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Visual gravity influences arm movement planning

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Sciutti A, Demougeot L, Berret B, Toma S, Sandini G, Papaxanthis C, Pozzo T. Visual gravity influences arm movement planning. *J Neurophysiol* 107: 3433–3445, 2012. First published March 21, 2012; doi:10.1152/jn.00420.2011.—When submitted to a visuomotor rotation, subjects show rapid adaptation of visually guided arm reaching movements, indicated by a progressive reduction in reaching errors. In this study, we wanted to make a step forward by investigating to what extent this adaptation also implies changes into the motor plan. Up to now, classical visuomotor rotation paradigms have been performed on the horizontal plane, where the reaching motor plan in general requires the same kinematics (i.e., straight path and symmetric velocity profile). To overcome this limitation, we considered vertical and horizontal movement directions requiring specific velocity profiles. This way, a change in the motor plan due to the visuomotor conflict would be measurable in terms of a modification in the velocity profile of the reaching movement. Ten subjects performed horizontal and vertical reaching movements while observing a rotated visual feedback of their motion. We found that adaptation to a visuomotor rotation produces a significant change in the motor plan, i.e., changes to the symmetry of velocity profiles. This suggests that the central nervous system takes into account the visual information to plan a future motion, even if this causes the adoption of nonoptimal motor plans in terms of energy consumption. However, the influence of vision on arm movement planning is not fixed, but rather changes as a function of the visual orientation of the movement. Indeed, a clear influence on motion planning can be observed only when the movement is visually presented as oriented along the vertical direction. Thus vision contributes differently to the planning of arm pointing movements depending on motion orientation in space.

motor planning; visual rotation; visuomotor conflict; vertical; internal model of gravity

WHEN SUBMITTED TO ALTERED visual feedback, subjects exhibit rapid and robust adaptation of visually guided arm reaching movements (Ghahramani et al. 1996; Helmholtz 1925; Krakauer et al. 2000). The reduction of systematic errors observed during adaptation indicates the development of a new mapping between movements and new visual context. Beside the learning process recurrently investigated by means of the rate of adaptation, these studies also raise a fundamental question: does the brain use the same motor plan before and after visuomotor remapping? By motor plan, we are referring to the choice of a specific motor pattern among the many ones that could satisfy the goal of the movement. Its content is accessible by examining movement characteristics that remain invariant under differing experimental conditions. For instance, when visual information on hand trajectory is artificially rotated, one might reach the target by using the same motor pattern (for example, straight hand path) as before visuomotor rotation; alternatively, one might adopt a new motor plan (for example, curved hand path) corresponding to the new spatial context. Differently stated, if visuomotor realignment to artificial rotation of the visual feedback can be achieved by several motor plans, which one will the central nervous system (CNS) prefer?

Traditional protocols, although interesting for examining visuomotor adaptation processes, present a limitation to address this question. Indeed, reaching different targets in the horizontal working space requires in general the same motor plan, that is, straight path and symmetric bell-shaped velocity profile (Morasso 1981). In the present study, to overcome this limitation, we took advantage of the motor planning process of vertical vs. horizontal arm movements. For single-joint movements, such as those investigated in this study, the motor plan relates to the shape of the velocity profile only (in single-joint movement, hand path remains constant). Previous studies (Gentili et al. 2007) have reported robust differences in hand velocity profiles between upward, downward, and horizontal arm movements. Precisely, acceleration duration is shorter than deceleration duration for upward movements, equivalent for horizontal (left or right) movements, and longer for downward movements. Berret et al. (2008) demonstrated that these asymmetries are due to a direction-dependent planning process that optimizes arm movements (by minimizing energy expenditure). Therefore, we assessed the effect of conflicting visual feedback on the motor plan by asking subjects to perform a reaching task in cardinal directions requiring specific velocity profiles. Two experimental phases were considered. We first checked subjects' motor performance during arm pointing in a virtual reality environment. In particular, subjects were asked to perform vertical (up and down) single-joint arm movements (rotation around the shoulder joint) while they visually perceived incongruent vertical movements (respectively, down and up). The underlying assumption, which to our knowledge has not been examined before, is that if the visuomotor conflict induces a new motor plan, arm velocity profiles should change in a predictable way, corresponding to those that subjects adopt when actually moving the arm along the visually perceived incongruent direction. Second, we tested whether such an effect would be vertical-dependent. Indeed, verticality seems to be central in motor planning, because vertical is the orientation of the gravitational force field, which our CNS has to continuously take into account in everyday life. Moreover, several

