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REVIEW

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Differential exploitation of the inertia tensor in multi-joint arm reaching

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Abstract The identification of the kinaesthetic information used for directing 3D multi-joint arm movements toward a target remains an open question. Several psychophysical studies have suggested that the ability to perceive and control the spatial orientation of our limbs depends on the exploitation of the eigenvectors (e_3) of the inertia tensor (I_{ij}), which correspond to the arm rotational inertial axes. The present experiment aimed at investigating whether e_3 was used as a collective variable to direct the masses toward the target and hence to control the spatial accuracy of the final hand position. Natural, unconstrained, three-dimensional multi-joint reaching movements were submitted to alterations of forearm mass distribution. Given the existence of several "sensorimotor strategies" for the control of arm movements, the participants were a priori contrasted and ranged in groups according to their reliance on either visual or kinaesthetic information. The results indicated (1) the dependency of the arm's directional control on I_{ij} parameters, (2) a non-linear relationship between the performance predicted by the inertia tensor and the observed performance, depending on the deviation amplitude and (3) the presence of a large inter-individual variability suggesting the existence of different strategies, including proprioceptive compensation mechanisms. This study validates in unconstrained multi-joint arm movements the exploitation of the inertia tensor by the central nervous system, thus simplifying the coordination of the segments' masses during reaching. The results also provide evidence for the existence of motor alternatives in exploiting proprioceptive information that may depend on spatial referencing modes.

Keywords Proprioception · Multi-joint free arm reaching · Sensorimotor strategies · Eigenvectors of inertia tensor · Mass compensation

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Introduction

Pointing at a target with the hand requires the spatial mapping between the endpoint of the arm and the target located in an external frame of reference. Classical computational approaches to motor control have analyzed the directional control of arm movements toward a target as a series of sensorimotor coordinate transformations, from a direction in a visual space to a direction in a motor space. More specifically, it has often been assumed (Kalaska and Crammond 1992; Soechting and Flanders 1992) that the central nervous system (CNS) performs a major computation in the conversion of a kinematic space (i.e., spatial target, hand displacement or joint motion) to a kinetic space (i.e., joint torque or muscular activity). When the arm's movements are out of sight throughout the progress of reaching toward a still visible target, the pointing task relies mainly on kinaesthetic cues and efferent commands. It is widely recognized that proprioceptive information from the muscles, joints and other receptors plays an important role in accurately controlling both the spatial and temporal features of the movement, as well as the final orientation of the hand (Sainburg et al. 1993). Patients deprived from proprioceptive feedbacks, due to large fiber-sensory neuropathy, show large errors in movement direction and curvature (Sainburg et al. 1995). It is well established that deafferented subjects have no ability to adjust their movements in the face of unexpected loads, or to maintain a steady joint angle without vision (Rothwell et al. 1982; Sanes and Shadmehr 1995). Precision in muscle timing, a known key factor for controlling limb interaction torques, is also dramatically impaired (Sainburg et al. 1993). For these patients, vision partially improves performance (Ghez et al. 1995). A significant aspect of this inaccuracy in the absence of vision is the inability to take into account the variation in inertia of the limbs during the reach. Despite the extensive research in animals and human subjects, the precise contribution of proprioception to motor control still remains poorly understood. One recurrent question is about the identification of the kinaesthetic invariants that are genuinely used for directing the arm toward the target.

Some experiments strongly support the notion that the CNS uses intrinsic criteria based on the arm's dynamics in the planning of the movement (Flash and Hogan 1985; Hogan 1984; Viviani and Flash 1995), including the inertial properties of the arm (Sabes and Jordan 1997, 1998). In healthy subjects, it has been established that the transient inertial loads, unexpectedly added or subtracted symmetrically from the spatial axes of a moving limb, leave the movement end-point unaffected. Nevertheless, contrasting with the above experiments are numerous investigations providing evidences that the directional control of the final hand position is affected when loads are affixed away and asymmetrically from the spatial axis of the forearm (Pagano et al. 1996; Sainburg et al. 1999), thereby leading to alterations in mass distribution.

According to Pagano and Turvey (1995), our ability to perceive the spatial orientation of a limb via kinaesthetic inputs is tied to the eigenvector (e_3) of the inertia tensor (I_{ij}). This mechanical invariant parameter quantifies the mass distribution of a segment or a rigid limb. Several studies have revealed that the eigenvector can be used in pointing the whole occluded arm toward a visible target (Pagano and Turvey 1995), in aligning the posture of the forearms (Pagano et al. 1996) or in matching the position of the hand with the position of another part of the body, such as the shoulder or the nose (Riley and Turvey 2001).

Previously, these questions have been investigated in pointing tasks involving arm movements limited to only a single degree of freedom. In the experiment described below, we examined the generalization of the inertia tensor hypothesis to unconstrained poly-articulated pointing arm movements. In single-degree-of-freedom reaching, this mechanical parameter is time-independent and coordinate-independent. In 3D multi-joint reaching, however, the continuous modification in the angular limb configuration leads this physical parameter to be coordinate-dependent.

