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Perception and Reproduction of Force Direction in the Horizontal Plane

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Toffin, D., J. McIntyre, J. Droulez, A. Kemeny, and A. Berthoz. Perception and reproduction of force direction in the horizontal plane. *J Neurophysiol* 90: 3040–3053, 2003. First published July 23, 2003; 10.1152/jn.00271.2003. In this study, we evaluated the capacity of human beings to perceive and reproduce forces applied to the hand. We tested for perceptive distortions and/or privileged directions in the performance of these two tasks. Subjects resisted a reference force applied by a joystick in a given direction, with instructions to keep the hand at a constant position. In a perception task, subjects subsequently resisted a second such force, the direction of which they could adjust with a potentiometer; the task was to reorient the second force to be in the same perceived direction as the reference. In a reproduction task, subjects were instructed to push against the now elastically constrained joystick with the same force that was required to resist the initially applied reference force. Twenty-four reference force directions in the horizontal plane were tested twice each. We observed systematic distortions in the reproduction of force direction that were not present in the perception task. We further observed that the distortions could be predicted by anisotropy of limb stiffness and could be affected by manipulating the mechanical impedance of the hand-joystick interaction. We conclude that human subjects specify and store forces to be applied by the hand not in terms of a perceived force vector, but rather in terms of the motor activity required to resist or produce the force—i.e., subjects possess a multi-dimensional "sense of effort."

INTRODUCTION

This study addresses two important questions concerning the perception and reproduction of forces by the hand: what are the control variables used to perceive and reproduce forces and in what reference frame are they encoded?

Reference frames for force perception

Questions concerning reference frames constitute a recurring theme in neuroscience, particularly in the area of motor control, where one may ask how the CNS interprets and processes sensorimotor information (Berthoz 1991; Droulez and Darlot 1989; Lacquaniti 1989; Lacquaniti and Caminiti 1998; Soechting and Flanders 1989b). Many studies exist on the distinction that can be made between different possible reference frames: egocentric frames that are referred to the subject's body and allocentric frames that are referred to environmental cues or spatial references (Luyat et al. 2001). One can identify several egocentric reference frames for haptic tasks, centered on the head (Soechting et al. 1990), the shoulder (Flanders et al. 1992; Soechting and Flanders 1989a,b), or hand (Flanders et al. 1992; Gordon et al. 1994a,b). Conversely, allocentric reference frames for haptic perception might be defined by external forces acting on the hand (such as the geocentric reference frame defined by the direction of the pull of gravity) or by contextual cues given by positions and orientations of objects within the visual or haptic environment (Carrozzo et al. 1999). We sought to identify the coordinate systems in which the CNS encodes force information at the level of perception and reproduction. To do this we tested for a phenomenon know as the oblique effect, which was introduced by Appelle for visual stimuli (Appelle 1972). An oblique effect exists when performance on a given task is in some sense better for a set of canonical axes (such as the horizontal and vertical axes) than for any other oblique orientation. It has been argued that the privileged axes that emerge from an observed oblique effect can be used to identify the reference frames employed by the CNS to represent orientation information. The existence of oblique effects for haptic stimuli have been frequently reported in the literature (Appelle and Gravetter 1985; Gentaz and Hatwell 1995; Kappers 1999; Lechelt and Verenka 1980; Lechelt et al. 1976). For example, in experiments on the haptic reproduction of orientation in absence of visual feedback (Kappers and Koenderink 1999), subjects were presented a reference bar in one of four orientations in the horizontal plane (0, 45, 90, or 135°). The subjects then had to modify the orientation of a test bar to be parallel with the reference bar. Their results showed the existence of an oblique effect for the haptic perception of object orientation—subjects were rather poor in the reproduction of oblique orientations (45 and 135°) and better in the reproduction of horizontal and vertical stimuli. One of goals of this paper was to test for such anisotropy in tasks requiring subjects to perceive and produce forces against the environment.

Control variables: a sense of force or a sense of effort?

A number of hypotheses exist concerning how forces exerted by the arm on external objects are programmed by the CNS. In studies from the early eighties, it was purported that mechanoreceptors like the Golgi tendon organs and the glabrous skin receptors allow a direct perception of force (Houk and Rymer 1981). On the other hand, other studies showed that subjects measure a "sense of effort" associated with the muscle

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activity required to produce the perceived force (Jones 1986; McCloskey et al. 1974). Support for the sense of effort hypothesis is given by the fact that perceptual constancy is not maintained for force perception; forces produced by fatigued muscles (which require higher activation levels for a given force level) are overestimated by the CNS (Jones and Hunter 1982, 1983), just as the maximum force produced by a muscle varies as a function of muscle length (Cafarelli and Bigland-Ritchie 1979) and the vibration of muscle tendon disturbs the perception of force (Jones and Hunter 1985). A fatigued muscle, for example, will produce less force for the same effort. If subjects employed a true sense of force, the variations in force levels due to fatigue would be corrected either through feedback control based on the sensed force output or through feedforward control in which the fatigued state of the muscle is taken into account. Instead, when subjects are requested to match two force levels, what appears to be matched are the efforts required to produce those forces, rather than the output forces themselves. The hypothesis of a sense of effort provides a more parsimonious view of force perception, given these psychophysical results and given what is currently known about the mechanoreceptors that are supposed to measure forces. For instance, Golgi tendon organs appear to measure *changes* in force (Jami 1992)—not absolute force level—and are more sensitive to active force change initiated by the CNS than to passive stretch imposed by the environment. Thus the CNS may not possess the sensors necessary to unambiguously measure constant force levels. In this case, the sense of effort provides a viable alternative that in most cases should be sufficient to the task.

As demonstrated in the preceding cited studies, the difference between a sense of force and a sense of effort in one dimension (single joint) manifests itself in terms of the amplitude of the force actually obtained for different mechanical or physiological conditions of the muscles. As we will show, a sense of effort applied in a multi-dimensional context can not only lead to discrepancies in the amplitude of the force produced by the hand, but can also produce variations in the direction of the exerted force. In the case of the human arm, variations in the direction of the force produced can arise from two main factors, as illustrated in the following examples.

FACTOR 1: NONLINEAR FORCE-TORQUE RELATIONSHIPS. First, the arm constitutes a nonlinear mechanical linkage. The same muscle forces or joint torques produced with the hand at different positions in the workspace will not produce the same force output at the hand in terms of either the amplitude or direction of the force vector measured in Cartesian space. Figure 1 illustrates this point for a hypothetical two-joint planar manipulator that is presumed to have pure torque generators at each joint. The joint torques necessary to produce a force in the direction of 45° when the endpoint (hand) of the manipulator is at the central position, will produce forces in a slightly different direction when the hand is situated at a nearby location. To accurately reproduce the same force direction at different locations in space, the control system must modulate the torque levels, either through feedback control of the measured force level or though feedforward control that predicts the relationship between force and torque as a function of the joint angles. Conversely, perceptual matching based on a sense of torque (which in this hypothetical example could be construed as a sense of effort) will result in differences in force direction when forces are compared or produced at different hand locations.

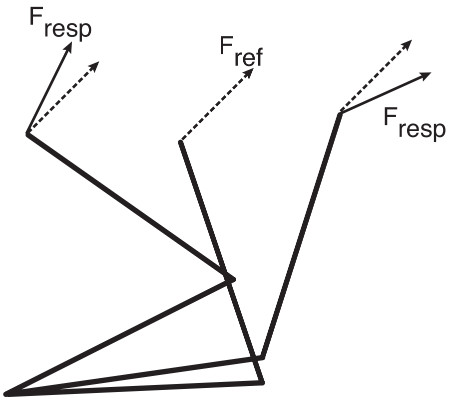

FIG. 1. Endpoint force variations as a function of position. The same joint torque applied in the central position to resist the reference force F_{ref} will generate forces in a slightly different directions when reproduced at different positions of the hand due to the nonlinear relationship between joint and hand space.

FACTOR 2: ANISOTROPIC IMPEDANCE. The second major factor affecting force reproduction involves the mechanical impedance (stiffness, viscosity, inertia) of the actuators, the linkage, and the environment. The actuators of the human arm are not pure force generators. The force produced by a muscle depends on a number of factors, including its level of activation, its length, and its rate of contraction. One cannot directly equate activation level with force output; the activation level of the muscle determines instead its mechanical state, which, although highly nonlinear, can be described to a first-order approximation in terms of its rest-length, stiffness and viscosity for small displacements around a given operating point. Simple reflex loops modify this behavior, making it in some cases more linear, but the overall effect is the same—muscles and reflexes engender spring-like behavior at the joints. In the same vein, mechanical interactions with the environment are seldom perfectly rigid. Pushing against a constraint will in general cause a (perhaps very small) displacement. Similarly, the forces in the muscles are transferred through the mechanical linkage, including nonrigid tendons and bones. A given set of muscle activations will determine the equilibrium state of the limb, but the actual force produced against the environment will depend on the interaction between the mechanical impedances of all these elements.