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recent results suggest that the vertical visual field is strongly embodied in the human neural system not only for motor control but also for visual perception (Indovina et al. 2005; Troje and Westhoff 2006; Zago et al. 2009). Therefore, it might be reasonable to expect that a feedback along the vertical (gravitational) orientation could have a higher relevance in inducing arm motor replanning than feedback in the horizontal direction. To test this hypothesis, we measured kinematics of vertical arm movements while subjects perceived incongruent horizontal movements, and vice versa. We found that altered visual information around the vertical but not horizontal axis strongly constrains the planning process of arm movements. In a control experiment, we verified that the observed changes in velocity profiles do not depend on continuous online corrections triggered by the visual feedback, but on the durable modification of the motor plan.

MATERIALS AND METHODS

Subjects

Ten right-handed subjects (2 women and 8 men, ranging in age from 23 to 33 yr, mean age 26.5 yr) took part in the main experiment. Six additional male subjects (ranging in age from 25 to 31 yr, mean age 29 yr) participated in the control experiment. All subjects were healthy, with normal or corrected to normal vision, and did not present any neurological, muscular, or cognitive disorder. Right hand dominance was determined by means of the Edinburgh handedness inventory (Oldfield 1971). All participants gave written informed consent before testing. The study was approved by the local ethics committee (Azienda Sanitaria Locale Genovese N.3), and all experiments were conducted in accordance with legal requirements and international norms (Declaration of Helsinki, 1964).

Experimental Device

The experiments were performed in a dark room. Subjects were comfortably seated on an adjustable chair in front of a black screen (190 cm wide × 140 cm high) at a distance corresponding to 110% of their fully extended right arm length. Two target-zones (total area = 1.68 m^2) were displayed on the screen by an Epson emp1815 LCD projector (70-Hz refresh rate), each one covering about 32% of the scene. These zones were delimited by white curved lines and were positioned either at the two sides of the screen (Fig. 1*A*) or at the top and the bottom of the screen (Fig. 1*C*). The curved shape was chosen to reduce as much as possible the environmental cues about vertical and horizontal references (see Le Seac'h and McIntyre 2007). In addition, a mask was applied on the projector to obtain a shaded circular picture contour. The subject was positioned slightly to the right and under the center of the projected screen (see Fig. 1*A*) to avoid the possibility that arm movements could occlude the visual display in any condition. Visual feedback about the position of the subjects' right arm was provided by a white dot (2-cm diameter) that moved on the screen in real time with their fingertip (see below for further details). Subjects were asked to perform (at a natural self-selected speed) single-joint arm movements (rotation around the shoulder joint, maintaining the arm completely extended) to drive the cursor from one target zone to the other (i.e., upward, downward, outward/rightward, and inward/leftward arm movements). Subjects wore goggles that hid the visible part of their limb and therefore restricted their visual field only to the screen. Moreover, they were required to keep their arm at an angle of about 5° (5.37 ± 0.8°, mean ± SE) under the horizontal plane crossing the shoulder (for horizontal motions) and about 6° (6.46 ± 0.7°) outward with respect to the vertical plane crossing the shoulder (during vertical motion) to ease hiding of their arm (Fig. 1*B*). This slight deviation from the horizontal/vertical planes did not modify the shape of velocity profiles. Indeed, when the visual feedback moved in the same direction as subjects' movement, the velocity profiles reproduced the same pattern of asymmetries reported in the literature (compare Papaxanthis et al. 1998c and 2003b with RESULTS, *Congruent Conditions*). This finding was not unexpected, because no significant changes in the velocity profile shape have been found even for 45° rotations, at least for vertical drawing movements (see Papaxanthis et al. 1998d).

