, we applied the gaze fixation task (GF135), in which subjects were instructed to make bent-arm pointing movements (elbow 135°) to targets while keeping their gaze fixed on the center target. Six subjects were tested doing the following five tasks in the light: C, V135, GF135, CL, C (in this order).

In general the fixation task caused no trouble for the subjects. The standard deviations (averaged across subjects) of horizontal and vertical direction of the eye in space (gaze) for the entire duration of the task were only 1.6 and 1.4°, respectively, indicating that during this task arm movements were effectively dissociated from gaze shifts. However, an examination of the 2-D upper arm trajectories in this task showed that subjects were still able to point toward the targets with reasonable accuracy.

The effect of gaze fixation on the 3-D orientations of the upper arm is summarized in Fig. 8, A and B, which shows the twist score (Fig. 8A) and the thickness scores (Fig. 8B) for the various tasks. Although the gaze fixation task tends to slightly increase the scatter of the fitted 2-D surfaces relative to control V135 data (see Fig. 8B), the differences for the thickness between the various task conditions were not statistically significant [$F(4,20) = 2.74, P = 0.06$]. So in the case of the arm, the accuracy of how well Donders' law is obeyed did not depend on gaze direction. Neither was the *shape* of the best-fit surface affected by the gaze fixation task (see Fig. 8A). Statistical analysis revealed no significant differences [$F(1,5) = 0.04, P = 0.85$] between the twist scores in the gaze-free bent-arm task (V135) and the gaze-fixed bent-arm condition (GF135). Thus the implementation of Donders' law for the upper arm appears to be independent of gaze direction.

A related question is whether Donders' law of the arm is

influenced by Donders' law of the eye. Straumann et al. (1991) suggested that the function of Donders' laws of the eye, head, and arm is to create a synergy between these segments for coordinated action in any part of their workspace. If such a linkage exists, then one might expect that a change in eye orientation might affect the way that the arm is oriented. It is well known that the eye in space obeys Listing's law when the head is fixed, whereas it obeys the Fick strategy when the head is free to move (Glenn and Vilis 1992; Radau et al. 1994; Tweed et al. 1990). Therefore we repeated the C and V135 task with both the head-fixed and -free conditions in four subjects for comparison. The results are shown in Fig. 8, C and D. As shown in Fig. 8C, this variable had no effect on the data: the upper arm best-fit surface continued to be consistently flat with the arm straight and consistently twisted with the arm bent vertically, independent of gaze kinematics.

Coefficients of the fitted surfaces

Up to this point, we have quantified the range of arm orientations on the basis of the twist score (parameter e in Eq. 2) of the fitted surface and the torsional shift (parameter a) compared with a common reference position (Fig. 6), thereby ignoring the values of the other coefficients characterizing the fits. Potentially, these other parameters could be important in developing a kinematic rule for arm control. To obtain insight in these parameters, Table 1 lists all six parameters for each of the various task conditions (C, CL, V45, V90, V90v, V90w, V135, GF135, and H90) averaged across the number of subjects (n) who performed the task in head-free conditions (except GF135). By using an ANOVA, we determined whether there are differences in the parameter values across tasks. The significance level, P , is given in the *bottom row* of Table 1. The average torsional thickness is given by σ , which ranged be-

