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Constraints on Arm Position When Pointing in Three Dimensions: Donders' Law and the Fick Gimbal Strategy

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SUMMARY AND CONCLUSIONS

1. While making saccades between targets with the head stationary, eye positions are constrained to two of the possible three degrees of freedom. Classically this constraint has been described by Donders' and Listing's laws. The objective was to determine whether these laws also apply for the straight arm when pointing between different targets. Thus we determined whether the arm adopts only one angular position for every pointing direction (Donders' law) and whether these positions can be described by rotations from a reference position about axes that lie in a plane (Listing's law).

2. The angular positions (orientations) of the arm in three-dimensional space were studied as subjects pointed with a straight arm at different targets. Arm position was measured with the search coil technique by means of coils attached to the back of the hand. Pointing was studied over a range of ±45° in all directions from a central target located 45° to the right of the straight-ahead position.

3. The positions of the arm in space were described by quaternion vectors, i.e., a particular position was described in terms of the axis and amplitude of a rotation from a reference position to that position. Using this description, it was found that the straight arm adopted a similar orientation (standard deviations ranged from 2.8 to 4.8°) when pointing at a particular target irrespective of which target from which it had moved.

4. The angular position vectors for arm positions associated with relatively small movements (e.g., less than ±30°) lay in a flat surface with minimal torsion. At first sight, this surface appeared to be similar to Listing's plane of the eye. However, for positions associated with larger movements (e.g., ±45°) it became apparent that, unlike the eye, the surface deviated from one obeying Listing's law, i.e., it was twisted and showed torsion like that produced by rotations around the horizontal and vertical axes of a Fick gimbal. (The characteristic of a Fick gimbal is that the vertical axis is fixed, whereas the horizontal axis moves with the gimbal.)

5. Although there were differences between subjects, all showed a twisted position vector surface. The twist was always in the same direction, and it was always less than that of a Fick gimbal.

6. This position vector surface had a similar shape whether the arm was stationary or was moving between targets, whether subjects pointed with or without vision, and whether the pointing arm had moved between targets or from a bent-elbow position on the lap.

7. The position vector surface showed a stronger alignment with gravity than with the body: it tilted from the vertical by an average of only 10° for body tilts of >60°.

8. Thus the straight arm when pointing is similar to the eye when reorienting gaze in that it achieves a similar angular position for a particular target, i.e., it is constrained to two of the possible three degrees of freedom and thus obeys Donders' law. However, the arm is different from the eye in that the positions adopted do not follow Listing's law. Instead, the arm, to various degrees, adopts positions similar to those of a Fick gimbal. This appears to be a neurally imposed strategy that may be the consequence of working against gravity.

INTRODUCTION

How the CNS plans and executes limb movements in three dimensions is a problem of great complexity (Smith and Humphrey 1991). For example, attempts to model movements in terms of desired hand trajectories indicate that three successive sets of computations must be performed: first, joint angle changes must be specified using inverse kinematic computations; second, torques must be calculated using inverse dynamics; and third, muscle patterns must be computed and generated. The problem of the complexity of such calculations has led to a search for simplifying principles by which movements are generated. Some that have been suggested include approximately linear hand trajectories (Flash and Hogan 1985; Morasso 1981), bell-shaped velocity profiles (Hogan and Flash 1987), constant ratio of joint angular displacement (Kots and Syrovegin 1966), fixed relation between shoulder and elbow angles (Lacquaniti and Soechting 1982), invariant velocity profiles with speed and load (Atkeson and Hollerbach 1985), minimum torque change (Uno et al. 1989), and determination of final position by length-tension equilibrium points (Bizzi et al. 1984; Feldman 1966; Hogan 1984, 1988).

Another suggested simplifying principle is that movements are controlled by means of synergies, which are control strategies that reduce the number of patterns of muscle activity that are available (Bernstein 1967). This in turn reduces the degrees of freedom of the movement and simplifies the control problem (see Macpherson 1991). One example of a synergy is found in the oculomotor system, where it is known as Donders' law. In the mid-nineteenth century, Donders discovered that for steady fixation the positions of the eye are restricted such that there is only one eye position for every gaze direction (Helmholtz 1867). Thus the eye is constrained to two of its possible three degrees of freedom. The positions the eye is constrained to were investigated by Listing and Helmholtz by observation of the tilt of afterimages in different gaze directions. They described eye positions with reference to a central eye position (primary position). Eye positions were described in terms of a rotation from this primary position. Their result, now known as Listing's law is that the eye assumes only those positions that can be achieved by single rotations from primary position about axes that lie in a plane that was then defined as having zero torsion. This plane, known as Listing's plane, lies orthogonal to the gaze direction when the eye is in primary position.

Can Donders' and Listing's laws be applied to the arm? Simple observation suggests that Donders' law applies for straight-arm pointing movements. For example, ask a subject to select three widely separated targets in front of him and to point randomly between them. It can be observed that, while the subject is pointing at a particular target, the position (orientation) of the wrist in space appears to be the same, irrespective of which target he just moved from. In theory, this need not be the case: for a particular pointing direction, the amount of twist of the arm around its own long axis could vary by >180°. Thus in pointing there appears to be a constraint on arm position. If born out by careful measurement, this would indicate that the arm when pointing is restricted to two degrees of freedom, i.e., it is restricted to a two-dimensional subspace of the three-dimensional position vector space of all possible orientations (Hepp et al. 1991). But which two-dimensional subspace is the arm restricted to? Can it be described by Listing's law, which requires that these position vectors be confined to a plane? It is not obvious from simple observation whether this is the case. It has been reported (Hepp and Hepp-Reymond 1989; Hepp et al. 1991; Straumann et al. 1990) that local Listing's planes exist for the arm, but these were for the upper arm and for movements of relatively small amplitude (±25° from a central target) compared with the full range of arm movements (greater than ±90°).

The overall objective of the present experiments was to investigate the strategy involved in straight-arm pointing. The specific objectives were *1*) to determine how accurately arm position follows Donders' law and *2*) to determine whether Listing's law applies, i.e., to determine whether, if arm positions are expressed in terms of single rotations from a reference position, the axes of these rotations lie in a plane. Preliminary results have been reported (Hore et al. 1990, 1991).