Pagano et al. (1996) have suggested that understanding movement control and coordination should be addressed in terms of the relative directions of the segmental inertia ellipsoids, rather than in terms of joint angles. However, they have equally concluded that the observed bias when manipulating e_3 is consistently less important than predicted. These contrasting results may suggest the existence of several strategies for the control of arm movements. As indicated by Adamovich et al. (1998), human subjects can use diverse perceptual information to achieve comparable final accuracy, but the details of the strategies employed may differ with the kind of information available.

Some authors (Isableu et al. 2003) have suggested that different levels of competence in using motor-somesthetic inputs can constrain the way sensory inputs are integrated for the control of balance, thereby leading to typical and stable sensorimotor "styles". This suggestion may explain the variability observed between subjects in both the perception and the control of spatial orientation. Indeed, strong differences are found in spatial orientation tasks between subjects who are visual field dependent (FD) and field independent (FI) (Asch and Witkin 1992; Isableu et al. 1998). We have decided to contrast three groups of subjects: two groups differed from each other in their extreme visual vs non-visual spatial referencing mode (FDI: independent or dependent to visual field); the third group was a group of gymnasts (GYM) known for their expertise in controlling body mass distribution. Recent experiments have suggested that GYM can be more attuned to somesthetic information than sedentary humans in motor activities (Vuillerme et al. 2001a, b) or in perceptual estimates of self-body orientation (Bringoux et al. 2000). Gymnasts present the particularity of being able to rapidly take into account alterations in proprioceptive information (Vuillerme et al. 2001a) when visual informations are altered or removed (Vuillerme et al. 2001b). We expected FI subjects and GYM to compensate for the alteration in their mass distribution in a more efficient way than subjects relying on a visual reference frame (FD subjects).

To summarize, we examined the contribution and degree of generalization of the inertia tensor hypothesis to unconstrained poly-articulated pointing arm movements. We also suggested a differential approach of the e_3 hypothesis by using contrasting groups in their reliance on different spatial referencing modes. We made the following hypothesis: if perception and control of arm orientation toward the target are constrained by the inertia tensor, pointing will consist in directing the eigenvector of the arm toward the target.

Materials and methods

Subject

Twenty-four right-handed males, aged from 19 to 25 years (±2–3 years), gave their informed consent to participate in the experiment. All participants were free from sensory, perceptual or motor disorders and had normal or corrected-to-normal vision. They were naïve about the purpose of the experiment.

Selection and screening test: Three groups of participants were formed. In order to obtain clear-cut groups of eight subjects, we selected from a non-athletic male population the extreme visual FD group, the visual FI group and (among an athletic male population) the expert GYM group (45 points, FIG code reference). The Oltman's rod and frame test (Oltman 1968) was used to select the extreme visual FD participants ($M=6.1°$; $SE=2°$) and the visual FI participants ($M=1.45°$; $SE=0.6°$).