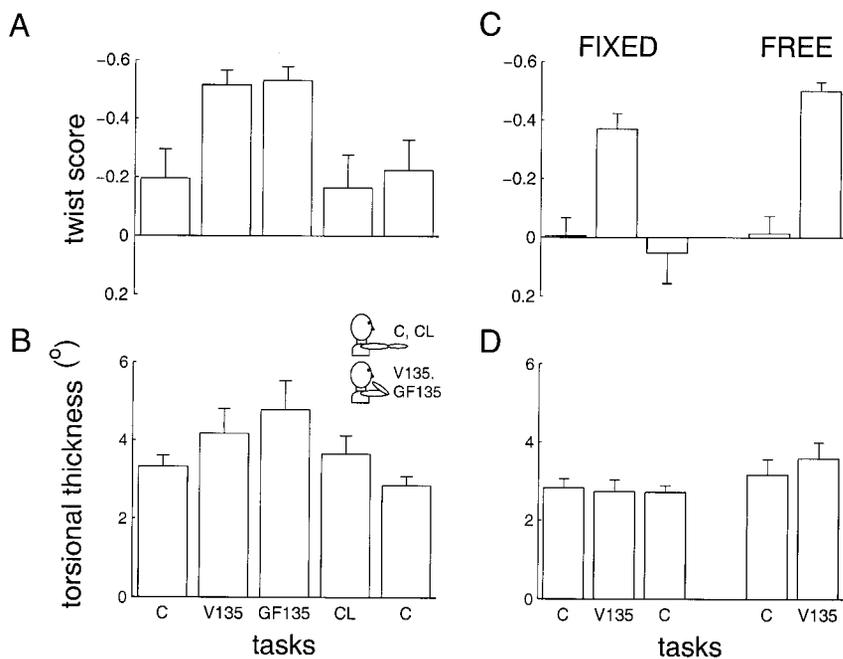


FIG. 8. *A* and *B*: gaze-dependency of 3-dimensional (3-D) upper arm movements. Average twist scores with standard error (*A*) and mean thickness scores with standard error (*B*) of the fitted 2-D surfaces. No significant differences were found for both the thickness and the shape of the 2-D planes between the gaze-free (V135) and the gaze-fixed task (GF135). *C* and *D*: effect of 3-D gaze kinematics on 3-D upper arm orientations. Four subjects were tested in a straight-arm or vertical-arm laser-pointing paradigm in both head-fixed and -free conditions. Each task consisted of 2 50-s pointing blocks. The 1st 3 bars represent the head-fixed condition of the experiment, while the 2 bars on the right show the results in the head-free condition. With regard to the twist score (*C*), the differences between the head-fixed and -free condition are not significant, neither for the control task [$F(1,3) = 1.47$, $P = 0.31$] nor for the bent-arm laser task [$F(1,3) = 3.45$, $P = 0.16$]. The differences in thickness (*D*) for different task conditions, varying between 2.7 and 3.6°, were not significant [$F(4,12) = 1.42$, $P = 0.29$]. V135, 135° vertically bent-arm task (gaze-free); GF135, gaze-fixed 135° vertically bent-arm task. The small icons indicate the initial arm configuration.

tween 2.6 and 4.8° and is not significantly different among tasks ($P = 0.08$).

Note that each task had its own reference position in this analysis. Therefore parameter a , which quantifies the torsional deviation relative to the reference position, was rather small and never significantly different from zero (t -test, $P < 0.05$). Coefficients b and c characterize the orientation of the plane. The value of parameter b , which specifies the linear relationship between torsion and the vertical arm orientation, ranged from -0.01 to 0.24 and was only significantly different from zero for positive values (t -test, $P < 0.05$). This reflects the arm's tendency to roll clockwise when pointing downward and counterclockwise when pointing upward. The c scores, quantifying the relationship between torsion and the horizontal arm orientation, differed only significantly from zero in the V90v task. Although an ANOVA revealed that parameters b and c are significantly different among tasks (see P value in bottom row of Table 1), each specific value remains close to zero, which indicates that the plane is nearly aligned with the yz plane of our coordinate system.

Parameters d , e , and f describe the curvature of the surface. Parameter d specifies the curvature along the torsional axis with the vertical arm orientation and is in some tasks significantly different from zero (t -test, $P < 0.05$). A negative score means that the arm rolls counterclockwise when pointing upward or downward. An ANOVA showed no significant differences of the d score among tasks ($P = 0.38$), indicating that parameter d remains constant for all task conditions. Similar results were found for parameter f , which ranged from -0.12 to 0.08 . This coefficient, which describes the curvature along the torsional axis with horizontal arm orientation, was not significantly different from zero for any of the tasks (t -test, $P < 0.05$). Also here, an ANOVA revealed that this coefficient remains fairly constant among the various task conditions ($P = 0.59$).

To conclude, as can be seen in Table 1, parameter e , describing the twist of the surface, was always negative and significantly different from zero in all tasks but one (H90;

t -test, $P < 0.05$). From the second-order terms, it turned out that only the twist score varied highly significantly among tasks ($P \ll 0.0001$). This suggests that most of the change in curvature in the fitted surfaces is captured by just one parameter (e), expressing the twist of the surface along a continuum, from Listing to Fick.