METHODS

Procedures

Experiments were performed on 12 adult human subjects. Three-dimensional arm position vectors were measured with the use of a modification of Robinson's (1963) magnetic field–search coil technique as previously described (Tweed et al. 1990). Arm movements were monitored with the use of two orthogonal search coils. The coils were taped to the back of the hand just distal to the wrist. This arrangement measured the position of the hand in three-dimensional space, and, with the arm straight, effectively measured the overall rotation of all arm joints. A second coil pair was taped to the upper chest to monitor body movements. The subjects sat in three 2-m diam orthogonal alternating magnetic fields (frequencies 62.5, 100, and 125 kHz) positioned so that the sagittal plane of the body was in the plane of the forward and vertical magnetic fields. The fields were uniform over a working range of ~1 m^3. Three voltages from each search coil induced by the field were sampled at 100 Hz, which gave the pointing direction of each coil.

Subjects performed two straight-arm pointing tasks. *1*) Randomly sequenced pointing between specified targets located at the center and corners of a square: for this task, subjects pointed between targets in response to verbal commands read from a random list. *2*) Spontaneous pointing to randomly chosen objects in the room: for both tasks, subjects were instructed to move naturally between targets at their own speed and to point accurately at the targets. No mention was made of hand or arm orientation until the end of the experiment, when some subjects were asked to change the orientation of the hand and then to continue pointing, or to deliberately twist their arm when moving between targets. The initial orientation of the wrist varied between subjects. As described in the following sections, this initial position, when the subject was pointing at the central target, was defined as the reference position. Subjects also pointed while leaning backward or forward. In these experiments, attempts were made to keep the shoulder at approximately the same point in space by moving the chair forward, and backward, up, and down. In additional experiments, five subjects pointed at the same targets, first with the arm straight and second starting with the hand resting on the lap with the elbow bent.

For the target pointing task, targets (8-mm circles) were located with respect to a central reference target. This central target was defined separately for each subject: it was placed so that arm position was horizontal and 45° to the right of the straight-ahead pointing direction. This position was chosen as center because it was approximately at the center of the mechanical working range of the arm. A potential problem exists in the location of targets due to the fact that subjects, when using vision, point with the finger tip on a line of sight from the eyes to the object, i.e., not on a line from the shoulder through the finger to the object (Taylor and McCloskey 1988). Thus, if the targets are symmetrically located with respect to the shoulder, the arm will not be symmetrically located when the subject uses vision to point at them. To minimize this problem, targets were located for each subject by positioning the arm, e.g., the upper left 30° target was located by moving the arm from the central target first horizontally to the left through 30° and then up vertically through 30°. The subject was then asked to specify visually the location of the target, which was then adjusted for that arm position. Targets were located ~10 cm from the fingertip.

Quaternion vectors

Arm position was computed off-line with the use of the algorithms described in Tweed et al. (1990). Arm position was defined in terms of quaternion (angular position) vectors. The properties and advantages of quaternions for describing position in three dimensions are described in Tweed and Vilis (1987). One advantage of quaternions for arm movement studies is that they give an accurate representation of position over 360°. In brief, a quaternion is a four-component object that can be regarded as the sum of a scalar and a vector: $q = q_0 + \boldsymbol{q}$. If the arm moves from the central reference position by a rotation of α degrees, the quaternion vector is $\boldsymbol{q} = \sin(\alpha/2)\,\boldsymbol{n}$, where $\boldsymbol{n}$ is the axis of the rotation and $\sin(\alpha/2)$ is its length. Thus arm position is represented by quaternion vectors where each point $\boldsymbol{q}$ depicts the rotation required to move the arm from its central (reference) position to its current position in terms of axis and amplitude. Over our operating range, there is an approximately linear relation between quaternions and angles and so, for simplicity, the scale was marked in angles.

Coordinate system

In this paper, arm position is specified with respect to a coordinate system that was fixed in space. Its orientation was defined with respect to arm position as the subject pointed at the central reference target (R) at the beginning of the experiment (Fig. 1). Thus the torsional axis was a straight line down the arm, whereas

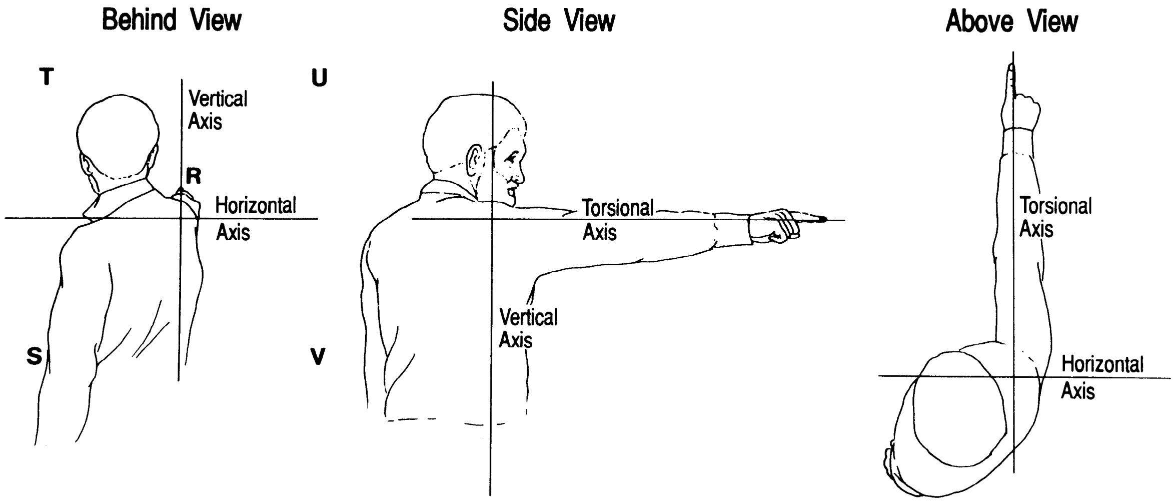

FIG. 1. Behind, side, and above views of the vertical, horizontal, and torsional axes that were fixed in space. S, T, U, and V are peripheral targets, and R is the central (reference) target. Subject is shown pointing at target R. This arm position was used at the start of the experiment to define the reference position.

the horizontal and vertical axes were at right angles to this. Arm position was described in terms of three views of this coordinate system: a behind view, which looked down the torsional axis, gave the horizontal and vertical components (note that the behind view was at 45° to a line through both shoulders); a side view at right angles to this, which looked down the horizontal axis, gave rotations torsionally and to the left and right (around the vertical axis); and an above view gave rotations torsionally and up and down (around the horizontal axis). Torsion, in keeping with standard practice in eye movement studies, is defined with respect to this simple orthogonal coordinate system. Confusion can arise unless it is realized that, for any pointing direction other than reference, torsion is not the same as twist (rotation) of the arm around its pointing direction. For example, consider the situation when the subject is pointing at the central reference target: rotation about an axis parallel to the arm produces movement around the torsional axis (generates torsion). However, if the arm is moved 90° to the right of reference position, now rotation about an axis parallel to the arm produces movement around the horizontal axis whereas up or down movements generate torsion. Thus torsion is defined as movement around an axis that is fixed in space.