Visual Feedback Characterization

The time delay between the real motion of the finger and its projection on the screen was <30 ms. After the experiment, all subjects verbally reported that they perceived the motion of the dot to be simultaneous with the motion of their arm. The scaling factor between arm movement amplitude and visual feedback was one (1); consequently, the distances covered by the fingertip and the moving dot were similar (70 cm, corresponding to a shoulder rotation of about 65°). The dot position was adapted individually; it was set in the center of the screen when the subjects' arm position was at the middle of the motion, i.e., at the level of the shoulder horizontal position for horizontal movements or at the shoulder height for vertical movements. In this way, the three-dimensional finger trajectory centered in front of the shoulder was presented in real time to the subject as a two-dimensional trajectory of the visual cursor centered in the center of the screen (see Fig. 1*A*). The projection of fingertip movement from three to two dimensions induced just a minimal change in the cursor velocity profile with respect to that of the actual movement. Indeed, the average absolute difference between the speed modulus computed with three- or two-dimensional data across all subjects and conditions was very small: 72.2 ± 10 mm/s, corresponding to <3% of speed amplitude (on average 2.76 ± 0.14%). Moreover, this difference did not change significantly among conditions (1-way repeated-measures ANOVA, Greenhouse-Geisser corrected, $P > 0.05$). In addition, the absolute change in the skewness of the velocity profile (measured as the relative duration of the movement acceleration phase) computed with three- or two-dimensional data across all subjects and conditions was only 0.012 ± 0.0005 and did not vary significantly among conditions (1-way repeated-measures ANOVA, Greenhouse-Geisser corrected, $P > 0.05$). Because these minor changes were balanced across all congruent and conflicting conditions, they did not interfere with the experimental procedure.

Motion Tracking

An Optotrak Certus system (NDI Northern Digital, Ontario, Canada) recorded the position of the subjects' fingertip at 100 Hz. The recorded position was then used to dynamically render the circle dot representing the visual feedback provided to subjects. Custom software (C++) was used to record data and to compute and display the appropriate rotation of visual feedback. Four active infrared markers were placed on the tip of the index finger, the shoulder (acromion), and the head. The two head markers were situated on the right side of the goggles, separated by 6 cm, and were subsequently used to evaluate subjects' head stability during motion by computing head angular displacement. These positions represented the Frankfort plane, which is usually adopted in head motion analysis (Pozzo et al. 1990).

Experimental Protocol

Each subject was presented with a set of congruent conditions followed by two incongruent, or conflict, conditions and realized a total of 168 movements. In all experimental phases, arm movements were initiated after the experimenter's verbal signal. Subjects were asked to perform natural and uncorrected movements (1-shot move-