DISCUSSION

This study has concentrated on the question of whether the control strategy of the upper arm is dependent on its peripheral linkage to the forearm. When our data are pooled across experiments and different elbow configurations, the results show (see Fig. 6) that the upper arm violates Donders' law (or at least does not obey a single Donders' law) corroborating the findings of Soechting et al. (1995). But strikingly, when one considers upper arm orientation when pointing with a specific forearm posture, Donders' law is consistently obeyed (see Fig. 5). Moreover, it turned out that the manifestation of this Donders strategy is different for different forearm postures. In cases where the forearm is fully extended or when it is horizontally bent, a Listing-type of strategy is used (see Figs. 1, *B* and *C*, and 7), whereas in cases where the forearm acts as an inverted pendulum, the upper arm uses a Fick-like strategy to position the forearm (see Figs. 1, *D* and *F*, and 2–4). These results suggest that the various forms of Donders' law observed in arm movements may provide glimpses into a more general set of kinematic rules. Since the control strategy of the upper arm was dependent on the forearm orientation, these kinematic rules can be interpreted as a coordination strategy. Furthermore, we were able to show that Donders' law for the upper arm does not coordinate with Donders' law of the eye and that its implementation is independent on gaze direction (Fig. 8).

Purpose of Donders' law for the arm

The kinematic redundancy of the arm has its basis in the number of joints as well as in the large number of muscles

acting across these joints. Because of the multiple degrees of freedom, the position of the hand in space can be reached by many joint configurations. Therefore one of the major problems in motor control is how the upper arm control system deals with this redundancy problem when controlling the forearm (Buchanan et al. 1997; Turvey 1990). Donders' law is one possible solution to the kinematic redundancy problem, reflecting a coordination strategy for specific upper arm-forearm interactions.

However, in cases where the kinematic redundancy is reduced, one could expect a break-down of Donders' law. For example, for the eye it has been shown that it violates Listing's law during the vestibuloocular reflex (Crawford and Vilis 1991). Also for the arm, it is clear that one can voluntarily rotate the arm about any axis in 3-D space, resulting in violations of Donders' law.

The present study examined several kinematically redundant pointing behaviors of the upper arm, and found that for a limited set of conditions (e.g., any fixed elbow angle) Donders' law held at least as well as for straight-arm pointing but took on different forms. Could this be a mechanical effect? Since we have not measured electromyographic (EMG) characteristics and other factors related to muscle forces and biomechanics, it cannot be ruled out that these have had an effect (Kamper and Rymer 1999). On the other hand, since we can freely rotate our arms torsionally, the arm is obviously not mechanically constrained to Donders' law. Two mechanical parameters were altered in our paradigms: the baseline level of torsional twist in the shoulder socket (potentially affecting muscle pulling directions) and the geometry of the arm's inertia. However, any torsional lag on the upper arm arising from forearm inertia would be expected to produce a one-dimensional curvature in the fitted surface—in opposite directions for the H90 and V90 tasks—rather than the flat or twisted surfaces (respectively) that were actually found. Moreover, the progressive increase in the twist score observed in the V45-V90-V135 series (where shoulder torsion did not change) is incompatible with either mechanical explanation. This suggests that it is the neural system that is choosing different forms of Donders' law. Clearly, the neural system cannot ignore muscle force and dynamic aspects of joint torques (Nishikawa et al. 1999). To the contrary, it must account in an exquisite fashion for these factors to optimize some variable.

Contrary to the observation of Straumann et al. (1991) and compatible with the conclusion of Theeuwens et al. (1993), the 2-D surfaces for the arm that we obtained do not coordinate with Listing's plane of the eye. The fitted surfaces of the upper arm were flat when pointing with the arm straight and twisted with the arm bent vertically, irrespective of 3-D eye orientation. This indicates that Donders' law does not serve as a synergistic control principle for eye and arm.

Nor was elbow angle alone the sole determinant of the 2-D surface for the upper arm because different forms of Donders' law were observed for the same 90° elbow angle depending on forearm orientation. Instead the important factor appears to be the *interaction* between elbow angle and torsional arm posture. In particular Donders' law of the upper arm appears to be influenced by forearm posture against *gravity*. Note that when the arm is fully extended, upper arm torsion has little or no

effect on the work done to maintain forearm posture against gravity. In this under-constrained condition, the upper arm thus used the best strategy to preserve Donders' law and still take the shortest route between any of two arm positions: Listing's law (Ceylan et al. 2000). However, when the elbow is bent, upper arm torsion determines the orientation of the forearm with respect to gravity (Fig. 1), possibly providing a new constraint on arm posture. Thus in the case where the forearm was aligned vertically like an inverted pendulum, the upper arm adopted a Fick-like strategy. From a purely phenomenological viewpoint—without getting into cause and effect—this clearly reduced torques on the forearm due to gravity.