Surface fitting

The data describing arm positions were fitted to a second-order surface defined by the equation

$$q_T = a_1 + a_2 q_V + a_3 q_H + a_4 q_V^2 + a_5 q_V q_H + a_6 q_H^2$$

where q_T, q_V, and q_H are the torsional, vertical, and horizontal components. The parameter a_5 was used to measure the amount of twist of the surface. The standard deviations to the fitted surface were also calculated (see Tweed and Vilis 1990).

RESULTS

Data format

As an aid to understanding the data format used in this paper, consider a theoretical movement that obeys Listing's law from the central target R to target U as viewed from behind (Fig. 1). The axis about which this rotation takes place is perpendicular to the pointing direction, i.e., it has a similar orientation to the line joining T and V. Now consider the representation of arm position while the subject is pointing at U in terms of a quaternion vector as viewed from behind (Fig. 2*A*, Behind). The vector lies along the axis as described above with its amplitude proportional to the angle of rotation. The direction of the vector is given by the right hand rule: if the thumb points in the direction of the position vector, the fingers curl round in the direction the arm is rotated away from reference position, i.e., in this case up and to the right. Inspection of the side view shows that the axis of this theoretical movement has a component along the vertical axis, whereas the above view shows that the axis also has a component along the horizontal axis. Because it has no torsional components, it lies in a plane with zero torsion.

Now consider the representation of arm position while the subject is pointing at target U after a second theoretical movement from target T (Fig. 1). The quaternion vector (axis and amplitude) describing position is the same, although the actual axis used to make the movement is quite different. Thus arm positions are defined in terms of theoretical rotations required to move the arm from its central (reference) position to its current position. These are not the same as the actual axes used to make the movements (except for those starting from reference).

Reproducibility of arm position when pointing

Now consider real movements to target U. Figure 2*B* shows quaternion plots of three such movements: from center target R, from target T, and from target V. Each of the many points on the three traces represents arm position, whether during the movement or when stationary. Each point represents the vector, i.e., it represents the tip of the arrowhead on the straight line from center. Inspection of the behind view shows that all three movements finished in approximately the same position. Inspection of the side view shows that the degree of torsion of the arm was similar after all three movements. This result is reinforced in Fig. 2*C*, which shows only the final positions for 11 movements from the three targets. The range of torsion in this final position was 6°. Table 1 shows that this result is representa-

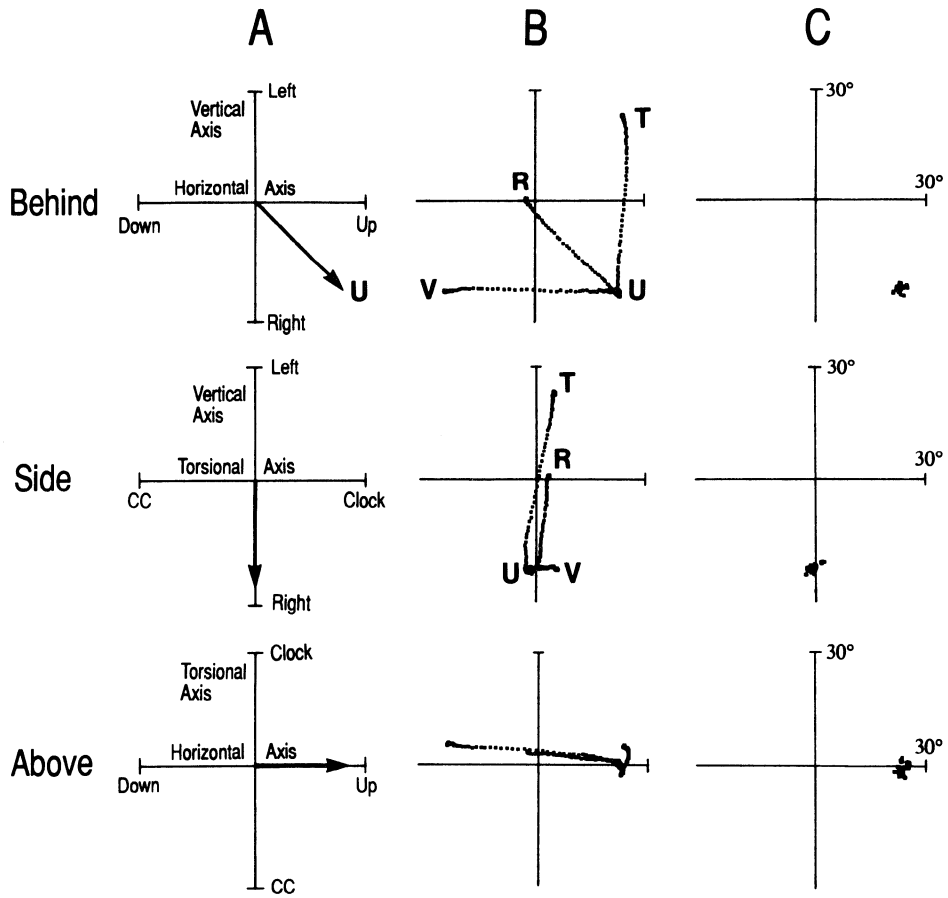

FIG. 2. Quaternion vector representation of arm position for movements to target U as viewed from the behind, side, and above. *A*: position after a theoretical movement from target R to target U (Fig. 1). Quaternion vector is at 90° to the straight line R-U in the behind view because it represents the axis of rotation of the movement and not the trajectory. *B*: data from actual movements from targets R, T, and V to target U. Each point during the movement and at the final position represents the quaternion position vector, i.e., the tip of the arrowhead on the straight line from center. *C*: final positions for 11 movements to target U. Clock, clockwise rotation; CC, counterclockwise rotation.

tive. Considering 332 movements to the five ±45° targets in the seven subjects that were studied, the mean of the range of torsion was 7.9°. The mean standard deviation of torsional position was 2.5°.

A further way to obtain a quantitative assessment of the degree to which Donders' law is obeyed is to determine the standard deviation of the thickness of the surface that fits the data points (see METHODS). Standard deviations of second-order fits ranged from 2.8 to 4.8° for the different subjects (Table 1), again indicating a good compliance with Donders' law. Thus, when the subject is pointing at a particular target, there is a major constraint on torsional arm position.

An analogue of Listing's law for the arm?