The mechanical impedance of muscles will therefore play an important role in determining the force that is produced for a given activation level and will thus be a factor that can be used to distinguish between a sense of force and a sense of effort. For the production of static forces, i.e., after all movement has subsided, one need only consider the rest-length and the length/tension relationship of the muscles, i.e., in this case impedance involves only stiffness for small changes of length. In the single joint case, or in the case of an isolated muscle, a given level of muscle activation will produce less force against a compliant (low stiffness) environment than against a more rigid constraint. This is because the compliant environment will "give," allowing the muscle to contract to a length closer to its rest-length before the system reaches its steady-state level of force. In analogy with the fatigued muscle example given

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above, reproducing a constant muscular activity (effort) will vary depending on the mechanical impedance, whereas a true sense of force should correct for such discrepancies.

The interaction of mechanical impedances in the multidimensional case can also affect the direction of the force produced for a given level of effort. Consider the idealized, linear system illustrated in Fig. 2 in which the actuators are tunable springs. The relative stiffness and rest-lengths of each of the springs will combine to define an equilibrium position (EP) at which the net force of the system is zero. When an external constraint displaces the system from this EP (or equivalently, if the EP is displaced away from the actual constrained position by re-tuning the actuators) a net force output will be produced. The force produced by a given EP displacement, however, depends critically on the mechanical interaction with the environment. For an isotropic stiffness field (equal stiffness in all directions) the force produced by a displacement of the EP in any direction will be in the same direction as the displacement itself (Fig. 2*A*). If, however, the impedance around the EP is anisotropic, the direction of the force produced by a given EP displacement can be significantly different from the direction of the EP displacement itself. Thus if the effect of a change in the control variable used to specify a force is in fact equivalent to a specified EP displacement, the actual force for a given change in the control variable will depend on the impedance of both the controlled mechanical system (the limb) and the environment (Fig. 2*B*). One can use this fact to test between a sense of force and a sense of effort: to the extent that muscles and reflexes can be considered as tunable springs, a central motor command (effort) will define the equilibrium position and impedance of the limb. If subjects can overcome these mechanical effects by sensing actual forces at the endpoint or by accurately predicting forces via feedforward models of the impedance, perception of the force direction produced should be independent of the mechanical impedance of the limb and the environment. On the other hand, if subjects specify and reproduce forces simply by exerting an effort in a given direction (which will be manifested by a change in the EP), the actual forces produced should be influenced by the impedance of the different mechanical conditions. Moreover if subjects remember two-dimensional (2D) efforts rather than 2D forces, predictable distortions in perceptual responses will occur depending on the total impedance of the coupled system.

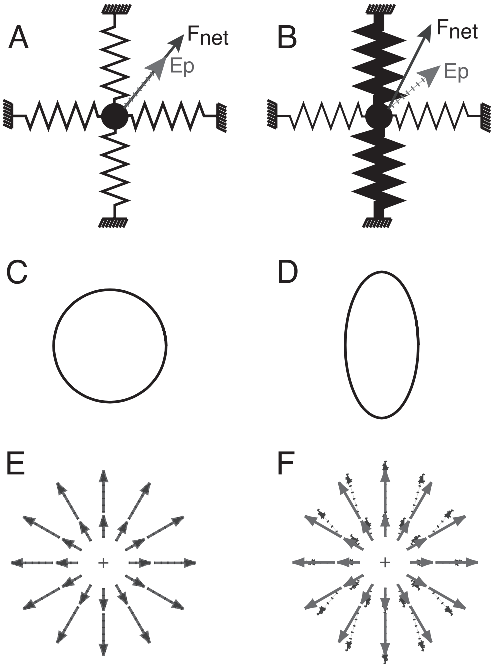

FIG. 2. *A*: isotropic, 2-dimensional spring. Equilibrium point displacement ΔEP required to produce a given force F_{net} is collinear with the force itself. *B*: anisotropic spring that is stiffer in 1 direction: F_{net} and ΔEP are generally in slightly different directions. *C* and *D*: graphical representation of a 2-dimensional stiffness by an ellipse representing the stiffness in each direction. *E* and *F*: EP displacements (dotted lines) required to produce forces in different directions (solid arrows). EP displacements and force vectors superimpose for all directions with an isotropic impedance (*E*) but vary systematically as a function of force direction with an anisotropic stiffness (*F*).

The purpose of the current study was to evaluate the capacity of human subject to memorize, compare, and reproduce different force directions without visual information. We performed a set of experiments where we *1*) evaluated the ability to compare two forces, *2*) measured the ability to actively reproduce a perceived reference force, and *3*) tested the influence of the mechanical impedance (including the impedance of the subject's arm) on the active reproduction of force. Note that for the human arm the effect of impedance will be confounded by the effects of the nonlinear linkage noted above. Pushing against mechanical loads having different impedances will cause the limb to be displaced in slightly different ways. Thus even if subjects are accurately reproducing joint torques against different environments, the resulting forces will not be identical if the changes of limb configuration are not taken into account. With this in mind, we considered the possibility that subjects may use a sense of torque (rather than force) when interacting with the environment. We used these experiments to ask the question: what is specified by the nervous system when perceiving and reproducing forces against the environment? By comparing experimental data with model predictions we asked the question: do human subjects specify forces, torques, or efforts when controlling mechanical interactions between the environment and the hand?

METHODS

Participants

A total of 10 male and 2 female university students aged 23–30 yr participated in this study, with different subgroups performing different protocols as noted below. All participants were right-handed and had no known problems of haptic perception or motor control. Participants gave their informed consent prior to starting the experiments and all protocols were carried out in accordance with regulations concerning the ethical use of human subjects.

Experimental equipment

The experimental setup was equipped with a seat, a force-actuated joystick, and a video screen connected to a computer to give instructions to the subject (test number, procedure to be used, etc.; see Fig. 3). Push buttons were used by the subject *1*) to initialize the system and *2*) to confirm and record perceptual responses. Subjects viewed the video screen through a face mask attached to the chair, which prevented them from seeing their hand but allowed them to see information displayed on the screen.

A force-actuated joystick, (ROBOTOP, Matra Marconi Space) was used to generate forces against the hand of the subject. This system had two degrees of freedom: *X* and *Y*. Each axis was coupled to a

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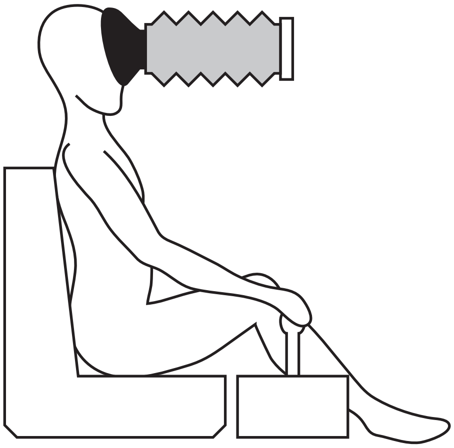

FIG. 3. Schematic profile view of the experimental equipment and subject.

motor through a gear reduction of 50:1 allowing a restitution of effort of ≤25 N. Each motor was connected to an optical encoder (100,000 points per turn) making it possible to obtain a position measurement with 0.09-mm resolution.

The base of the joystick was attached rigidly to the chair, with the shaft of the joystick oriented vertically upward at the central position. The two degrees of freedom of the joystick thus allowed movements roughly in the horizontal plane. More precisely, the distance between the center of the grip (a 2.5-cm radius ball) and the joystick's two intersecting axes of rotation was 15 cm, allowing movement of the hand along the surface of a 15-cm-radius sphere. A sensor integrated in the shaft of the joystick provided measurements of the forces applied between the hand and the grip of the joystick, with a range of ±40 N and a resolution of ±0.02 N (see McIntyre et al. 1995). The force sensor was rigidly connected to the grip of the joystick without any intervening bearings or couplers. Thus the force sensor measured the true contact force between the hand and the joystick independent of any friction acting on the joystick axes. Because displacements of the hand from the central position in this experiment were small (1–2 cm), measured movements and forces were considered to lie in the horizontal plane, i.e., neglecting the true motion of the joystick across the surface of a sphere.

Subjects were seated in a comfortable upright position with the joystick grip located at waist level to the right and in front of the subjects torso (Fig. 3). The torso and shoulder were unrestrained, but the fixed position of the mask relative to the seatback restricted movements of the body with respect to the joystick.