To understand this point, note that gravity will produce no torsional torques on an inverted pendulum that is held to be perfectly vertical, as in the Fick constraint (Fig. 1D), but will exert growing torques for increasing off-Fick tilts, like those seen in the Listing strategy (Fig. 1A). These torques may seem negligible compared with the overall work-load of the arm, but over time, and particularly when bearing a heavy load, they become energy costly and even mechanically dangerous. Now, it is another matter to speculate that the system is actually *designed* to account for these factors, but one way to test this idea would be to perform our experiment with the subjects' bodies tilted on their sides to see whether the kinematic strategies for the V90 and H90 conditions reverse.

In critique of these ideas, the question arises why subjects did not implement a more pronounced Fick strategy (more negative twist score) when pointing with the 1-kg weight (V90w-task), where the potential gravitational torques are even larger. Furthermore why did the Fick-like twist not decrease from the V90 condition to V135 task, where gravity would have less effect? One has to bear in mind that the advantages of Listing's law do not go away for the bent arm—this just brings in potential disadvantages. One possibility is that in our (somewhat unnatural) tasks there was an internal competition between the factors that weigh the system toward the Listing versus Fick strategies with elbow angle tending to tip the scales toward the latter. However, once again this is all just speculation—the important point, addressed in the next section, is that an upper-arm control strategy resembling Donders' law was obeyed in these tasks and that this strategy was systematically modified as a function of arm configuration.

How general is Donders' law as a control principle for the upper arm?

In the case of the eye, where Donders' law has long been studied, we have seen a progression of accepting Donders' law, rejecting it and then revising it into more complex forms. For example, Donders assumed that his law applied to all eye movements. Then it was thought that Listing's law for the eye does not hold for near vision. Later work, however, has shown that the Listing plane of each eye rotates as vergence increases (Minken and Van Gisbergen 1996; Mok et al. 1992). Now we know that a higher form of Donders' law called L2, which incorporates both eye "joints," captures the behavior more completely (Tweed 1997). Could the same general principle also apply to arm movements?

If so, then one might explain an apparent discrepancy between results in the literature: some authors found that Donders' law is obeyed during straight-arm pointing move-

ments (Hore et al. 1992; Miller et al. 1992; Straumann et al. 1991; Theeuwens et al. 1993), whereas others found violations of Donders' law under less restricted conditions (Desmurget et al. 1998; Gielen et al. 1997; Soechting et al. 1995). Even when we consider only our limited set of tasks, it is clear that Donders' law does not hold up in general. However, for each specific task, one finds a certain range of arm orientations emerging, dependent on the limited conditions that were set, like elbow angle and forearm orientation.

Taking these ideas one step further, if one considers an even wider set of orientations than those in the current study, including all upper arm and forearm orientations, elbow angle, effects of dynamic and static forces, and their cross-correlations, they may all be optimized according to certain learned or preprogrammed rules. These context-dependent rules could form a lawful set of equations within a *kinematic hyperspace*, where they could optimize for both kinematic and dynamic factors (Kelso et al. 1991; Soechting et al. 1995; Turvey 1990).

Viewed this way, if one looks at all possible kinematically redundant hand paths (at least where paths are not constrained), there are arrangements—such as those explored in the current study—for which Donders' law can be preserved at least for the movement end points (Crawford et al. 1999). But there are also situations that are not kinematically redundant (like turning a door-knob) or where dynamic factors override kinematics, requiring a violation of Donders' law. For example, Soechting et al. (1995) demonstrated situations where large torsional rotations in the upper arm provide a clear advantage in minimizing kinetic energy. Thus our various Donders surfaces could be viewed as various slices cut along iso-Donders surfaces through the kinematic hyperspace, whereas the task employed by Soechting et al. (1995) might be viewed as cutting tangentially (or orthogonally) to these slices.

As shown in our study, the fitted 2-D surfaces resemble a kinematic strategy for the upper arm related to how the forearm is held. Thus the idea of a kinematic hyperspace must be incorporated into the idea of *coordination* (although the latter also includes temporal dynamics which were not addressed here) (Buchanan et al. 1997; Turvey 1990). In this respect, our results provide a good analogy with the head-movement study of Ceylan et al. (2000), where similar task-dependencies govern the manifestation of Donders' law for the head when controlling the eye.