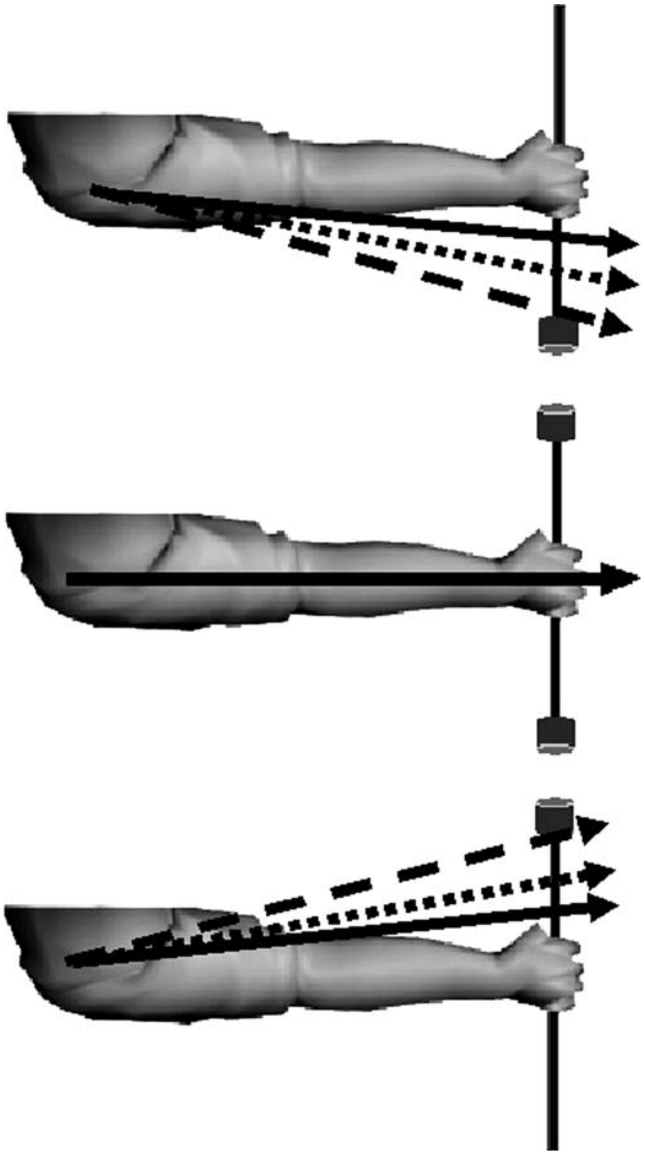

Fig. 1 Side view of the experimental apparatus illustrating the target in front of the tested subject. A mask obscured the sight of the arm throughout the pointing, while the target (*the vertical line*) remained visible. Deviation of the e_3 eigenvector in the experimental conditions. e_3 was deviated 1.7° (*solid arrow*); 3.2° (*stippled arrow*) and 6.8° (*dashed-dotted arrow*) in the 100, 200 and 500 g mass conditions, respectively, to the right side (**a**) or left side (**c**) of the arm. When the mass was added on each side of the arm, the eigenvector was aligned with the longitudinal axis of the arm (**b**)

Setup

Participants sat on a chair with their trunk fixed against the back. The center of the target was directly aligned across the joint center of rotation of the right acromion, such that the shoulder formed a 90° angle with the trunk when the arm was fully extended on the target. The distance separating the subject from the target was equal to the length of each subject's arm. In the starting position, the right arm was supported on a rest. As illustrated in Fig. 1, the participants wore a mask that obscured the sight of the arm throughout the pointing, while the target (a vertical line) remained visible.

The participants held an apparatus that allowed their wrist to be fixed. With this system, a rod was adjusted perpendicularly to the forearm axis (the z-axis), measuring 60 cm in length and 1 cm in diameter. The mass distribution of the right arm was modified via a cylinder placed on this axis, at 28 cm from the center of the hand. Masses, weighing 100 g, 200 g and 500 g, were located either symmetrically—the z eigenvector being aligned with the longitudinal axis of the arm—or asymmetrically (allowing rotation of the z eigenvector), thus breaking its alignment with the longitudinal axis of the arm. The participants were required to maintain the forearm/object system on a horizontal plane during the reaching movement. No physical limitation was used to constrain this planar movement, so that the rotation resistance was conserved. Nevertheless, a visual inspection was carried out to exclude the trials in which a rotation of the system arm/object higher than 5° were observed. This resulted in the exclusion of ten trials for the entire experiment. Under these conditions, the subjects were instructed to point as accurately as possible toward the target.

Eigenvector calculation

The estimation of body parameters was based on Kwon's method (Kwon 2002), adapted from Hanavan's geometric model (Hanavan 1964). Masses, centers of masses and principal moments of inertia were computed by using the regression equation and the procedures provided by Kwon. The forearm and the upper arm were modeled as truncated cones, the hand as an ellipsoid of revolution and the mass was added to the arm as a cylinder. We calculated the inertia tensor when the arm was fully extended. The principal moments of inertia, I_{xx}, I_{yy} and I_{zz} of each segment of the arm were calculated about their respective centers of mass. The origin for I_{ij} could be translated from the joints of each segment to some other location in order to test the sensitivity of the arm/forearm system to the inertial deviation. Huygens theorem was used to obtain the components of the total moment of inertia (the inertial rotation quantity of the forearm/arm system) about the shoulder. The following equation was used:

$$I_{/S} = \sum I_{/G} + \sum H \tag{1}$$

where $I_{/S}$ is a 3×3matrix (kg m^2) about the joint center of the shoulder, $I_{/G}$ the inertia tensor of all elements of the arm/object system about their respective center of mass and H the moment of inertia of the mass center about the shoulder rotation axis. The direction and magnitude of the principal moments of inertia, that is, the eigenvectors and eigenvalues, were obtained by diagonalizing the inertia tensor, minimizing the inertia products. The eigenvector (e_3) related to the new axis of the arm's inertia tensor had the smaller eigenvalue. When the arm was extended, the e_3 eigenvector deviated from the longitudinal axis of the arm by 1.7, 3.2 and 6.8° in the 100, 200 and 500 g conditions, respectively (see Fig. 1). The displacement of the eigenvector was coded negatively to the left of the arm and positively to the right of the arm.

Procedure

A learning session allowing the subjects to become familiar with the movement time was included at the beginning of the experiment. Movement duration was fixed to 1.3 s, thereby corresponding to natural reaching movements. During 50 trials, the subjects performed pointing movements under the same restricted protocol used in the test session, without any additional mass, feedback or vision of the arm. During the learning session, the participants performed the trials with two auditory signals announcing the start and the end of the pointing movement. If the participants lost the tempo during the test trials, additional trials with the auditory signals were repeated in order to rescale the duration of reaching. Trials out of the ±10% limits of this fixed duration were withdrawn and immediately repeated. The experimental trials combined for each group (FI, FD and GYM) three masses (100, 200 and 500 g) and three localizations (left-asymmetrical, symmetrical and right-asymmetrical). The trials were grouped by mass conditions in a single experimental session. The order of mass and localization conditions was randomized for each subject. On the other hand, the three trials in each condition were repeated in succession. The participants never received any visual or proprioceptive feedback about the onset, trajectory or endpoint of their movements.