Experiment 1—force perception and reproduction

In an initial pair of experimental protocols, we measured subjects' ability to perceive and reproduce forces applied against the hand. Each task consisted of a *reference* and a *response* phase. In the perception task, a given trial began by having the joystick apply to the hand a reference force along a given direction. The force ramped up at a rate of 0.75 N/s to a constant level of 5 N. Subjects resisted this force with instructions to keep the hand at a constant position. At steady state, the force applied by the subject and the force applied by joystick were equal and opposite (neglecting friction). When subjects felt they had a good perception of this force direction, they pressed a button with the left hand, causing the reference force to ramp back down to zero (−0.75 N/s). Immediately afterward, a variable-direction test force was generated by the joystick along a direction ±30° from the reference direction. Again the force ramped up at a rate of 0.75 N/s to a constant magnitude of 5 N. Subjects twisted a potentiometer with their left hand to adjust the direction of the test force to any direction in the horizontal plane. The task was to reorient the test force to be in the same direction as the initial reference force. When subjects estimated that the test force matched the reference force, they pressed a button to validate their response, terminate the trial, and start the next. During the two phases of each trial (reference and response), applied force and joystick positions were measured and recorded for *X* and *Y* axes at a frequency of 75 Hz. Twenty-four reference force directions distributed uniformly around a circle in the horizontal plane were tested twice each in an experimental session lasting approximately 20 min.

For the reproduction task the reference phase of each trial was the same as for the perception task described above. Subjects resisted a reference force applied by the actuated joystick in a given direction, with the instruction to keep the hand at a constant position. After this first step and when subjects felt that they had achieved a good perception of this force direction, they pressed a button with the left hand to pass to the response phase. At the beginning of the response phase the joystick moved automatically to the central position. The joystick was reprogrammed to be at rest in the central position with a stiffness of 2.25 N/cm in all directions. Subjects were instructed to push against the elastically constrained joystick with the same force that was required to resist the initially applied reference force. When subjects estimated that they were producing a steady-state response force in the direction of the previously perceived reference force, they pressed the button with their left hand. Subjects were requested to concentrate on the direction of the response force; no instructions were given about the required magnitude. During the two phases of each trial (reference and response), the force and the joystick position were measured and recorded for the *X* and *Y* axes at a frequency of 75 Hz. The same 24 reference force directions in the horizontal plane were tested twice each during a second 20-min session immediately following the perception session previously described. Trials were self-paced, with pauses allowed to avoid fatigue. Six subjects (5 males and 1 female) performed this experiment.

Analysis

For each type of trial, we calculated two bi-dimensional force vectors, the measured reference force F_{ref} and the measured steady-state response force F_{resp} at the end of the trial. The direction of the force θ is equal to $\tan^{-1}(Fy/Fx)$; thus we obtained θ_{ref} and θ_{resp} measured in the reference and response phases, respectively.

Errors for the two tasks (perception and reproduction) were first characterized by the mean signed error in force direction across all 24 reference directions. A mean error significantly different from zero would indicate a systematic rotation of all responses in a given direction. The RMS error about the ideal response of $\theta_{\mathrm{resp}} = \theta_{\mathrm{ref}}$ provides an indication of response deviations for different reference directions, which is expected to comprised of two components: the first arising from distortions in response directions that are systematically dependent on the direction of the reference force and the second arising from random noise in the response and measurements.

To measure the systematic direction–dependent component, we approximated the transformation between the reference and response forces as a linear transformation, which we call the 2 × 2 distortion matrix Q, where $F_{\mathrm{resp}} = QF_{\mathrm{ref}}$. This linear formulation was chosen because *1*) it constitutes a first-order approximation of local distortions in transformation from the reference to the response force (McIntyre et al. 2000) and *2*) because such linear distortions are to be expected from the 2D impedance of the hand/joystick interaction if subjects reproduce muscular efforts (and thus EP displacements) rather than forces, and if displacements are small. For each subject and each set of 48 trials, we computed the best-fit Q that minimized the angle between F_{ref} and F_{resp}. The matrix Q can be depicted graphically as an ellipse which is in turn characterized by it's shape and orientation. The anisotropy in a given ellipse can be described by an anisotropy vector V defined as the major eigenvector of the matrix Q weighted by the anisotropy factor $D = (\lambda_{\max}/\lambda_{\min}) - 1$ where $\lambda_{\min}$ and $\lambda_{\max}$ are the minimal and maximal eigenvalues of Q. This vector

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indicates the orientation and magnitude of the expected distortion. The length of V reduces to zero for an isotropic (undistorted) transformation.

The clustering of anisotropy vectors for the group of six subjects was tested using the Raleigh test for uniformity of distributions on a circle, and the mean directions were compared for the perception and reproduction tasks using the Watson F test for axial data (Watson and Williams 1956). The amount of distortion was compared for the two tasks by applying a standard paired t-test to the anisotropy factor D and by the nonparametric Wilcoxon signed-rank test. In addition, we computed the best-fit 2×2 distortion matrix that describes the transformation between the measured reference force vector, averaged across all six subjects, and the measured response vector, also averaged across subjects. From these two distortion matrices, we computed the "combined" anisotropy factor D and anisotropy vector V. We computed the RMS residual error as the difference between the response force direction predicted by the linear transformation Q and the actual measured response directions. RMS residual values were used to determine what percentage of the overall variance between trials could be explained by the distorted linear transformation versus that explained by the ideal response of $\theta_{resp} = \theta_{ref.}$

Experiment 2—effects of the nonlinear arm linkage and limb impedance

We hypothesized that the subjects might reproduce either the same joint torque or the same EP displacement of the hand when reproducing a remembered force. In the former case, the force produced in the reproduction task could depend on the actual position of the limb during the response phase compared with the position of the limb maintained during the sensation of the reference force. To test this hypothesis, we modeled the arm as a two-joint linkage having two degrees of freedom at the shoulder and one at the elbow (see APPENDIX A), and we computed the position dependent Jacobian matrix that relates hand forces in Caretesian space to torques applied at the joints. For each reference force direction we computed the joint torques required to resist this force, taking into account the measured position of the hand during the reference phase. We then predicted the hand force that would result if the subject applied the same torque at the position measured in the response phase. This leads to a predictable transformation between the reference and response forces as follows

$$F_{\text{resp}} = (J^{\text{T}}_{\text{resp}})^{-1} J^{\text{T}}_{\text{ref}} F_{\text{ref}}$$

where J_{ref} and J_{resp} represent the Jacobian of the joint-to-hand transformation at the reference and response positions, respectively. The deviations in the response force from the reference force could thus be predicted for each reference force direction and compared with the actual error produced on average across subjects. Note that the joystick did not allow displacement along the vertical axis, nor did we actually measure forces applied along this direction. For the purposes of these simulations, we first assumed that P_z and F_z were both equal to zero. Further simulations showed that the XY force variations predicted by this model are relatively independent of any unmeasured vertical force that the subject may have applied to the Z axis of the joystick (see APPENDIX B).

To test whether the impedance of the arm and joystick interaction could be the source of the observed distortions in the force reproduction task, we evaluated the arm stiffness K_{Arm} of three subjects from the original group using a procedure similar to that of Mussa-Ivaldi et al. (1985). Subjects held the joystick at the neutral position. The joystick imposed small position perturbations of 10 and 15 mm in eight different directions (0, 45, 90, 135, 180, 225, 270, and 315°), presented in random order. Subjects were required to maintain a stable posture around the nominal position but were instructed to not actively intervene when the joystick imposed a displacement. Force (*Fx*, *Fy*) and position (*Px*, *Py*) at the beginning and end of each displacement were measured, and from these, we computed ΔP and ΔF. Through a linear regression on these values, we obtained the best-fit stiffness matrix corresponding to the arm stiffness

$$\Delta F = K_{\text{Arm}} \Delta P$$

Using the measured stiffness values, we estimated what would be the transformation matrix Q resulting from the mechanical interaction between the joystick and the hand if the subject regulates a control variable such that the EP shift required to resist the reference force ($\Delta \text{EP}_{\text{ref}}$) and to produce the response force ($\Delta \text{EP}_{\text{resp}}$) was the same ($\Delta \text{EP}_{\text{ref}} \equiv \Delta \text{EP}_{\text{resp}}$). Assuming that the stiffness of the joystick was zero during the reference phase (the joystick is assumed to generate a constant force, independent of the position), the net impedance of the arm + joystick is equal to that of the hand alone and the EP displacement required to resist a given reference force F_{ref} is computed by

$$\Delta \text{EP}_{\text{ref}} = C_{\text{Arm}} \Delta F_{\text{ref}}$$

where $C_{\text{Arm}} = K^{-1}_{\text{Arm}}$ is the mechanical compliance of the arm. In the reproduction phase, the subject pushed against the joystick through a series connection of the arm and joystick impedances. The net compliance is thus equal to the sum of the hand and joystick compliances and the force resulting from a given EP displacement is given by

$$\Delta F_{\text{resp}} = K_{\text{Arm+Joystick}} \Delta \text{EP}_{\text{resp}}$$

$$\Delta F_{\text{resp}} = (C_{\text{Arm}} + C_{\text{Joystick}})^{-1} \Delta \text{EP}_{\text{resp}}$$