Relation to other models of the control system

In the past, many different types of models have been proposed to describe the kinematics of human arm movements. Usually, the validity of these models was tested by comparison of predicted and measured postures of the arm or movements trajectories of the hand. However, hardly any studies have discussed these various models in the context of degrees of freedom of movement control.

EQUILIBRIUM-POINT HYPOTHESES. One of the best-known models for movement control is the so-called equilibrium-point hypothesis (Feldman et al. 1998; Polit and Bizzi 1978). In the context of Donders' law, the final equilibrium point for antagonistic muscle forces need incorporate not only the pointing direction of the arm but also its orientation. The question is, does the brain determine this final orientation by explicitly computing the corresponding muscular equilibrium points?

Since it is undeniably true that the mechanical plant must have some equilibrium point at any one time—that will not equal current position during motion—it is difficult to argue against this theory on the basis of behavior alone, but as a control strategy, it poses certain problems (Gottlieb 1998). For example, in the oculomotor system, it is clear that movements are not generated by equilibrium-point commands but rather by velocity commands that are sent directly to the plant and to a neural integrator that computes a tonic 3-D eye orientation signal (Crawford et al. 1991; Robinson 1975). In a sense, the latter provides an equilibrium point command to the ocular motoneurons, but this only specifies *current* eye position and is computed in somewhat passive fashion in response to movement commands. Likewise, we suggest that Donders' law of the arm is implemented through similar kinematic commands (see NONHOLONOMICS AND VELOCITY CONTROL).

TRAJECTORY MINIMIZATION. As explained by Ceylan et al. (2000), Listing's law is optimal for pointing in the sense that it guarantees the shortest route between any of two arm positions under the constraint of Donders' law. But it does not provide the absolute shortest path between joint positions, for to do so consistently for all paths and positions predicts systematic violations of Donders' law (Ceylan et al. 2000; Crawford et al. 1999; Tweed and Vilis 1990). Therefore the finding that arm torsion does not depend on starting position (see Fig. 5) is incompatible with "minimum-rotation" principles or at least a strict interpretation of them that would hold across all situations (Rosenbaum et al. 1999; Soechting et al. 1995; Uno et al. 1989). The Fick strategy does provide the shortest path rotation for vertical movements, but only at the cost of lengthening the path for most horizontal movements (Hore et al. 1992).

TRAJECTORY MINIMIZATION AGAINST GRAVITY. Again, in the present study, a tendency to minimize rotation of the upper arm was only observed for a subset of movements (vertical) at a subset of elbow configurations (bent-vertical). Does this mean that the Fick strategy was primarily being used to minimize angular arm displacements for work against gravity, as suggested by Hore et al. (1992)? Unlikely because these displacements became less optimal (i.e., less Fick and more Listing) as the elbow extended—increasing the work load against gravity, leading us back to the postural arguments that we began with. Moreover, it would appear that the Fick-like behavior first reported by Hore et al. (1992) may pertain more closely to the hand (which is what they measured) and so relate to factors other than those that we are considering.

NONHOLONOMICS AND VELOCITY CONTROL. Based on our discussion so far, one is left with the idea that arm movements for pointing to (distant) targets are planned in unconstrained, kinematically redundant coordinates that must then be converted into the appropriate points in a kinematic hyperspace. The various theories of trajectory minimization—in their strictest sense—are not compatible with our data but can be incorporated together with various Donders' strategies into the rules for a kinematic hyperspace, as discussed in the preceding text. So how then would the brain implement these rules? One possibility is that the brain could have a little box for each little sub-rule by learning and maintaining internal models to determine the motor commands required to perform specific tasks (Kawato 1999; Kawato and Wolpert 1998). But there may be a more parsimonious alternative.

We propose that there is just one control system, adjustable by different parametric inputs (e.g., proprioceptive signals, efference copies, muscle-spindle signals). In basic principle, such a system could resemble the relatively simple model used by Ceylan et al. (2000) for head-movement control. These authors proposed a velocity-constraint box, which could implement the control mode (Fick, Listing, or whatever) at the level of velocity commands rather than position commands. One advantage of using such commands is that they can be used downstream to derive postural commands—as in the oculomotor system—but more importantly, they offer a more flexible solution to the control problems observed in limb coordination.