Were Listing's law to apply for the arm, it would require that the axes of the rotations from reference position to the adopted arm positions (i.e., quaternion vectors) should all lie in a plane. To determine whether this was the case, the quaternion vectors for positions during all movements and at all final positions for the same experiment shown in Fig. 2 were plotted for the behind and side views (Fig. 3*A*). When viewed from the side, it can be seen that there is a major constraint on torsion, i.e., all positions have minimal torsional components. This constraint on torsion can be clearly seen by comparing this side view with that obtained while the subject made spontaneous pointing movements over the same target range but deliberately twisted the arm (Fig. 3*B*). It can be seen that the torsion developed while pointing at the five targets (Fig. 3*A*) is a small fraction of that which the arm is capable of achieving. A similar constraint on torsion was seen while the subject pointed spontaneously at randomly located objects in the room over this same range (Fig. 3*C*). If subjects were instructed to change the orientation of the arm, e.g., from a horizontal wrist position to one rotated by 90° clockwise, they tended to maintain this new orientation while pointing in subsequent trials. This resulted in a planar surface that was shifted along the torsional axis.

Is this data equivalent to Listing's plane of the eye? Figure 3*D* shows the behind and side view of the equivalent eye movement data recorded with the same equipment, but with the coil in a contact lens on the eye in a different

TABLE 1. *Range of torsion at targets*

Subject	Targets, ±45° R	T	S	U	V	SD of Surface Thickness
PRE	9 ± 2.2	15 ± 5.7	11 ± 4.0	8 ± 2.3	7 ± 2.1	4.79
NAS	5 ± 1.5	10 ± 3.3	8 ± 3.0	8 ± 2.8	3 ± 1.2	4.32
SHE	9 ± 3.0	12 ± 4.1	12 ± 3.5	3 ± 1.2	6 ± 2.2	4.47
JON	8 ± 2.2	6 ± 1.9	3 ± 1.2	3 ± 1.1	5 ± 1.4	2.78
HOC	8 ± 2.7	9 ± 3.2	8 ± 2.3	4 ± 1.3	5 ± 1.7	3.79
DER	10 ± 3.0	10 ± 3.8	8 ± 2.7	11 ± 5.3	3 ± 1.1	4.50
MAR	10 ± 3.1	8 ± 2.2	11 ± 2.7	12 ± 2.8	9 ± 1.2	3.55

Values are means ± SD in degrees of torsion at each of the five targets. Subjects (n = 7) made ~10 movements to each target. R, central target; T, S, U and V, peripheral targets.

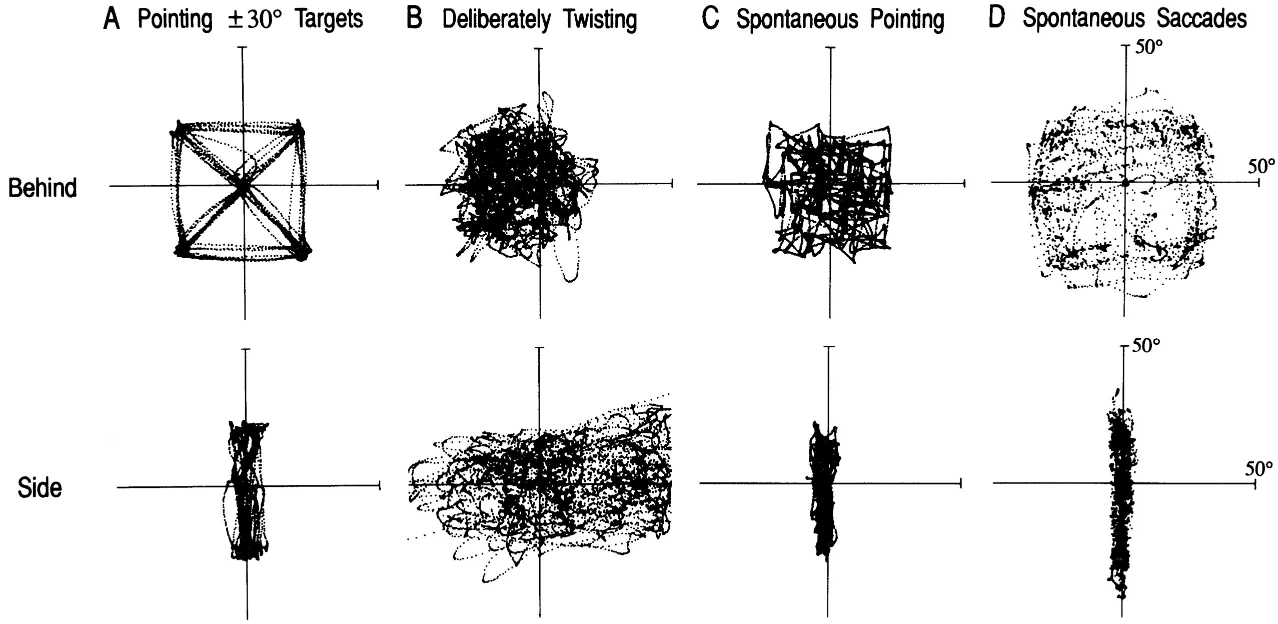

FIG. 3. Comparison of degree of torsion developed in position for arm pointing movements and eye saccades. Quaternion vector representation of positions as in Fig. 2. *A*: arm pointing between center and ±30° targets. *B*: spontaneous pointing, but with arm deliberately twisting. *C*: spontaneous pointing within ±30° target range. *D*: spontaneous saccades. The side view in *D* shows the experimental recording of Listing's plane. *A–C*: subject HOC. *D*: subject SHE.

subject. The subject with head stationary made spontaneous saccades over the full oculomotor range. The side view shows the data corresponding to Listing's plane, i.e., torsion is severely constrained such that all points lie within about ±5° of a single plane. Comparison of the eye and arm movement data indicates that some similarities exist, although the torsion is slightly greater for the arm. Thus, over this ±30° target range, an analogue of Listing's law appeared to hold for the arm. However this was not born out by further investigation.

Failure of Listing's law

Because the arm has a range of about ±90° from the central (reference) target, we investigated whether this apparent Listing's analog applied for larger movements. Figure 4 shows the results for a second subject. Again while the subject was pointing at the ±30° targets (Fig. 4*A*), the side view shows that torsion was constrained, in this case to a range of ~15°. However, considering results from movements over the ±45° target range (Fig. 4*B*), there is a large increase in torsion that now varies over a range of >30°. In theory, this could result from a breakdown in Donders' law, thereby producing a uniformly thicker plane. However, inspection of the data for each corner revealed that Donders' law was still approximately obeyed (Table 1, PRE). Thus it is clear that these points do not lie on a plane, i.e., Listing's law does not apply.