At the end of each pointing movement, we expected the angle between the target and the arm to be equal to 0° when the arm and target axes coincided, to be positive when the hand was positioned to the left of the target and negative when it was positioned to the right of target. Constant errors (CE), mean angle between the tip of the stylus, the acromio-clavicular joint and the vertical target-line location at the end of movement (Darling and Gilchrist 1991; Rossetti et al. 1994) were analyzed in ANOVAs with group (3) and deviation by mass conditions (9) as factors. Planned post hoc comparisons were used to detail the main analysis. The statistical regression method was also used to estimate the relationship between the errors predicted by the model and the observed pointing errors. This method was based on a linear regression quantifying, by mean slope and R^2 values, the fit between the predicted and observed bias. The final pointing errors were normalized by subtracting the y-intercept of each deviation condition from each pointing error.

Results

Target accuracy

A 9×3 ANOVA, with mass and group factors was carried out on the average constant error (CE). It indicated a significant main effect for group ($F(2,21)=3.66$, $P<0.05$). Planned comparisons ($P<0.05$) showed a difference in CE between the FD group ($M=2.53°$) and the two other groups ($M=0.53°$ for FI, $P<0.05$; $M=1.82°$ for GYM, $P=0.06$). This result revealed the existence of a gap between the felt (proprioceptive) target localization (mean bias by group) and the visual target. On an average, the pointing performance for the FD participants deviated more from the real target (large constant error) than for the FI participants ($P<0.05$). The FI and GYM groups did not differ ($P>0.05$). To compare the effect of the eigenvector deviation, the set of end pointing errors was adjusted by subtracting the constant error of each group by e_3 deviations. In addition, the symmetric conditions were collapsed, as they were not affected by the added mass ($P>0.05$).

Effect of eigenvector deviation

A regression was plotted on the adjusted data, showing the significant relation between the mean predicted bias,

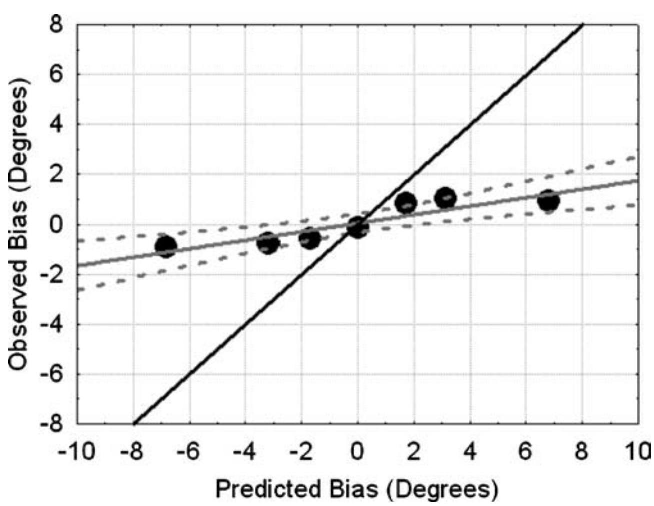

Fig. 2 Mean observed angular constant errors as a function of predicted angular eigenvector deviation ($y=0.17x$)

Table 1 Individual and mean slope and adjusted R^2 values in each deviation condition

	1.7°		3.2°		6.8°		All deviations	
	Slope	R^2	Slope	R^2	Slope	R^2	Slope	R^2
S1	0.01	0.00	0.24	0.69*	0.17	0.20	0.17	0.26*
S2	0.83	0.56*	-0.14	0.00	0.00	0.00	0.01	0.00
S3	0.64	0.07	0.09	0.00	0.16	0.67*	0.17	0.04
S4	0.61	0.73*	0.21	0.97*	0.09	0.82*	0.14	0.42*
S5	0.13	0.00	0.41	0.31	0.10	0.28	0.16	0.13*
S6	0.15	0.00	-0.03	0.00	-0.01	0.00	0.00	0.00
S7	0.25	0.03	0.20	0.54	0.14	0.30	0.15	0.31*
S8	0.21	0.12	0.01	0.00	0.15	0.34	0.13	0.28*
S9	0.06	0.00	0.10	0.00	0.13	0.13	0.12	0.09
S10	0.67	0.32	0.63	0.59*	0.38	0.86*	0.43	0.67*
S11	0.47	0.62*	0.23	0.41*	0.10	0.23	0.13	0.31*
S12	0.94	0.87*	0.78	0.81*	0.31	0.93*	0.42	0.68*
S13	0.00	0.00	0.10	0.00	0.14	0.30	0.13	0.22*
S14	−0.05	0.00	0.04	0.78*	0.04	0.07	0.03	0.00
S15	0.32	0.00	0.22	0.07	0.04	0.00	0.08	0.00
S16	0.29	0.00	0.10	0.00	0.01	0.00	0.04	0.00
S17	0.47	0.27	0.01	0.00	0.02	0.00	0.04	0.00
S18	0.75	0.73*	0.00	0.00	0.04	0.00	0.05	0.01
S19	0.45	0.21	0.39	0.86*	0.11	0.28	0.17	0.30*
S20	0.29	0.58*	0.07	0.00	0.07	0.89*	0.08	0.13*
S21	0.07	0.46*	0.05	0.04	0.13	0.35	0.11	0.35*
S22	1.70	0.73*	0.96	0.74*	0.62	0.78*	0.71	0.69*
S23	−0.21	0.10	0.22	0.42*	0.05	0.05	0.07	0.09
S24	0.63	0.30	2.11	0.94*	0.34	0.28	0.54	0.34*