Note that many of the rules in the kinematic hyperspace of the arm are probably *nonholonomic* (Wongchaisuwat et al. 1984), i.e., they cannot be controlled with the use of rules describing desired orientation—as in the equilibrium-point hypothesis among others—but can be controlled using velocity rules (Ceylan et al. 2000). In particular, the correct velocity can always be computed on the basis of current arm orientations and desired extrinsic pointing direction. In this respect, a flexible velocity-based control system has the flexibility to choose a Donders-type strategy or to violate Donders' law so as to minimize kinetic energy (Nishikawa et al. 1999; Soechting et al. 1995), depending on the context (Kelso et al. 1991). Thus the suggestion of Nishikawa et al. (1999)—that the arm is under control of velocity constraints—is in good agreement with the idea of nonholonomic modeling. Such a control system is probably the best way to implement the rules that determine the allowable positions in the arm's kinematic hyperspace.

We thank L. Sergio, L. Harris, and E. Klier for critical comments on the manuscript.

This study was supported by a grant (MT-13357) from the Canadian Medical Research Council (MRC). During the period of this study, D.Y.P. Henriques was supported by an E. A. Baker Foundation–Canadian National Institute for the Blind/MRC Doctoral Research Award, and J. D. Crawford was supported by an MRC scholarship.