To determine whether these points could be described by a surface, and if so, to determine its shape, the data were fitted by a second-order surface fitting program. This revealed more clearly what can be seen in the original data: there is a surface, and it is twisted and has torsion (Fig. 4, Side Surface Fit). The twist, viewed from the side, was like that produced as follows: hold a sheet of paper vertical as if to read it, with the left hand holding the left edge and the right hand holding the right edge, fold the right hand over the left, then raise the right hand vertically by 10 cm. Thus the thick line in Fig. 4 represents the near and bottom edge of such a surface. Moving down this near edge from top to bottom corresponds to a torsional change from clockwise to counterclockwise (c.f. Fig. 2*A*, Side). This twisted surface was observed in all subjects who were studied over the ±45° range. Examples of the corresponding surfaces seen from the above and side views for four further subjects are shown in Fig. 5.

The degree of twist of the surface was determined quantitatively by means of the surface fitting program, which provided a numerical value for the degree of twist. This value was the a_5 parameter (see METHODS). Its magnitude was independent of the initially chosen reference position. Values for the other parameters were inevitably smaller, usually by at least an order of magnitude. The values for the degree of twist for the surfaces for the seven subjects who performed the ±45° target pointing were −0.75, −0.79, −0.88, −0.61, −1.10, −0.90, and −0.67. These values can be compared with a value of 0 (no twist) and −1.23 (twist displayed by a Fick gimbal, see DISCUSSION).

This twisted surface had a similar shape for positions while the arm was moving (Fig. 4*C*) and while it was stationary (Fig. 4*D*). The values for the degree of twist for the surfaces shown in Fig. 4, *C* and *D*, were −0.75 and −0.74, respectively. Similar degrees of twist were also found for the surfaces when the arm was moving and when it was stationary while the subject was spontaneously pointing. For example, values for the spontaneous pointing shown in Fig. 3*C* were moving −0.45, stationary −0.49.

The position vector surface was also twisted and displayed torsion for positions adopted in movements without vision, whether these were made on command to remembered target positions (Fig. 6*A*) or were made spontane-

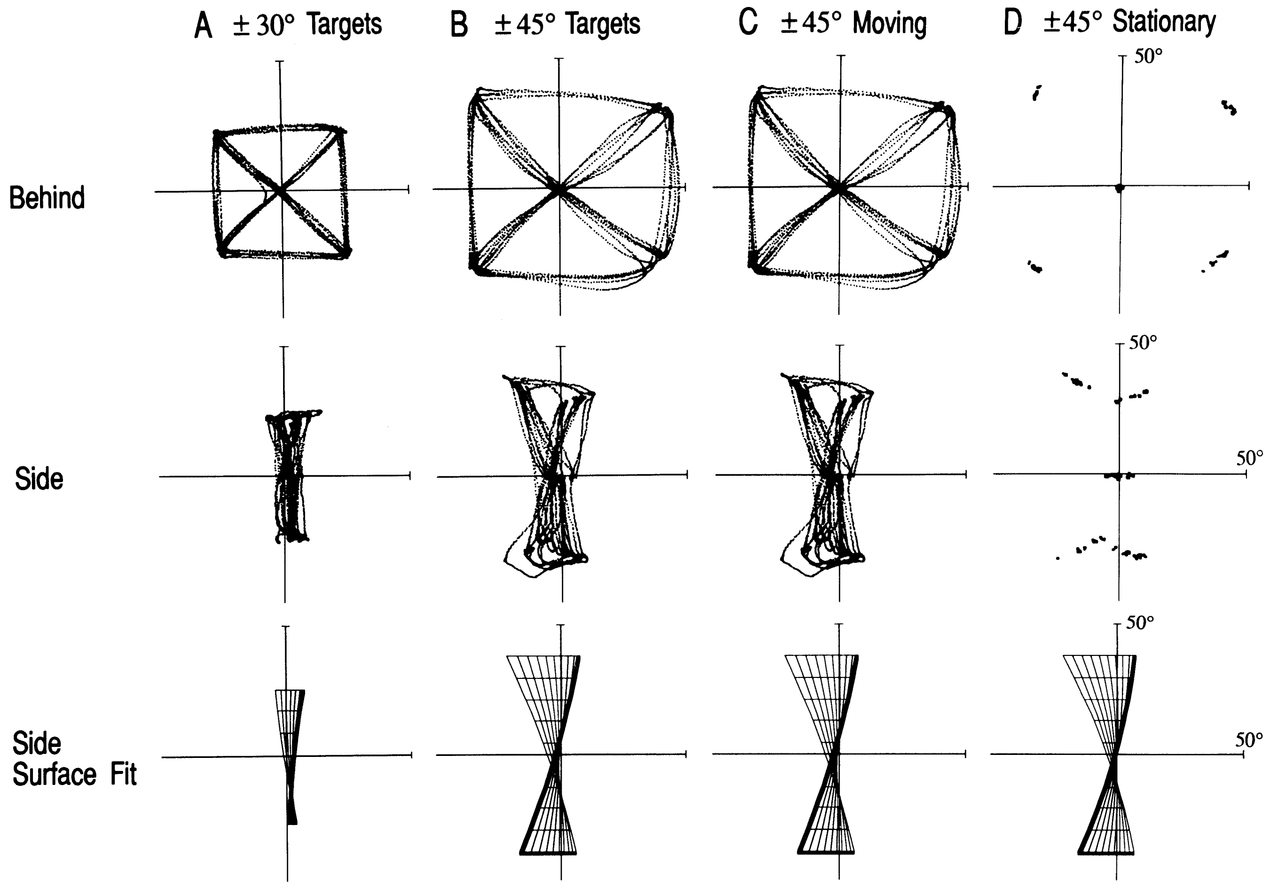

FIG. 4. Development of large torsions and a surface twist for positions associated with large arm pointing movements. Quaternion vectors shown from behind and side views as in Fig. 2 and from side view when data were fitted by a 2nd-order surface fitting program. *A*: ±30° targets. *B*: ±45° targets. *C*: arm positions while only moving for same movements as in *B*. *D*: arm positions while stationary for same movements as in *B*. Subject PRE.