From this hypothesis, one can predict the response forces for a set of reference forces as

$$\Delta F_{\text{resp}} = (C_{\text{Arm}} + C_{\text{Joystick}})^{-1} C_{\text{Arm}} \Delta F_{\text{ref}}$$

One can therefore define the distortion matrix predicted by the impedance change as

$$Q_{\text{impedance}} = (C_{\text{Arm}} + C_{\text{Joystick}})^{-1} C_{\text{Arm}}$$

To test whether $Q_{\text{impedance}}$ could adequately explain observed patterns of error in the force reproduction task, we computed errors in response force direction that would be produced by the transformation $Q_{\text{impedance}}$ and compared these to the actual measured response errors. We computed the percentage of the overall variance explained by the $Q_{\text{impedance}}$ model and compared this to that explained by the ideal response of $\theta_{\text{resp}} = \theta_{\text{ref.}}$ Furthermore, we compared qualitatively the characteristics of the distortion matrix (i.e., the direction and length of the anisotropy vector V) predicted from the arm impedance $Q_{\text{impedance}}$ to that of the best-fit matrix Q estimated directly from the measured reference and response forces.

Experiment 3—effects of the joystick impedance

If subjects reproduced the remembered value of a control variable such that displacements of the EP are the same in both the reference and response phases, the response force should be a function of both the limb impedance and the impedance of the environment. To test this hypothesis we modulated the impedance of the joystick between the reference and response phases on each trial. In a first set of trials, six subjects (2 from the subgroup tested in *Experiment 1* plus 4 others) performed the force reproduction task in which two trials were performed for reference forces in each of the 24 different directions. The response phases for these 48 trials were performed with the same isotropic joystick impedance used in *Experiment 1*. Randomly interspersed between these normal trials were 16 perturbation trials, all of which had the reference force at 45°, but in which the joystick impedance was modified to be anisotropic. In these perturbation trials, the major axis of the joystick stiffness ellipse was oriented +45° (K_{CCW}) or −45° (K_{CW}) from the reference force direction (i.e., stiffer

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along the *Y* or *X* axis, respectively). The stiffness along the major and minor axes for the perturbed trials was calculated such that a given displacement of the EP along the 45° direction would generate the same amplitude of force as that produced against the isotropic joystick impedance used in control trials. In this way, subjects would be less likely to perceive any change in the amount of effort required to produce the response force for perturbed versus control trials. Indeed, no subject reported sensing a change in the mechanical characteristics of the joystick for these trials.

In a second set of trials, 24 directions were tested each twice and we set the joystick impedance to be anisotropic on each trial. The shape of the joystick impedance (ratio of the stiffnesses along the major and minor axes) was constant across all trials and on alternate presentations of each direction the major axis of the stiffness ellipse was oriented +45° (K_{CCW}) or −45° (K_{CW}) from the direction of the reference force. A total of six subjects performed this part of the experiment (4 of which had previously performed one or more of the other protocols).

Analysis

If the response force direction is effectively the result of an EP displacement and the net impedance of the hand-joystick interaction, reorientation of the joystick stiffness by ±45° predicts a systematic deviation of the response away from the force direction that would be produced against an isotropic external constraint. The response will deviate in the positive direction (counterclockwise) for K_{CCW} and in the negative direction (clockwise) for K_{CW}. For both sets of perturbed trials, we measured the direction of the response force as a function of the orientation of the joystick stiffness (K_{CW} or K_{CCW}). We tested for a systematic change in the orientation of the response force using a Watson *F* test for directional data with the joystick stiffness orientation as a within-subjects factor.

The change in joystick impedance might also engender a change in the position of the hand during the response phase. Thus variations of response force direction as a function of joystick stiffness could arise either from a reproduction of joint torques without compensating for changes in the Jacobian or by the reproduction of an EP shift without compensating for the differences in mechanical stiffness. To test between these two hypotheses, we computed the predicted changes in force direction for the same joint torques, taking into account the measured position of the hand for each of the two joystick stiffnesses. We also computed the changes predicted for the same EP shift, taking into account the different combined joystick/limb impedance. These predicted values could be compared with actual measured differences in force directions for the two different joystick stiffnesses, if any. Finally, we computed $Q_{\text{impedance}}$ for each of the two joystick stiffnesses and compared the resulting anisotropy vectors *V* to those arising from the corresponding best-fit distortion matrices *Q*.

Experiment 4—transfer of force information

In a final protocol, we tested transfer between the right and left hand to see how variations of limb impedance might affect the reproduction of force direction. Subjects resisted the applied reference force with the right hand as in the tasks described above. They then reproduced the reference force with the same hand (ipsilateral reproduction) or they reached across the body with the left arm to exert the response force against the joystick (contralateral reproduction). Twenty-four directions were tested each twice for each of the two conditions (ipsilateral and contralateral), and we estimated the stiffness matrix for the right and the left arms at the nominal working position of the joystick using the displacement technique described above.

Analysis

Using the measured stiffness values, we estimated what would be the transformation matrix *Q* resulting from the mechanical interaction between joystick and the hand for ipsilateral and contralateral reproduction

$$Q_{\text{ipsilateral}} = (C_{\text{Right}} + C_{\text{Joystick}})^{-1} C_{\text{Right}}$$
$$Q_{\text{contralateral}} = (C_{\text{Left}} + C_{\text{Joystick}})^{-1} C_{\text{Right}}$$

From these estimates, we predicted systematic rotations of the response vectors that would arise if the subjects specify forces as EP displacements (see RESULTS). We tested for a significant rotation of the responses according to the hand used using the Watson *F* test for directional data. We compared the predicted average rotation to the measured values, and we also compared the predicted and measured distortion vectors.

RESULTS

Errors in force perception and reproduction

Figure 4 shows the responses of a typical subject plotted against the reference forces for both the force perception and the force reproduction tasks. In general the responses are grouped around the ideal values of $\theta_{\text{resp}} = \theta_{\text{ref}}$. Calculations of the mean error are shown in Table 1. In neither case do the average error values differ significantly from zero ($F_{(1,6)} = 0.43$, $P < 0.53$), indicating that there was no global rotation of responses common to all reference directions. RMS error computed for each protocol shows that deviations of responses

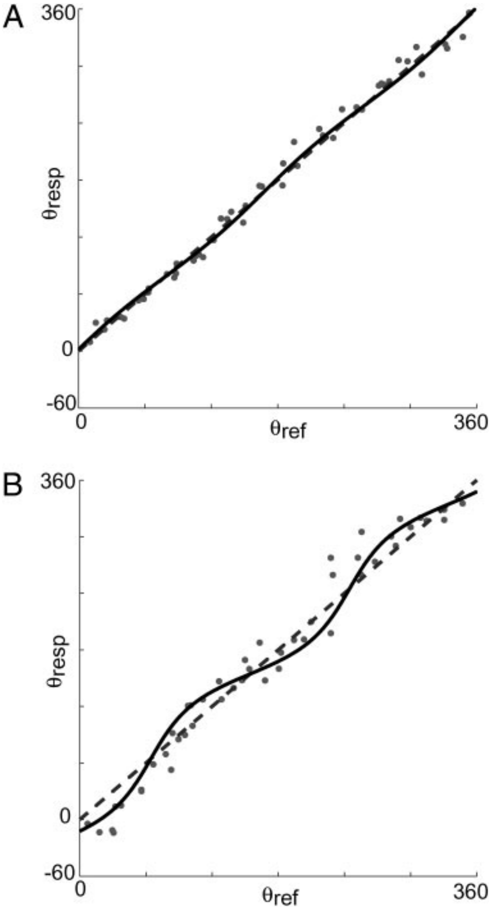

FIG. 4. Response force direction as a function of the reference force direction compared with the ideal response $\theta_{\text{ref}} = \theta_{\text{resp}}$ (dashed line) and the predicted responses based on the best-fit linear transformation *Q* (solid line). Results for 1 subject for the force perception task (*A*) and the force reproduction task (*B*).