*Indicates a significant regression

that is, the e_3 deviation, and the mean observed bias ($y = 0.1703x$, R^2 adjusted = 0.78, $P < 0.05$). This result indicates that, overall, the participants aligned the direction of e_3 on the target (see Fig. 2). An ANOVA performed on (absolute values of) error amplitudes comparing left and right deviations of e_3 relative to the symmetrical condition indicated a symmetric effect of e_3 deviation ($F(5, 115) = 1.20$, $P > .05$). This result extends previous findings (Pagano et al. 1996) to the case of pointing with a natural multi-joint arm movement. However, close inspections of slope values by e_3 deviation conditions indicate different relationships between predicted and observed bias ($F(3, 210) = 10.08$, $P < 0.05$). The slope values were 0.38 for 1.7° (R^2 adjusted = 0.06, $P < 0.05$), 0.26 for 3.2° (R^2 adjusted = 0.11, $P < 0.05$) and 0.13 for 6.8° (R^2 adjusted = 0.09, $P < 0.05$) e_3 deviations. This result shows that pointing errors did not increase after the intermediate e_3 deviation.

Differential effects of eigenvector deviation

The general effect for eigenvector deviation did not completely fit the predicted bias. Table 1 presents the R^2 and slope values for each individual regression between the predicted bias in e_3 deviation and the observed bias in degrees. From the series of the 24 slope values, a continuum of arm pointing responses can be observed. As illustrated in Fig. 3a, the slope values extended from 0.00 to 0.69. This continuum suggests a differential sensitivity to the inertia tensor. What can account for this large inter-individual variability in the specification of the final hand position?

As illustrated in Fig. 3, two types of behavior were identified: one type was close to the inertia tensor predictions (e_3/target alignment); the other type was close to the given experimental instructions (hand/target alignment). We will refer to the first behavior as the "tensor strategy" (TS) and to the second as the "other strategy" (OS). The TS group corresponded to the participants that presented a regression slope value close to one (perfect fit), as illustrated in Fig. 3b for a typical participant of this group ($y = 0.68x$, R^2 adjusted = 0.67, $P < 0.05$). The OS group corresponded to the subjects that presented a regression slope value around zero. The data from one typical participant of this group are illustrated in Fig. 3c, showing no pointing error ($M = 0.01°$; $SE_1 = 0.40$) and no effect of the eigenvector deviation ($y = 0.12x$, R^2 adjusted = 0.88, $P < 0.05$). Figure 4 shows the distribution of OS and TS behaviors by condition of e_3 deviation. It should be stressed that the distribution between the two behaviors changed as a function of the deviation conditions. The TS behavior was largely present for the small eigenvector deviation. The pointing errors decreased when the added mass increased. The distribution of the slope values was largely flattened for the larger deviation of e_3 (see Fig. 4) toward OS behaviors. Only few subjects remained altered by the 6.8° deviation of e_3. Furthermore, one of the 24 participants tended to overestimate the deviation of the inertia eigenvector for the 100 g mass and another for the 200 g mass.