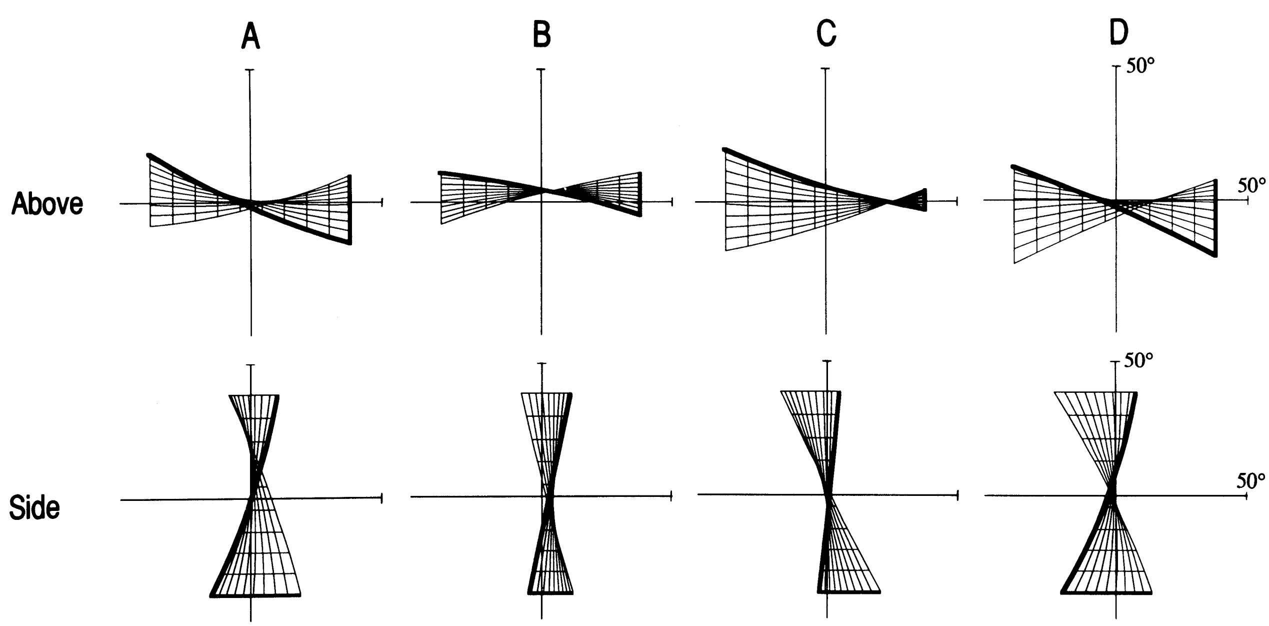

FIG. 5. Second-order surface fits of quaternion vector data for 4 representative subjects who made movements to ±45° targets. Surfaces show torsion and are twisted. *A*: subject NAS. *B*: subject HOC. *C*: subject SHE. *D*: subject JON.

ously (Fig. 6*B*). The degree of twist of these surfaces was −0.97 and −0.73, respectively.

Pointing from a bent-arm starting position

Do the final angular pointing positions in space depend on having started from a straight arm position? Would a similar final position vector surface occur if the arm started from a bent-elbow position? To answer these questions, we performed additional experiments on five subjects in which they pointed to the same targets as before but started with the hand resting on the lap with the elbow bent. They also performed the straight-arm pointing as before. The final position vector surface was determined in both cases while the arm was stationary, pointing at the targets. Although there was some variability between tasks and between subjects, overall the position vector surface for the bent-arm pointing was similar to that for the straight-arm pointing. The average degree of twist of the surface for the five subjects was bent arm −0.63, straight arm −0.65. The values (bent arm, straight arm) for the individual subjects were −0.56, −0.60; −0.74, −0.62; −0.46, −0.67; −0.90, −0.42; and −0.49, −0.94, respectively. This indicates that under these conditions similar pointing positions were achieved irrespective of whether the arm was initially straight or bent.

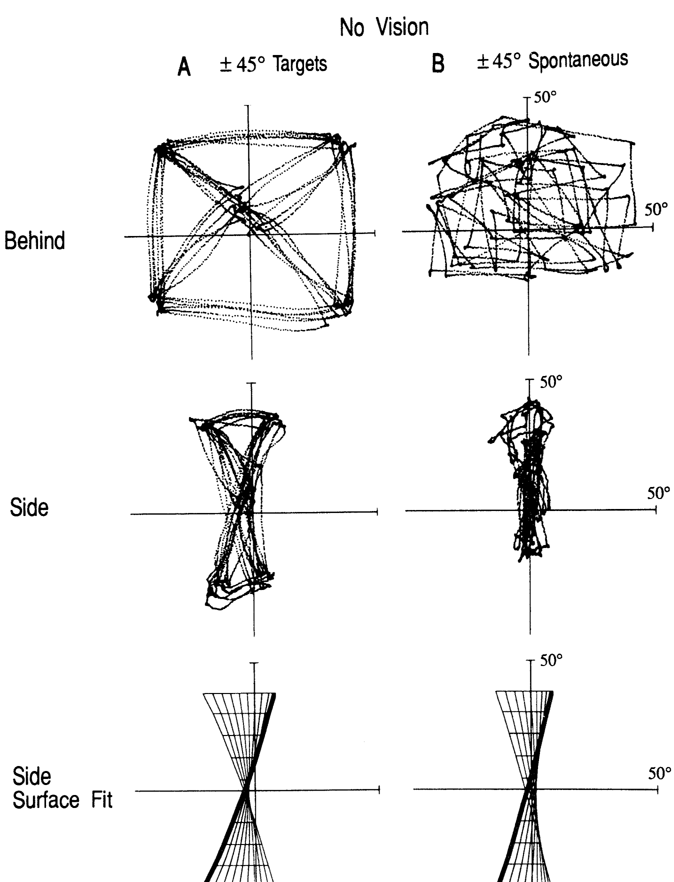

FIG. 6. Large movements made without vision also show torsion and surface twist. Same data format as Fig. 4. *A*: positions for movements to remembered ±45° targets. *B*: positions for spontaneous movements. Subject PRE.

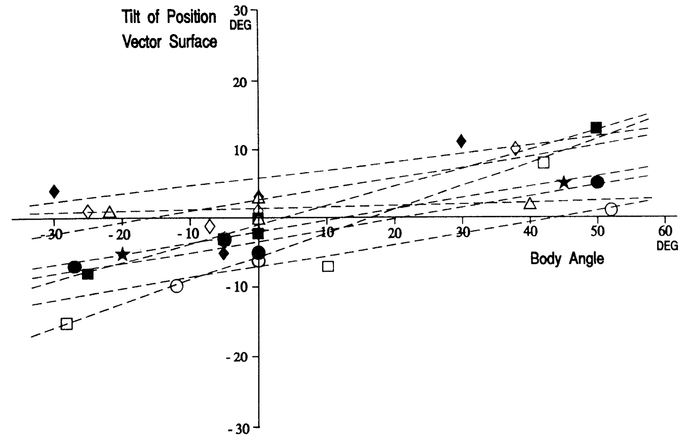

FIG. 7. Relation of tilt of the position vector surface to tilt of the body. The orientation of the position vector surface was determined mathematically; the orientation of the body was determined from the search coil taped to the chest. Measurements were made with the body in a natural upright position leaning against a vertical board, leaning forward, and leaning backward. A different symbol is used for each of the 8 subjects. Dashed lines are the best linear fit to the data for each subject.