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TABLE 1. *Results of Experiment 1 for the perception and reproduction task*

	Force Perception Task				Force Reproduction Task			
Subjects	Mean Error	ε_{RMS}	δ_{RMS}	Anisotropy Factor D	Mean Error	ε_{RMS}	δ_{RMS}	Anisotropy Factor D
S1	0.51	9.74	9.32	0.16	1.78	22.59	20.79	1.02
S2	0.54	17.15	16.96	0.15	1.13	21.70	20.67	0.51
S3	−4.24	19.54	19.72	0.12	−2.02	19.74	19.36	0.18
S4	−3.90	25.96	25.03	0.45	−2.67	25.54	22.76	1.28
S5	0.78	14.47	14.22	0.15	2.40	23.14	21.02	0.47
S6	−2.34	19.73	19.63	0.11	0.96	18.23	17.82	0.35
Combined	−0.60	6.39	5.80	0.13	0.10	10.34	8.95	0.30

from the ideal were somewhat smaller for the force perception task value than for the force reproduction task (6.39 vs. 10.34°).

Superimposed on Fig. 4 are the predictions of the best-fit linear transformation between the reference and response force vectors. The RMS of the residual variance for an undistorted versus distorted transformation are reported in Table 1. In both the perception and the reproduction tasks, the best-fit linear transformation reduces the variance of the residual compared with the ideal model in which subjects reproduce the reference force without distortion. However, the reduction in residual variance was significant at the $P < 0.01$ level only for the reproduction task. The more important point, however, is that the anisotropy in the distortion matrix Q was systematically greater in the reproduction task for all subjects, as measured by the distortion factor D. This was true for each subject considered separately and when the analysis was applied to the responses for each reference direction averaged across subjects ("Combined" subject shown in Table 1). The differences in D between tasks where confirmed by a paired *t*-test ($P < 0.01$) and by the nonparametric Wilcoxon signed-rank test ($P < 0.02$), the latter being a less powerful test that makes no assumption about the normality of the distribution of D.

The anisotropy vectors for each subject are plotted in Fig. 5. The fact that the anisotropy is smaller for the perception task is illustrated by the shorter length of these vectors in Fig. 5*A* than in Fig. 5*B*. Variability in the direction of the distortion vectors was high for both tasks (±61.20° for the perception task and ±44.23° for the reproduction task). Only for the reproduction task could the distribution of distortion vectors be considered nonuniform, as indicated by the Raleigh test for uniformity of axial data ($P < 0.15$ for the perception task and $P < 0.03$ for the reproduction task). The average direction was nevertheless significantly different between the two tasks, as indicated by the Watson F test for axial data ($P < 0.001$). The matrix Q computed from data averaged across all subjects combined yielded a distortion vector that lies along the Y axis (93.38°) for the force perception task, whereas this vector points along an oblique axis (153.05°) for force reproduction.

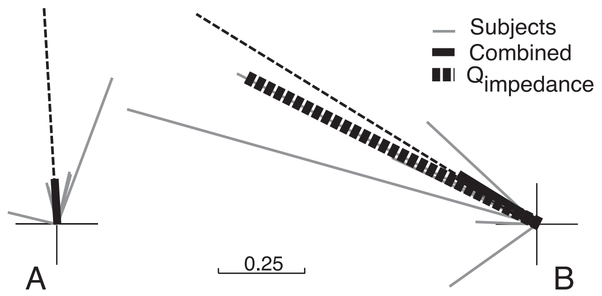

FIG. 5. Anisotropy vectors V for each subject in the force perception task (*A*) and the force reproduction task (*B*). Thin dashed lines indicate the direction of the anisotropy vector computed for all subjects combined. In *B*, the direction of the anisotropy vector $V_{impedance}$ predicted by the distortion $Q_{impedance}$ induced by the limb impedance is also shown (thick dotted line).

Estimation of arm stiffness

Figure 6 shows the measured stiffness ellipses for one subject around the central position of the joystick (Fig. 6*A*) and the average across three subjects tested on this protocol (Fig. 6*B*). Stiffness shape (2.8), size (19.79 $[\mathrm{Ncm}^{-1}]^2$), and orientation were similar to those found by Mussa-Ivaldi et al. (1985). Maximum stiffness attained a value of 4.2 Ncm^{-1} and was aligned approximately with the forearm. Minimum stiffness in the perpendicular direction was 1.5 Ncm^{-1}. Computed stiffness ellipses were of the same shape and size for displacements of both 10 and 15 mm, indicating that the approximation of a linear stiffness was valid for these small displacements. All three subjects exhibited similar hand stiffnesses.

Effects of limb stiffness

Figure 7 shows the reference-response curves predicted by either a reproduction of joint torques, without adjusting for the effects of changing limb position on the torque-to-force relationship, or by the reproduction of an EP shift, without compensating for the anisotropy of the overall limb/joystick impedance. The reproduction of joint torques does a poor job of predicting systematic errors in the reproduced force directions. The RMS residual error not explained by this model is in fact greater than that obtained from the comparison with the ideal response (12.31 and 10.34, respectively). Conversely, reproducing the equivalent to a shift in the EP of the limb reduces the RMS residual value to 9.14. The EP shift hypothesis explains a significant part of the residual variance (22%) not explained by the ideal response model $\theta_{resp} = \theta_{ref}$ ($P < 0.01$).

The estimated stiffness averaged over all three subjects predicts the distortion matrix $Q_{impedance}$ that would result if subjects reproduce EP displacements. The anisotropy vector $V_{impedance}$ corresponding to this predicted distortion is plotted in Fig. 5*B*. $V_{impedance}$ falls well within the range of measured anisotropy vectors in terms of both the amplitude and the direction of the distortion.

Effects of the joystick impedance

Figure 8 describes the methods and results of the experiment in which the stiffness of the joystick was anisotropic and varied from trial to trial. Subjects' responses were directly influenced by the

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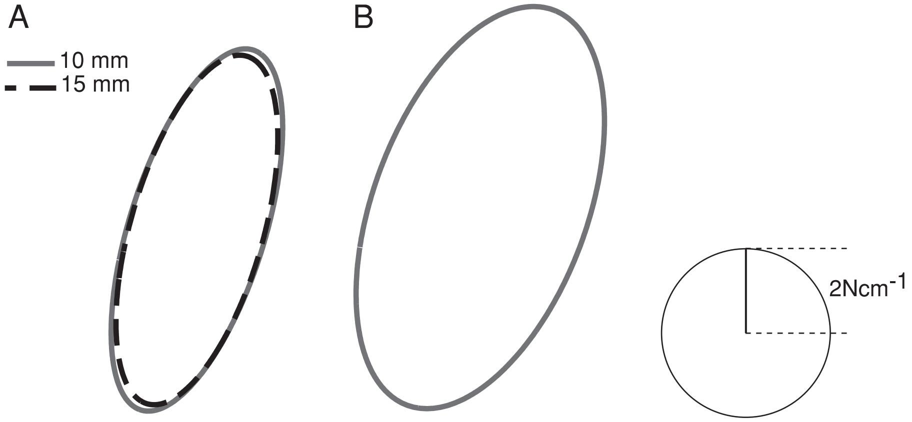

FIG. 6. *A*: graphical representation of arm stiffness measured for 1 subject for 2 small displacements (10 and 15 mm). *B*: estimated stiffness for the 2 displacements averaged across 3 subjects.

joystick impedance. Response vectors were reoriented in the clockwise direction for K_{CW} and in the counterclockwise direction for K_{CCW}, as predicted by the EP displacement hypothesis. An Watson *F* test analysis revealed a significant effect of the direction of the joystick anisotropy for both parts of the experiment: $F = 29.23$, $P < 0.001$ for trials where joystick stiffness was modified only for a reference force of 45° and $F = 129.76$, $P < 0.001$, when the joystick stiffness was modified for all 24 directions.

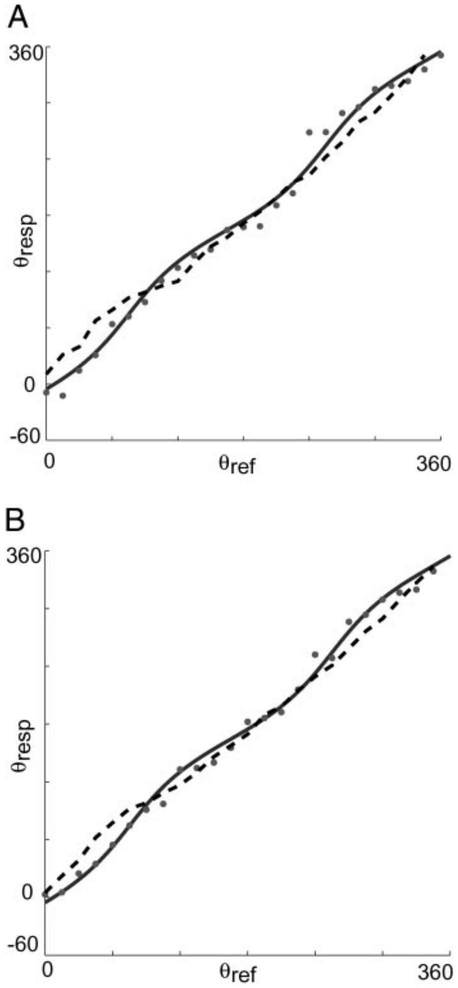

FIG. 7. Comparison of measured responses vs. predictions of 2 models. Solid lines indicate the pattern of responses predicted by the reproduction of an EP displacement (effort) coupled with an uncompensated effect of the mechanical impedance of the limb. Dotted lines indicate the predicted errors of a reproduction of joint torque with uncompensated changes in the limb Jacobian. *A*: data from a single subject. *B*: average across all subjects.