REFERENCES

- BERNSTEIN N. *The Coordination and Regulation of Movements*. Oxford, UK: Pergamon, 1967.
- BUCHANAN JJ, KELSO JA, AND DE GUZMAN GC. Self-organization of trajectory formation. I. Experimental evidence. *Biol Cybern* 76: 257–273, 1997.
- CEYLAN MZ, HENRIQUES DYP, TWEED DB, AND CRAWFORD JD. Task-dependent constraints in motor control: pinhole goggles make the head move like an eye. *J Neurosci* 20: 2719–2730, 2000.
- CRAWFORD JD, CADERA W, AND VILIS T. Generation of torsional and vertical eye position signals by the interstitial nucleus of Cajal. *Science* 252: 1551–1553, 1991.
- CRAWFORD JD, CEYLAN MZ, KLIER EM, AND GUITTON D. Three-dimensional eye-head coordination during gaze saccades in the primate. *J Neurophysiol* 81: 1760–1782, 1999.
- CRAWFORD JD AND VILIS T. Axes of eye rotation and Listing's law during rotations of the head. *J Neurophysiol* 65: 407–423, 1991.
- CRAWFORD JD AND VILIS T. How do motor systems deal with the problems of controlling three-dimensional rotations? *J Mot Behav* 27: 89–99, 1995.
- DESMURGET M, GREY H, AND PRABLANC C. Final posture of the upper limb depends on the initial position of the hand during prehension movements. *Exp Brain Res* 119: 511–516, 1998.
- DONDERS FC. Beitrag zur Lehre von den Bewegungen des menschlichen Auges. *Anat Physiol Wiss* 1: 105–145, 1848.
- FELDMAN AG, OSTRY DJ, LEVIN MF, GRIBBLE PL, AND MITNITSKI AB. Recent tests of the equilibrium-point hypothesis. *Mot Control* 2: 189–205, 1998.
- FERMAN L, COLLEWIJN H, AND VAN DEN BERG AV. A direct test of Listing's law. I. Human ocular torsion measured in static tertiary positions. *Vision Res* 27: 929–938, 1987.
- GIELEN CCAM, VRIJENHOEK EJ, FLASH T, AND NEGGERS SFW. Arm position constraints during pointing and reaching in 3-D space. *J Neurophysiol* 78: 660–673, 1997.
- GLENN B AND VILIS T. Violations of Listing's law after large eye and head gaze shifts. *J Neurophysiol* 68: 309–318, 1992.
- GOTTLIEB GL. Rejecting the equilibrium-point hypothesis. *Mot Control* 2: 10–12, 1998.
- HAUSTEIN W. Considerations on Listing's Law and the primary position by means of a matrix description of eye position control. *Biol Cybern* 60: 411–420, 1989.
- HENRIQUES DYP, KLIER EM, SMITH MA, LOWY D, AND CRAWFORD JD. Gaze-centered remapping of remembered visual space in an open-loop pointing task. *J Neurosci* 18: 1583–1594, 1998.
- HORE J, WATTS S, AND VILIS T. Constraints on arm position when pointing in three dimensions: Donders' law and the Fick gimbal strategy. *J Neurophysiol* 68: 374–383, 1992.
- KAMPER DG AND RYMER WZ. Effects of geometric joint constraints on the selection of final arm posture during reaching: a simulation study. *Exp Brain Res* 126: 134–138, 1999.
- KAWATO M. Internal models for motor control and trajectory planning. *Curr Opin Neurobiol* 6: 718–727, 1999.
- KAWATO M AND WOLPERT D. Internal models for motor control. *Novartis Found Symp* 218: 291–304, 1998. Discussion 304–307.
- KELSO JA, BUCHANAN JJ, AND WALLACE SA. Order parameters for the neural organization of single, multijoint limb movement patterns. *Exp Brain Res* 85: 432–444, 1991.
- KLIER EM AND CRAWFORD JD. Human oculomotor system accounts for 3-D eye orientation in the visual-motor transformation for saccades. *J Neurophysiol* 80: 2274–2294, 1998.
- MEDENDORP WP, MELIS BJM, GIELEN CCAM, AND VAN GISBERGEN JAM. Off-centric rotation axes in natural head movements: implications for vestibular reafference and kinematic redundancy. *J Neurophysiol* 79: 2025–2039, 1998.
- MEDENDORP WP, VAN GISBERGEN JAM, HORSTINK MWIM, AND GIELEN CCAM. Donders' law in torticollis. *J Neurophysiol* 82: 2833–2838, 1999.
- MILLER LE, THEEUWEN M, AND GIELEN CCAM. The control of arm pointing movements in three dimensions. *Exp Brain Res* 90: 415–426, 1992.
- MINKEN AW AND VAN GISBERGEN JAM. Dynamical version-vergence interactions for a binocular implementation of Donders' law. *Vision Res* 36: 853–867, 1996.
- MOK D, RO A, CADERA W, CRAWFORD JD, AND VILIS T. Rotation of Listing's plane during vergence. *Vision Res* 32: 2055–2064, 1992.
- NISHIKAWA KC, MURRAY ST, AND FLANDERS M. Do arm postures vary with the speed of reaching? *J Neurophysiol* 81: 2582–2586, 1999.
- POLIT A AND BIZZI E. Processes controlling arm movements in monkeys. *Science* 201: 1235–1237, 1978.
- RADAU P, TWEED D, AND VILIS T. Three-dimensional eye, head, and chest orientations after large gaze shifts and the underlying neural strategies. *J Neurophysiol* 72: 2840–2852, 1994.
- ROBINSON DA. Oculomotor control signals. In: *Basic Mechanisms of Ocular Motility and Their Clinical Implications*, edited by Bach-y-Rita P and Lennerstrand G. Oxford, UK: Pergamon, 1975, p. 337–374.
- ROSENBAUM DA, MEULENBROEK RG, VAUGHAN J, AND JANSEN C. Coordination of reaching and grasping by capitalizing on obstacle avoidance and other constraints. *Exp Brain Res* 128: 92–100, 1999.
- SOECHTING JF, BUNEO CA, HERRMANN U, AND FLANDERS M. Moving effortlessly in three dimensions: does Donders' law apply to arm movement? *J Neurosci* 15: 6271–6280, 1995.
- STRAUMANN D, HASLWANTER T, HEPP REYMOND MC, AND HEPP K. Listing's law for eye, head and arm movements and their synergistic control. *Exp Brain Res* 86: 209–215, 1991.
- THEEUWEN M, MILLER LE, AND GIELEN CCAM. Is the orientation of head and arm coupled during pointing movements? *J Mot Behav* 25: 242–250, 1993.
- TURVEY MT. Coordination. *Am Psychol* 45: 938–953, 1990.
- TWEED D. Visual-motor optimization in binocular control. *Vision Res* 37: 1939–1951, 1997.

- TWEED D, CADERA W, AND VILIS T. Computing three-dimensional eye position quaternions and eye velocity from search coil signals. *Vision Res* 30: 97–110, 1990.
- TWEED D AND VILIS T. Geometric relations of eye position and velocity vectors during saccades. *Vision Res* 30: 111–127, 1990.
- UNO Y, KAWATO M, AND SUZUKI R. Formation and control of optimal trajectory in human multijoint arm movement. Minimum torque change model. *Biol Cybern* 61: 89–102, 1989.
- WONGCHAIWAT C, HEMAMI H, AND BUCHNER HJ. Control of sliding and rolling at natural joints. *J Biomech Eng* 106: 368–375, 1984.