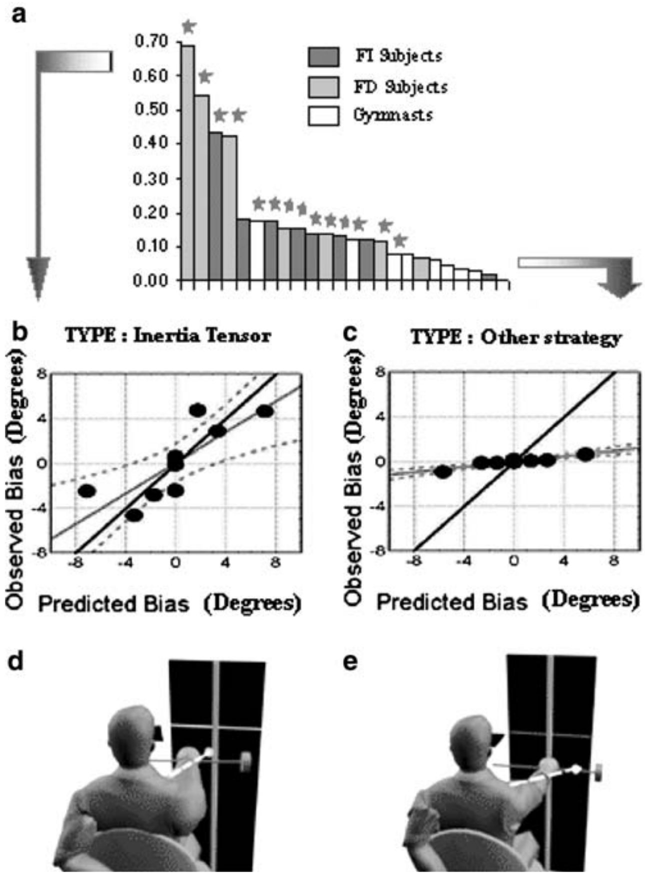

Fig. 3 Different strategies in using the inertia tensor during pointing: (**a**) the 24 individual regression slope values (one regression/subject) showing a continuum in the range [0.00; 0.69]; (**b**) a typical response from one participant of the inertia tensor strategy (TS) and; (**c**) from one participant of the other strategy (OS); (**d**) Illustrations of a perfect inertia TS, (**e**) and of another strategy (OS). *Indicates a significant regression

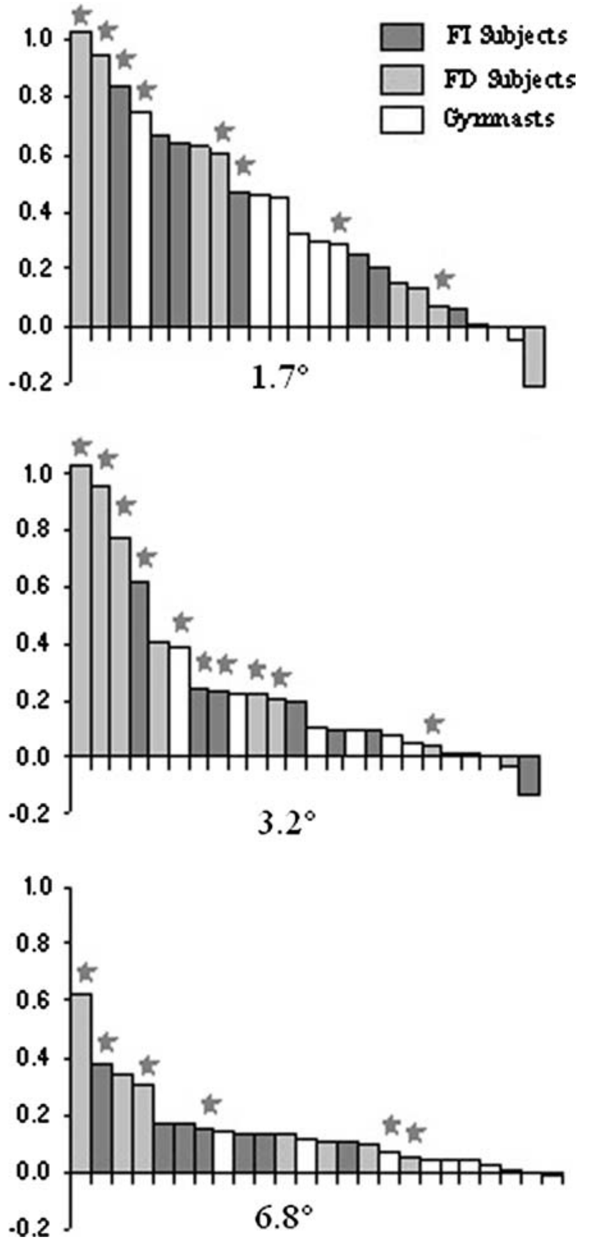

Fig. 4 Continuum of individual slopes (*between observed vs predicted pointing errors*) by e_3 deviation conditions. Responses are differentiated for each group (*FI* field independent, *FD* field dependent, *GYM* gymnasts). The proportion of subjects altered by the e_3 deviation decreased with the increase in mass. *Indicates a significant regression

A separate analysis was carried out on the slope values, with categorical FDI and continuous (e_3 eigenvector deviations) predictors as factors. It revealed a significant interaction between the two factors ($F(3, 162)=9.59$, $P<0.05$). This result confirms that the relationship between the e_3 predictors and the observed pointing errors differed between groups. A significant regression ($y=0.2717x$, R^2 adjusted $=0.68$, $P<0.05$) for the FD group indicated that the end pointing errors followed the predicted bias with a slope of 0.27, but only with a slope of 0.16 for the FI group ($y=0.1652x$, R^2 adjusted $=0.87$, $P<0.05$). Finally, the flat regression for the GYM group suggested that the observed pointing errors did not vary with the predicted eigenvector deviation ($y=0.0801x$, R^2 adjusted $=0.57$, $P<0.05$), as expected. The separate slope analysis carried out with the categorical FDI factor in each e_3 condition suggested a differential sensitivity to e_3 between groups for the 3.2° ($F(3, 66)=6.17$, $P<0.05$) and for the 6.8° ($F(3, 66)=4.20$, $P<0.05$) deviations. Pointing errors for the FD group continuously increased for the largest e_3 deviation. The relationship between the predicted and observed pointing errors in the FI group reached its highest value in the intermediate e_3 condition and then decreased for the largest e_3. By contrast, the GYM group never showed any relationship with e_3 in any deviation condition.