Alignment of position vector surface with gravity

An interesting feature of the data shown so far is that the arm position vector surface appears to be oriented vertically (see Figs. 3–6, side view). This was not the case for the equivalent data for eye positions, which, when viewed from the side, were tilted by ≤20° from the vertical when the head was in its natural upright position (Tweed et al. 1990). This suggested that the position vector surface for the arm may be oriented with respect to gravity rather than to the body. To investigate this possibility, subjects were asked to point between targets with a straight arm as before, but when their body was upright, tilted forward, tilted backward, then upright again. The results of these maneuvres are shown in Fig. 7, in which tilt of the position vector surface is plotted against tilt of the body for the eight subjects investigated, three of whom were used in the previous experiments. Two points can be seen. First, for the upright posture (defined as 0 body angle in the first trial), there is only a very small tilt of the position vector surface for all eight subjects. This confirms that the position vector surface was aligned relatively vertically. Second, for all subjects, there was a relatively small degree of tilt of the surface for different body tilts. Considering the average of all subjects, when the body tilted forward (positive values) by 45°, the position vector surface tilted forward (positive values) by 8°; when the body tilted backward by 22°, the surface tilted back by an average of 2°. Overall, for an average body tilt of 67°, the position vector surface tilted by 10°. This result indicates that the arm position vector surface was more strongly aligned to gravity than to the body.

DISCUSSION

The rationale for this study was that the principles used by the CNS to control saccadic eye movements may be the same as those used to control straight-arm pointing movements. Saccades have some intriguing properties that reflect their CNS control, i.e., eye positions are constrained in a particular way as described by Donders' and Listings laws. The present results show that there are similarities and differences between saccades and straight-arm pointing. Like the eye, the arm when pointing adopts the same orientation for a particular target, i.e., it approximately obeys Donders' law. Unlike the eye, arm positions do not obey Listing's law: the position vector surface that describes them is not a plane but is a surface that is twisted and has torsion.

Although previous studies of pointing over a small range reported a Listings-like plane (Hepp and Hepp-Reymond 1989; Hepp et al. 1992; Hore et al. 1990; Straumann et al. 1990), this plane is likely to be the result of having revealed only a small portion of the overall surface (cf. Figs. 3 and 4). In fact, these small portions, although they have minimal torsion, cannot be described as being a plane because they have a twist. This can be seen for the ±30° movements in the side surface fit in Fig. 4*A* and in the numerical value of −0.58 for its degree of twist (where 0 equals no twist).

Analogy to a Fick gimbal

What is the significance of the shape of this position vector surface? Interestingly, this surface has similarities to the position vector surface that describes the positions that can be achieved by a Fick gimbal. A gimbal is a device in which a system of axes is nested within each other. One example of a gimbal is the set of three metal rings that are pivoted, one within the other, that maintains a ship's compass on a horizontal plane. A gimbal in which the "horizontal" axis is mounted inside the "vertical" axis is called a Fick gimbal. An example of a Fick gimbal is an earth-fixed telescope: the telescope can rotate horizontally about the fixed vertical axis and can rotate vertically around a mobile horizontal axis (Nakayama 1983). A consequence of this system is that, when scanning the environment, the horizontal crosshair in the eye piece always lines up with the horizon.

Figure 8*A* shows diagrams of a Fick gimbal. To avoid confusion with the labeling of the axis system used in this paper, which is fixed in space, the axes of the gimbal will be described by use of quotation marks. Again note that the

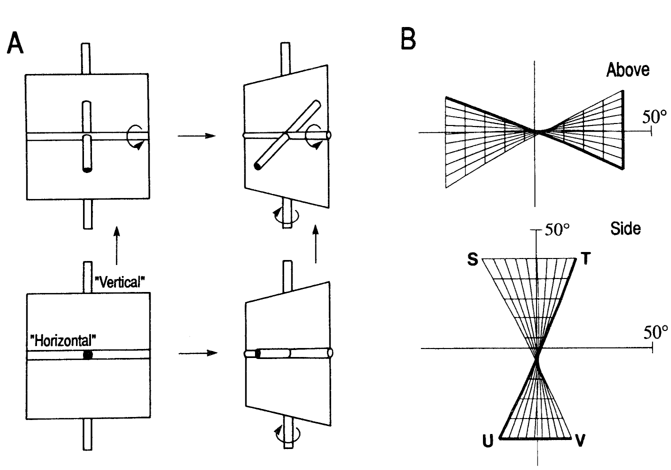

FIG. 8. Arm pointing movement modeled by a Fick gimbal. *A*: movement from reference target R to target U (Fig. 1) is achieved by rotations around the "horizontal" and "vertical" axes in either order or around both simultaneously. *B*: 2nd-order surface fit of quaternion vectors measured as the gimbal was rotated in order by 90° around the "horizontal" and "vertical" axes between targets S, T, U, and V (Fig. 1).

"horizontal" axis of the gimbal is mobile, whereas the "vertical" axis is fixed in space. Now consider movement of the gimbal from its position shown in Fig. 8*A*, *bottom left*, to that shown in the *top right*, i.e., such that its pointing direction is up and to the right when viewed from behind. This is equivalent to the pointing movement of the arm from target R to target U as described in Figs. 1 and 2*A*. To get to this position, the gimbal can move first around its "horizontal" axis (*bottom left* diagram to *top left*) and then around the "vertical" axis (*top left* diagram to *top right*). Alternatively, the gimbal can be rotated first around the "vertical" axis and then the "horizontal" axis. A direct diagonal movement can be made by simultaneously rotating about both axes.

To determine the positions that can be adopted by a Fick gimbal when rotated around these two axes, a coil was attached to the pointing arm (3rd axis), and the gimbal was rotated by 90° in succession around its "horizontal" and "vertical" axes, i.e., the gimbal pointed in succession to the four corners of a square. This was like the ±45° arm pointing task but differed in that it did not return to the center target. The positions adopted by the gimbal in terms of quaternion vectors are shown in Fig. 8*B*. The above and side views show that the surface has torsion with respect to the fixed coordinate system and is twisted in a similar manner as the arm while pointing (Figs. 4–6).