Superimposed on the measured response force directions (Fig. 8*B*) are the predictions of the hypotheses by which it is the joint torque (open squares) or EP shift (filled circles) that is reproduced during the response phase. Reproducing the same joint torque predicts very little difference in the direction of response forces for the two joystick stiffness, although both stiffnesses predict a small (approximately 5°) counterclockwise rotation of the response vector away from the ideal direction of 45°. Otherwise stated, the changes in Jacobian induced by the small differences in the limb position for the two cases have a minimal effect on the force that would be produced for equivalent joint torques. Not shown is the prediction of the true sense of force hypothesis, which would predict an average response force at 45° independent of the joystick stiffness. Clearly, subjects reproduce neither the ideal reference force nor the joint torques required to produce that force. On the other hand, if what is reproduced corresponds to an effective change of the limb EP (as would be predicted by a sense of effort), the response forces predicted by this hypothesis do a much better job of reproducing the actual measured responses. The predicted directions of the response forces for the two joystick impedances, which takes into account the anisotropic impedance of the limb as well, fall within one circular SE of the response vector averaged across subjects. A similar result holds when response force errors are averaged across all 24 directions (Fig. 8*D*). Neither a reproduction of force nor a reproduction of joint torques predicts an overall error different from 0° nor a systematic difference between the two joystick stiffness orientations. On the contrary, reproducing EP shifts does predict an symmetric ±20° average error for the two different stiffness orientations, a prediction that is born out by the measured data.

Transfer of force information

Figure 9*A* shows the measured stiffness ellipse for the right and left arm, as measured at the location of the joystick to the right of the subject (subjects reached across the body to attain this position with the left hand). Stiffness shapes and orientations were similar to those measured in *experiment 2*, where the maximum stiffness was aligned approximately with the forearm, and we found clear differences between the orientation of the stiffness ellipses for the right (72.91°) and the left arm (39.12°).

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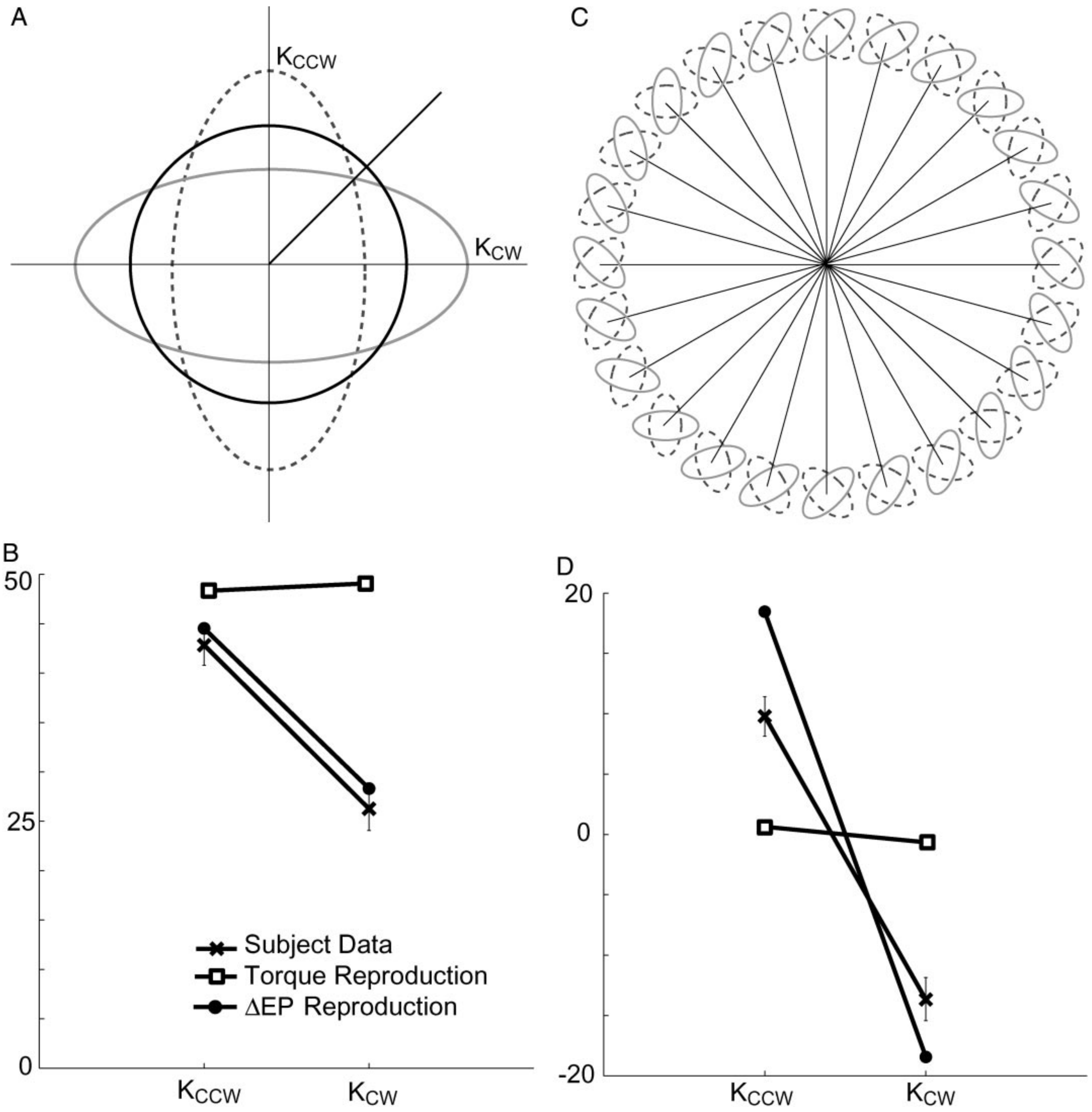

FIG. 8. *A*: stiffness ellipses for the joystick oriented ±45° from the reference force direction (K_{CW} and K_{CCW}) *B*: responses averaged across subjects for a reference force at 45° for each of the 2 different anisotropic joystick stiffnesses K_{CW} and K_{CCW} (×, error bars ± circular SD) compared with predictions of for reproduction of joint torque (squares) or EP shift (circles). *C*: joystick stiffness K_{CW} and K_{CCW} for all 24 directions of the reference force. *D*: average responses when the joystick stiffness was modified for all 24 directions (×) compared with average responses predicted by joystick stiffnesses K_{CW} and K_{CCW} for either a reproduction of joint torque (squares) or a reproduction of EP shift (circles).

Patterns of distortion varied as a function of whether the subject reproduced the reference force with the left or right hand. The anisotropy vector for all subjects combined are plotted in Fig. 9*B*. We observed a different orientation for ipsilateral reproduction (151.43°) and contralateral reproduction (108.09°) comparable to the values predicted by the EP displacement hypothesis (157.56° and 94.17°, respectively), but with no difference in anisotropy factor ($D = 0.40$).

The differences in limb impedance for ipsilateral and contralateral reproduction predict differing effects on the orientation of the response force, depending on the reference direction. Directions in the horizontal plane can be divided into two

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zones (Fig. 9*C*). In Zone 1 (from 30 to 120° and from 210 to 300°) angular errors in the reproduction of the reference force should be more positive (responses more counterclockwise) for the left hand than for the right hand. Conversely, in *zone 2,* angular errors should be more positive for the right hand than for the left hand. These predictions were born out in the measured results. In *zone 1,* errors were on average positive for the left and negative for the right hand, while *zone 2* showed positive errors for the right hand and negative errors for the left. In an Watson *F* test analysis, the relative errors between the right and left hand as a function of zone was significant ($P < 0.001$, see Fig. 9*C*).

DISCUSSION

Using only haptic sensorimotor information in the absence of visual feedback, subjects were able to carry out very well a perceptive comparison between two directions of force (force perception task). We found no specific oblique effect in this task that would clearly indicate an underlying reference frame for haptic force directions. There is, however, a tendency for anisotropy vectors to point along the *Y* axis. This effect could arise from either an egocentric reference frame corresponding to the front-back and left-right directions for the subject or to an allocentric reference frame provided by the experimental apparatus and the surrounding visual environment. Nevertheless, due to the low level of anisotropy exhibited for the force perception task, one cannot firmly conclude that there is a coding of force information in terms of either of these two reference frames.