Discussion

Our research provides evidence that proprioceptive control of reaching movements exploits the directional features dictated by inertial dynamics of our moving limb's mass distribution. Our results show that, in general, the control of the final position of a poly-articulated arm is affected by the deviation of the inertial eigenvector (e_3). Indeed, the participants pointed at the target by directing the eigenvector on it. This extends previous studies to the case of a multi-joint, multi-degree-of-freedom, reaching system (Garrett et al. 1998; Pagano 2000; Pagano and Turvey 1995; Pagano et al. 1996). However, it should be noted that the manipulation effect was less important than predicted, mostly when the asymmetry in mass distribution became very large (Garrett et al. 1998; Pagano and Turvey 1995). Three main results of our experiment are now discussed in detail: (1) the dependency of the arm's directional control on I_{ij} parameters, (2) the emergence of pointing errors' stabilization when the participants were faced with large alterations in their arm's mass distribution and (3) the presence of a large inter-individual variability suggesting the existence of various sensorimotor strategies.

Dependence on inertia tensor parameters

The observed tuning of the motor system to inertia tensor parameters indicates that the participants had chosen the eigenvector e_3 as the spatial reference axis for directing the movement toward the target. In this case, I_{ij} must take a diagonal form and the inertia products toward e_3 are minimized. Within this view, e_3 can be deemed as a reliable collective variable used for coordinating the segmental masses and hence, for positioning the fingertip on the referent target. This behavior was principally observed for the 1.6° e_3 deviation, and then it monotonically decreased with the increase in e_3 deviation. The number of subjects evidencing a close e_3 alignment with the target was high in the smallest deviation condition and then gradually decreased with increasing e_3 deviations.

Previous studies on the inertia tensor allowed participants, in each trial, to explore the properties of the arm/object system before pointing at the target (Garrett et al. 1998; Pagano 2000; Pagano and Turvey 1995; Pagano et al. 1996; Riley and Turvey 2001). In this experiment, we have considered that the three trials by condition realized in succession and the multi-joint nature of the movement allowed the participants to explore the inertial dynamic of the limb. Our results indicate that the inertial properties of the limb were perceived and exploited online during the pointing movement in spite of the absence of an exploratory phase.

Parameters for mass compensation

Inertia tensor parameters

The second main outcome of this study is that pointing errors culminated in the intermediate condition of e_3 deviation. The subsequent reduction in the pointing errors could indicate that subjects better detected the changes in the inertial structure of the mass distribution when asymmetries became very large. Prominent (e.g., asymmetric) inertial configurations could lead to fast behavioral compensations. We cannot rule out the possibility that subjects have shifted their arm's direction by continuously extracting information about the inertia tensor, thereby compensating for the deviation of the eigenvector. We claim that the inertia products bring forth to the resistance feeling, which in turn disclose information about the spatial inertial structure of the arm in relation to a given physical referent. According to this view, compensation for large e_3 deviations would entail a differential exploitation of the inertia tensor, requiring in this case the maintenance of the inertia products at a (constant) specific value, and the production of a suitable muscular torque in order to compensate during the movement toward the target the effect of alterations in mass distribution. Some authors (Gribble et al. 2003) have shown that increasing muscular co-contraction (and hence, joint stiffness) may be a relevant strategy to increase the movement's accuracy of multi-joint arm movements, although energetically expensive. In a three-dimensional unconstrained obstacle avoidance experiment, Sabes et al. (1998) have suggested that the CNS can use inertial information in the planning of obstacle avoidance movements, a conclusion that echoes our findings.

Other strategies

Garrett et al. (1998) suggested another interpretation accounting for the effect of e_3 lower than expected. This author evoked a motor organization of the limb that fixes a particular posture in accordance with Feldman and Latash's approach (1982a, b). Compensation could also be achieved on the basis of a joint geometry-based strategy (Soechting and Flanders 1992). This strategy involves the accurate reproduction of a specific angle between the arm and the trunk or the head used as a reference frame (spatial geometry). Such spatial geometry-based compensations could be also viewed as relevant and reliable strategies for bypassing continuous changes in mass distribution. Indeed, it has been recently shown that the perception of shoulder angle (with respect to the trunk) and elbow angle was very accurate, about 0.6–1.1° (van Beers et al. 1998). The finding that such mechanisms were not observed for the smallest e_3 deviation—participants adopting dominantly a tensor strategy—still remains puzzling and does not totally support this strategy, although it could not be excluded for some subjects of our sample. Note however that angular coding supposes the scaling of the magnitude or the duration of applied forces in order to fulfill the specified angular value. The scaling of force parameters implies that alterations in the inertial structure of the arm during the movement have been perceived.