In an attempt to obtain a quantitative assessment of this similarity, the degree of twist of the surface was calculated for all the data. A value of 0 indicates no twist, i.e., this would indicate a plane and a perfect correspondence with Listing's law. As expected, the eye data (Fig. 3*D*) at −0.04 was close to 0. At the other end of the range is the Fick gimbal (Fig. 8) with a measured value of −1.23 over the ±45° range and −1.07 over the ±30° range. Data was also expressed as a percentage of the value of the gimbal when moved through the same range. Comparison over the same range was necessary because the twist of the surface fitted to a Fick gimbal increases as the angle of rotation increases (because the twist is inversely proportional to the cosine of half this angle). Inspection of the data in RESULTS reveals that the values for arm movements lie somewhere between the value for Listing's law (0) and that for the Fick gimbal (100%). For the seven subjects who performed the ±45° straight-arm target task, the mean was 66% with a range of 50–90%. Thus the arm, when pointing, is more Fick gimbal–like than Listing's law–like.

Significance of similarity to Fick gimbal

What is the significance of this similarity? What does it tell us about the strategy the brain uses to make these movements? This similarity may be the consequence of five properties of a Fick gimbal that the arm follows to various degrees. The first is that when pointing forward and moving via rotations around only its "vertical" and "horizontal" axes, the Fick gimbal obeys Donders' law. The significance of this is that it indicates there is a constraint on position: for a particular target, the gimbal always points with the same orientation. Thus positions for both the arm and the gimbal are restricted to a two-dimensional subspace of the three-dimensional vector space of all possible positions. In the case of the arm, the advantage of this for the CNS is that, irrespective of the starting point of the arm, there is a need to specify only one command for the final arm position at every target.

The second property of a Fick gimbal is that, for these same conditions, there is no accumulation of torsion. Although torsion is generated by a rotation around one axis, it is dissipated by rotation around the other (cf. Figs. 1 and 8*B*).

A third important property of a Fick gimbal is that vertical movements always occur via the shortest path. This is because shortest-path movements involve rotation about an axis that is orthogonal to the pointing direction (which, in this case, is achieved by rotations around the "horizontal" axis). The significance of this property for the arm is that, because vertical movements are made with or against gravity, this strategy ensures that vertical movements will be of the minimum amplitude, i.e., they will occur via the shortest path. This appears to be relevant in terms of minimizing energy expenditure. In contrast, horizontal movements, made when the gimbal points up or down, involve rotations around the "vertical" axis and do not occur via the shortest path.

A fourth property of a vertically oriented Fick gimbal is that movements around the "vertical" axis are always made in a horizontal arc. Thus, for the arm when making horizontal movements, constant work is performed against gravity. If the gimbal (or body) is tilted, movements around the tilted "vertical" axis occur in an arc that is variably influenced by gravity: sometimes gravity assists the movement, whereas in other cases it opposes the movement. Thus, for the arm, the simplest and most energy-efficient arrangement would appear to be with the gimbal oriented vertically with respect to gravity. This may be the explanation as to why the arm position vector surface is aligned vertically when subjects sit upright and why it remains relatively vertical when the body tilts (Fig. 7).

A fifth property is that the pointing arm of the gimbal is always aligned horizontally. Thus, if the arm follows a Fick gimbal strategy, wrist orientation with respect to the horizon, and with respect to line of sight, will remain constant. However, there is nothing special about the initially chosen orientation, because subjects who had their wrist orientation changed by the experimenter continued pointing with the new orientation. This can be demonstrated on oneself: it is just as comfortable to point with the hand vertical as with it horizontal. Again, in both cases, movements are made using the Fick gimbal strategy.

Neural representation

It follows from the preceding that the parameter controlled by the brain in straight-arm pointing is not final arm position (i.e., the position vector surface was dependent on initial arm orientation). This suggests that the brain could be controlling the actual axes about which movements take place, and these would be Fick gimbal–like. In contrast, the findings from bent-arm pointing argue that final arm position is the important parameter (i.e., similar positions are achieved independently of initial arm orientation). Does this latter finding invalidate the advantages discussed for the Fick gimbal for straight-arm pointing? We do not think so. The interesting point is that, whatever the task, position vectors are constrained to a surface, the surfaces always have a twist, it is always in the same direction, and the direction is that of a Fick gimbal. This suggests that there is something ubiquitous about a Fick gimbal strategy, whether it be in the specification of axes or in a coordinate scheme for final position.

In fact, the present findings are consistent with the coordinate scheme proposed by Soechting and colleagues (e.g., Flanders and Soechting 1990; Soechting and Flanders 1989). They have investigated the nature of the transformation from the representation of target location in three-dimensional space to the representation of intended arm orientation. They propose that this transformation is parceled into two separate channels: in one channel, representation of target azimuth is transformed into arm yaw angle (the angle measured in the horizontal plane relative to the anterior direction), whereas in the other channel, representation of target elevation and distance are transformed into a representation of arm elevation angle. As far as arm representation is concerned, arm yaw angle is equivalent in the present experiments to movement around the "vertical" axis, whereas elevation is equivalent to movement around the mobile "horizontal" axis. Thus, in both schemes, arm position is defined by the same two parameters.

Why should there be this ubiquitous Fick gimbal–like behavior? One suggestion is that it arises from attempts to minimize energy expenditure because the arm constantly works against gravity. There may be many arm movements, e.g., at the shoulder, that are Fick gimbal–like whether or not there is additional movement at elbow and wrist. In these cases, the advantages of the Fick gimbal strategy, previously discussed for the straight arm when pointing, would apply. However there is an important qualification. These advantages will only apply to the extent that the arm movement resembles that of a Fick gimbal. Further experiments will have to be performed to determine more precisely the causes of the failure of the arm to perfectly follow the Fick gimbal model and to determine which of these properties of the Fick gimbal are the most important in determining positions and trajectories of the different arm segments under a variety of conditions.

In conclusion, it has been demonstrated that, like the eye, the straight arm when pointing obeys Donders' law, but unlike the eye does not obey Listing's law. Instead, the arm follows, at least to some extent, a Fick gimbal strategy. Because there is no apparent mechanical relation between the shoulder and a Fick gimbal, this strategy is presumably neurally imposed. One suggestion is that these differences between the properties of straight-arm pointing movements and the properties of saccades occur because the CNS has to take gravity into account for the arm but not for the eye.

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