On the other hand, for the production task in which subjects had to voluntarily reproduce a remembered force direction (rather than comparing the direction of 2 imposed forces) a much stronger pattern of errors was observed. Systematic deviations from the ideal responses were greater for reproduction than for perception and the best-fit transformation between the reference and response vectors were much more anisotropic in the former case. Subjects reproduced neither the same force direction nor the same joint torques between the reference and the response phases. Instead, it was shown that distortions in the reference-to-response transformations could be due to the interactions between a shift in the equilibrium position resulting from the reproduction of the same effort and the impedance of the mechanical interaction between the hand and the joystick. This hypothesis was supported by the fact that the measured limb impedance predicts the observed patterns of errors when subjects pushed against an isotropic mechanical environment and further confirmed by the fact that responses varied systematically when either the joystick or the limb impedance was changed between trials. These observations were illustrated qualitatively by the good correspondence between the direction of the anisotropy vectors *V* predicted by the limb/joystick impedance and the anisotropy vectors resulting from the best-fit approximation to the measured force data. The predictions of the sense-of-effort hypothesis were validated statistically by predicting how response forces should vary for different joystick or limb stiffnesses and by testing for such differences in the measured data.

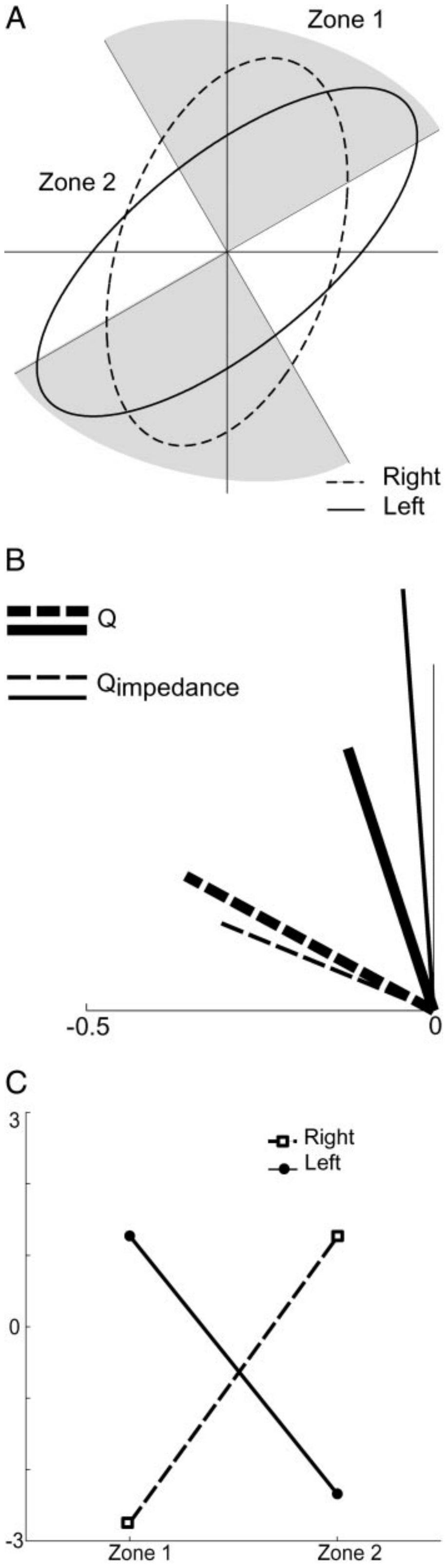

FIG. 9. *A*: measured stiffness of the left and right hand when operating the joystick located to the right of the subject. *B*: anisotropy vectors $V_{\mathrm{impedance}}$ predicted by the measured hand stiffness for ipsilateral and contralateral force reproduction (solid lines) vs. the measured anisotropy vector *V* computed for all subjects combined. *C*: planar directions may be divided into 2 zones based on the predictions of the EP displacement hypothesis: in *zone 1* (*zone 2*) errors produced by the left (right) hand are expected to be more positive than for the right (left) hand (see *A*). Average angular errors follow the predictions of the EP displacement hypothesis for the 2 hands in each of the 2 different zones.

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Patterns of error were different between the perception and the reproduction tasks. One might conclude from these observations that force perception and force production are carried out in different frames of reference. However, the preferred directions indicated by distortions in the reproduction task cannot be related to an easily identified egocentric or allocentric reference frame. Nor does the difference in error patterns observed for the force perception and reproduction tasks of *Experiment 1* imply that the motor strategies used in this two tasks were different. The difference is more easily explained by the differences of the mechanical conditions between the two tasks coupled with a sense of effort that leads to matching of equivalent EP shifts. In the perception task the joystick impedance remained the same (zero) for both the reference and response phases of the task. Therefore the applied forces in this task could be specified internally as muscular efforts. Because the limb impedance is not isotropic, one would expect that the EP displacement resulting from the change in muscle command would not be in the same direction as the applied force. Nevertheless, the subject could make accurate comparisons of the relative direction of applied forces based on the representation of the muscular effort or EP displacement because the deviations would be the same for both phases of the task. In the reproduction task, however, the joystick impedance was modified between the reference and the response phases of each trial (stiffness was 0 during the reference phase and finite during the response phase). Thus the same muscular effort or EP shift produced in both phases of a trial would be expected to produce a response force direction different from the reference force direction.

Subjects did not appear to encode and store force information in terms of a veritable force vector. In the response phase of the force reproduction task, subjects could have adjusted motor commands so as to match the remembered force sensation experienced in the reference phase of each trial based on afferent information. According to the results of these experiments, however, the specification of a desired output force appears instead to be related to the muscular effort or motor command required to produce the desired force. This leaves open the question of what exactly is being stored in the nervous system. Conceivably subjects might remember the actual motor commands used during the reference phase of each trial and then simply play back the same command as the required response. However, in the case where the reference force was sensed with the right hand and the response was reproduced with the left, both the actuators, and the impedance of the effector limb changed. The latter occurred due to the asymmetric configuration of the joint angles required to reach the joystick with the right and left hands. It is obvious, therefore, that the system is sophisticated enough to re-map motor commands to different muscles and different arm configurations, as shown by the cross-manual transfer task. Had subjects simply applied the muscle activations used by the right arm to the homologous muscles in the left arm, the forces applied by the left hand in the response phase would have been grossly out of line with the force produced the right arm. A similar argument applies to the hypothesis of reproducing joint torques. The joint torques were necessarily recomputed in the transfer from the right to left hands. It is clear, however, that muscular activities or joint torques were not being regulated to compensate for different impedances of the hand or joystick. The hypothesis that the CNS specifies and controls force or joint torque could not predict the patterns of distortion observed across the ensemble of experiments performed here.

Overall, the results described here indicate that EP displacements of the limb as a whole are much more invariant between the reference and response phases than either hand force, joint torques or even muscle activations (as shown by the cross-manual transfer task). This suggests that the CNS might in fact internally encode and store EP displacements as a means of specifying an output force. The EP displacement would then be mapped onto the appropriate muscles when the desired force is actually produced. The re-mapping does not, however, take into account changes of impedance. Subjects appear to blindly program a motor output without regard to sensory information that could indicate impedance changes for the limb or the environment. It remains to be seen whether under more radical conditions the CNS could account for different mechanical conditions, perhaps based on internal representations that include both an EP displacement and a specification of the limb impedance.

The observations reported here are consistent with hypotheses under which the fundamental control variable used by the CNS to regulate posture and movement is the equilibrium posture of the mechanical system. EP control hypotheses propose that the CNS simplifies movement planning by specifying a desired equilibrium trajectory as the descending motor command to the spinal cord (Bizzi et al. 1982; Feldman 1966, 1986; Gomi and Kawato 1997). Forces required to produce the movement and to ensure dynamic stability are generated by the viscoelastic properties of the muscles, i.e., the so-called α model proposed by Bizzi, and colleagues (Bizzi et al. 1982; Flash 1987; Hogan 1984), and by reflex pathways, as originally proposed by Feldman in his so-called λ model (Feldman 1966, 1986). Recent studies indicate that the EP hypothesis is probably not sufficient by itself to explain all classes of movements, at least not in the sense of a simple servo-control mechanism (McIntyre and Bizzi 1993). It is likely that feedforward control coupled with inverse dynamic models are used by the motor system to better control movement (Gomi and Kawato 1996; Wolpert et al. 1995). Nevertheless, it is clear that the motor system benefits from specifying stable equilibrium positions to maintain posture and to reject disturbances during movement. As shown here, EP hypotheses may also be applied to the generation of forces against an external object. By specifying a virtual equilibrium point that lies away from the actual position of the limb imposed by the environment, the elastic properties of the limb will generate a force that would move the limb toward the equilibrium if the externally imposed constraint were not there.