Therefore, although the use of the inertia tensor is not questionable when pointing errors match the e_3 deviation on the target, its (non-)use when pointing is accurate remains an open question that we view important for future research.

Differential exploitation of the inertia tensor

Our results provide a clear demonstration of a differential exploitation of the inertial parameters, as evidence by the large inter-individual variability observed. The previous sections identified two behavioral strategies related to either the inertia tensor exploitation (e_3 axis or an inertia products-based compensation) or to a spatial geometry-based compensation (angular coding). Our differential approach (FDI and GYM subjects) was intended to a priori screen the individual preferential or prevalent mode of spatial referencing. Note that the athletes participating in closed-skill sports (acrobatic sports such as gymnastic) are generally ranged as FI subjects, and a high level of expertise is known to correlate with increasing field independence (McLeod 1985). The supposed prevalent use of non-visual referents by FI subjects and GYM showed an interesting covariation with the two main reaching behaviors identified (TS and OS). Indeed, the differential regressions obtained for the three groups may imply different spatial referencing modes. A small asymmetric mass distribution of the arm can enhance the prominence of the arm inertial structure (e.g., enhanced resistances) that, in turn, may lead GYM and FI subjects toward compensations based either on a differential exploitation of the inertia tensor parameters or on a shift toward a spatial geometry-based strategy (angular joint coding). This result confirms recent experiments (Vuillerme et al. 2001a, b) and provides complementary suggestions that GYM detect somesthetic information better in motor activities (such as postural control).

Categorization of sensorimotor strategies is common in the motor control literature. Desmurget et al. (1998), for instance, suggested that the search for general theories may be vain, the CNS being able to use different strategies both in encoding the target location with respect to the body and in planning the movement of the hand. Research on the inertia tensor does not escape this discussion, for several studies have reported pointing errors in the opposite direction of the e_3 hypothesis, that is, in the direction of the added mass (Flanagan and Lolley 2001; Ghez et al. 1994; Gordon et al., 1994; Sainburg et al. 1999).

Ghez et al. (1994) and Gordon et al. (1994) have for instance found that, in planar reaching movements, hand acceleration varies with direction. Ghez et al. (1994) suggested that these variations are not planned and, instead, arise as a consequence of the interaction between limb mechanics and motor commands that do not take inertial anisotropy into account. In addition, systematic errors in amplitude and direction were reported by these authors (Ghez et al. 1994; Gordon et al. 1994) that primarily depend on the direction of hand movement and the initial position of the hand, respectively. They showed that low and high inertia movements overshoot and undershoot their targets, respectively. The finding that hand acceleration varies with direction-dependent changes in limb inertia was replicated by Flanagan and Lolley (2001), but with an opposite interpretation. They rather suggested that the CNS knows about inertial anisotropy and uses this knowledge to appropriately scale normal forces for direction-dependent variations in hand acceleration. They reported the same pattern of direction errors, but considered that their results indicate that the motor system maintains an accurate representation of this inertia anisotropy.

In Craig and Bourdin's experiment (Craig and Bourdin 2002), the apparent non-use of e_3 during pointing can be explained by the minimization of gravitational torque due to the apparatus employed (Riley and Pagano 2003). Nevertheless, a close inspection of their data revealed a significant relationship between the inertia tensor and pointing errors, but only in two of the target conditions among the four presented (−30, −15, +15, +30°/participants' body midline) (Riley and Pagano 2003). Craig and Bourdin's data reveal an effect of the e_3 manipulation when targets were located to the right of participants' body midline that is of a magnitude about equal to what has been observed previously (e.g., Pagano and Turvey 1995, Figs. 3, 4). Their data seem to reveal a limited role of e_3 for perceiving limb position, but only when the joint angles approach maximal limits (i.e., when the arm motion is blocked by the trunk). This can be viewed as an important and novel contribution of Craig and Bourdin's (2002) study, suggesting that the inertia tensor may play less of a role when the limbs are positioned at extreme joint angles.

Outcomes of Sainburg et al. (1999) clearly differ from the e_3 hypothesis. In Sainburg et al.'s study, the subjects performed multi-joint reaching movements supported on a horizontal plane by mean of a frictionless air-jet system, thereby withdrawing from the control possibilities the exploitation of rotations. Mass distribution and interaction torques were manipulated by altering the inertial load of the forearm. The pointing errors were on average in the direction of the mass location in the surprise trials (opposite to the e_3 hypothesis and to our data). The initial direction of their reaching responses also corresponded completely with the predictions of a forward model. Their results, although at first sight at odds with our data, confirm that compliant and differently-constrained movements can involve different control strategies (Desmurget et al. 1997, 1998).

All together, the results of this research indicate a differential use of the eigenvector e_3 of the inertia tensor of the arm during natural 3D pointing movements, depending on amplitude deviation and spatial referencing modes. Current research now explores the kinematics of both the inertia tensor and the arm during natural reaching movements.

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