In a recent set of studies on single-joint force control, Burgess et al. (1995) discussed whether the sense of “effort” corresponds to EP or torque control. The main results of their experiments was to show that perceived effort can be the same whether the subject intervenes to resist an increased force load (the descending EP command must change) or whether the subject allows the limb to be displaced without conscious intervention (the EP remains constant). Burgess argued that this is evidence for the “dynamic torque adjustment” (DTA) model in which equal effort means equal joint torques. According to Latash, however, effort would be equated to a shift

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in the specified EP of the limb that could be affected both by central commands and by afferent information. One could postulate that effort corresponds to the difference between the actual position and the virtual equilibrium position of the limb (i.e., the equilibrium position that would be assumed if there were no externally applied forces). This would coherent with the fact that afferent information is essential to force perception and reproduction even if the CNS is specifying and controlling forces in terms of effort (Sanes and Shadmehr 1995). The results of the experiments reported here are consistent with this interpretation and extend the interpretation of a sense of effort to the multi-dimensional case.

One might then ask the question as to what coordinate system could be used to specify the EP shift in multiple dimensions. Three logical candidates would be the equilibrium length of each muscle, the equilibrium orientation of each joint or the equilibrium position of the hand in space. While the experiments reported here cannot rule out any one of the these possibilities, the results of the cross-manual task argue for a representation of the hand EP. It seems unlikely that the same shift in muscle rest-lengths or joint equilibrium positions would have resulted in the same force exerted by the left and right hands, but this has yet to be proven. The memorization of an EP shift of the hand, however, whether it be in an egocentric coordinate system or allocentric Cartesian reference frame, would constitute an internal specification that need not change depending on the limb or muscles used to exert the force. On the other hand, specifying EP shifts of the hand would be inconsistent with what is known about motor adaptation in which learning to overcome dynamic force disturbances during repeated arm movements appears to occur in joint space (Shadmer and Mussa-Ivaldi 1994). In light of these conflicting results, additional work would seem necessary to ascertain the coordinate frame used by the CNS to encode and store the effort associated with a desired force output.

The interpretation that the CNS encodes forces as efforts or EP displacements is consistent with recent observations on the tuning of cells within primary motor cortex. It has been postulated that cells in these areas are broadly tuned, but respond preferentially to forces produced in a particular direction in 3D space (Georgopoulos et al. 1992; Taira et al. 1996). If these cells explicitly encode force, a given cell would fire equally for any given force vector independent of where in the workspace that force is being generated. It has been noted, however, that the preferred direction of individual cells changes as a function of the workspace position of the hand and the configuration of the arm (Sergio and Kalaska 2003). If instead of encoding 3D forces, these cells specify a displacement of the EP of the limb (a generalization of the EP hypothesis in which higher-order structures encode EP displacements as well), this behavior is to be expected. The same force produced in different workspace regions would require different EP displacements depending on the impedance of the limb at that location. Cell activity would reflect the differing EP displacement requirements and would thus also vary with hand location for the same net force. It remains to be shown, however, whether a given pattern of activations in a population of these neurons is better correlated with an EP displacement than with the actual force produced, as would be predicted by our hypothesis.

CONCLUSIONS

The experiments reported here provide evidence that human subjects do not directly control forces or joint torques in a force reproduction task. Forces appear to be specified via control signals that modify the equilibrium position of the limb without regard for the impedance of the interaction with the environment. These results give credence to the idea that humans possess a "sense of effort" as opposed to a true "sense of force" when controlling forces in multiple dimensions.

APPENDIX A: JACOBIAN COMPUTATION

Two steps are performed to compute the position of the hand M in the shoulder-centered coordinate system R0 (see Fig. 10).

1) $X(X_1, Y_1, Z_1) = \text{Rotation}(R_1 \rightarrow R_2)\, M(X_2, Y_2) + E(X_1, Y_1, Z_1)$

2) $M(X_0, Y_0, Z_0) = \text{Rotation}(R_0 \rightarrow R_1)\, M(X_1, Y_1, Z_1)$

The result is

$$M\begin{pmatrix} x \\ y \\ z \end{pmatrix} = \begin{cases} L_1 \cos\theta_s \cos\varphi_e + L_2 \cos\theta_s \cos(\varphi_e + \varphi_s) \\ L_1 \sin\varphi_e + L_2 \sin(\varphi_e + \varphi_s) \\ -L_1 \sin\theta_s \sin\varphi_e - L_2 \sin\theta_s \sin(\varphi_e + \varphi_s) \end{cases}$$

The Jacobian can be derived from the relation above

$$\begin{pmatrix} \mathrm{d}x \\ \mathrm{d}y \\ \mathrm{d}z \end{pmatrix} = J \begin{pmatrix} \mathrm{d}\varphi_e \\ \mathrm{d}\varphi_s \\ \mathrm{d}\theta_s \end{pmatrix}$$

The Jacobian matrix relates hand forces to joint torques

$$T = J^{\mathrm{T}}F$$

APPENDIX B: INFLUENCE OF *FZ*

The prediction of the response force direction if the subject reproduces the same joint torques is given as follows

$$F_{\mathrm{resp}} = (J^{\mathrm{T}}_{\mathrm{resp}})^{-1} J^{\mathrm{T}}_{\mathrm{ref}} F_{\mathrm{ref}}$$

For the experiments reported here, positions and forces are represented by Dvectors. Using the 2D joystick, the third degree of freedom (*Z*) is restricted to 0 for the position of the hand, while the *Z* component of the force is not measured. To test the predictions that subjects reproduced joint torques, we computed the joint torques required to reproduce the measured 2D forces, assuming that the vertical component of the force is equal to zero. We then repeated the joint torque calculations assuming different nonzero values for the *Z* component of the force.

Figure 11 shows that the predictions of the hypothesis in which subjects reproduce joint torques are insensitive to any force that may have been applied in the *Z* direction. Figure 11*A* shows the predicted pattern of errors for forces in the horizontal plane for three different

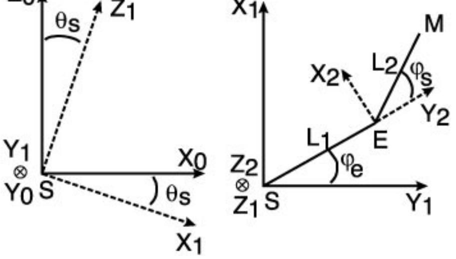

FIG. 10. Representation of the different coordinate systems used to compute the Jacobian of the transformation from hand coordinates to joint angles. *M* is the end effector, *E* is the elbow, and *S* is the shoulder. Angles correspond to the rotation in R_2 (X_2, Y_2, Z_2) for φ_S and R_1 (X_1, Y_1, Z_1) for φ_E.

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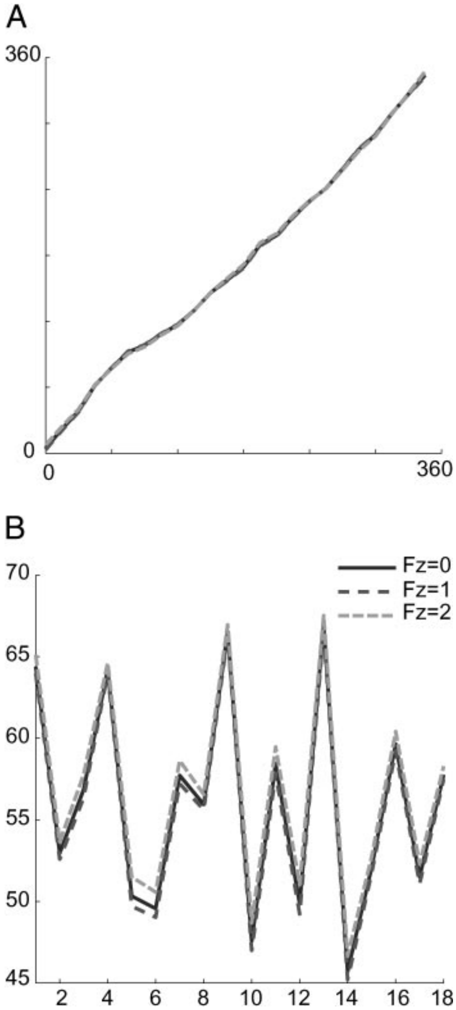

FIG. 11. Influence of 3 different values for the *Fz* composante in the estimation of the force direction obtain by the torque reproduction. *A*: for all directions. *B*: for 1 subject for the direction 45°.

values of vertical force. The predicted relationship between reference and response force directions in the plane are essentially identical. Figure 11*B* shows the predictions of the torque reproduction hypothesis for eight trials with the reference force at 45°. The expected difference in planar force directions due to changes in vertical force are much smaller than the variability between trials to the same reference stimulus.

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DISCLOSURES

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