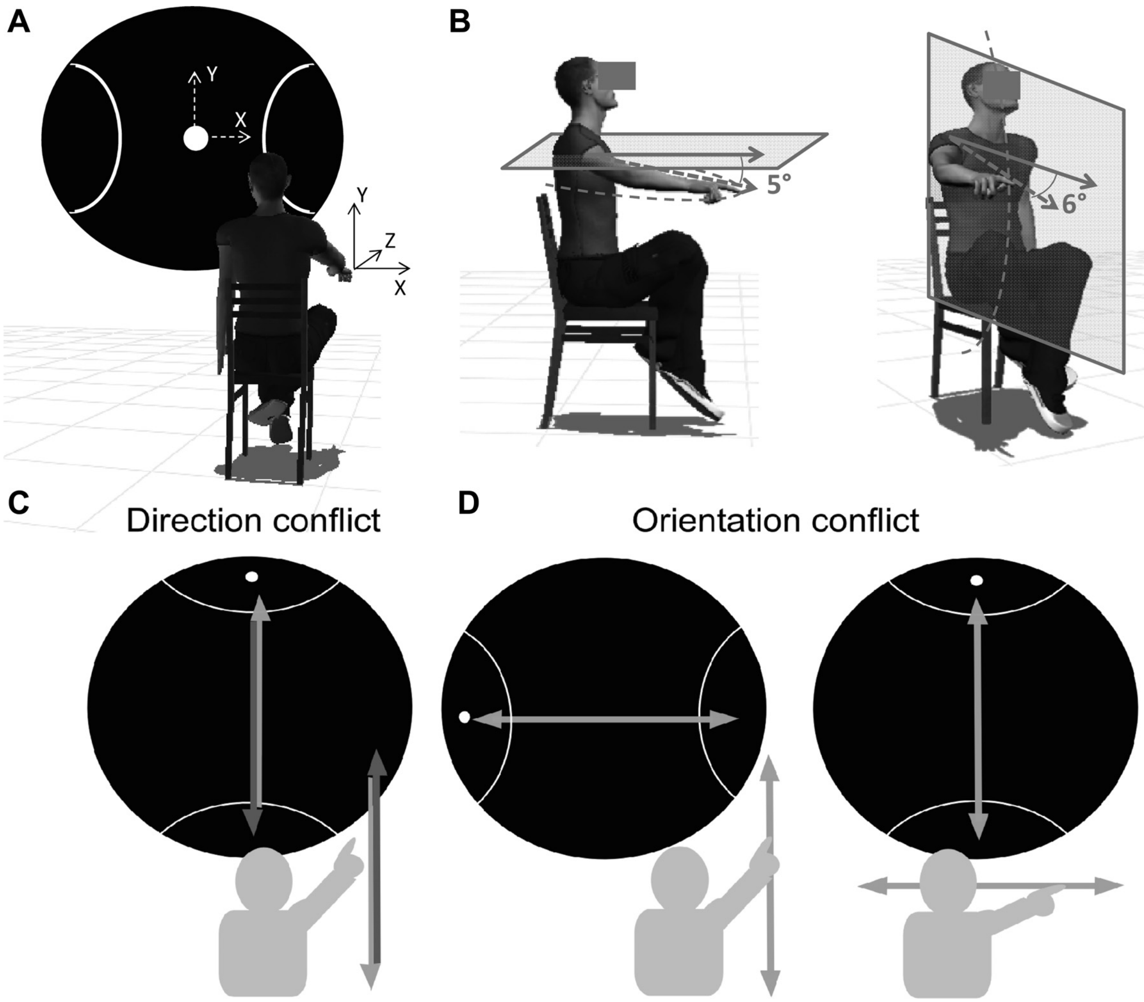

Fig. 1. Schema of the experimental incongruent conditions. Subjects sat in front of a screen on which the visual feedback of hand motion was projected as a white dot on a black background. *A*: the 3-dimensional position of the subject's fingertip was presented in real time as a 2-dimensional dot. The movement was centered in the center of the screen. The subject was positioned slightly to the right and under the center of the projected screen to avoid the possibility that arm movements could occlude the visual display in any condition. *B*: subjects wore goggles that hid the visible part of their limb and were required to keep their arm at an angle of about 5° under the horizontal plane crossing the shoulder (for horizontal motions) and about 6° outward with respect to the vertical plane crossing the shoulder (during vertical motion). *C*: first experimental phase: direction conflict. Upward movements are associated with a downward visual feedback (condition U-d), and downward movements are associated with an upward visual feedback (condition D-u). *D*: second experimental phase: orientation conflict. At *left*, upward and downward movements are associated with horizontal visual feedback (conditions U-h and D-h, respectively). At *right*, horizontal movements are associated with upward or downward visual feedback (conditions H-u and H-d, respectively).

ments) without paying attention to final accuracy. At the end of each trial, subjects were requested to maintain the final position for about 2 s. To avoid fatigue, they relaxed the arm during a resting period of 1 min every 8 trials.

Congruent Conditions

In the congruent conditions, the visual feedback of arm movements (white dot on the screen) was in the same direction and orientation as the actual arm movements. Precisely, subjects performed upward, downward, leftward, and rightward arm movements while observing on the screen the visual cursor moving in the same direction as the movement they produced. The initial position of the dot on the screen was at the top for downward motions, at the bottom for upward motions, at the left for outward motions, and at the right for inward motions. Congruent movements were performed in two sessions: *1*) vertical, composed of 12 upward movements alternated with 12 downward movements, and *2*) horizontal, composed of 12 outward movements alternated with 12 inward movements. The order of the two sessions was randomized.

Incongruent Conditions

In the incongruent conditions, the visual feedback of arm movements (white dot on the screen) was in conflict with actual arm movements (e.g., the dot was initially located on the top target area while the arm and the hand were starting from the bottom end of the movement trajectory). Visual feedback was computed as the real-time rotated two-dimensional projection of the actual arm movement, centered at the center of the screen. Therefore, subjects observed the dot moving with an instantaneous velocity exactly corresponding to that of the movement they were executing, just rotated with respect to the real movement direction. We conducted two experiments, with two different kinds of conflicts (see Fig. 1, *C* and *D*).

First experimental phase: incongruent direction conditions. In the direction conflict (Fig. 1*C*), the actual arm movement and its visual feedback had the same orientation but followed different directions (e.g., one upward and the other downward). Specifically, vertical arm motion was associated with vertical visual feedback as follows: *1*) move down while view up (D-u condition) and *2*) move up while view down (U-d condition). The initial position of the dot on the screen depended on the orientation and direction of the visual feedback. It was at the bottom for upward visual feedback (associated with downward actual arm motion) and at the top for downward visual feedback (associated with upward actual arm motion). Subjects performed this experimental phase in a single session composed of 12 D-u motions alternated with 12 U-d motions.

Second experimental phase: incongruent orientation conditions. In the orientation conflict (Fig. 1*D*), the actual arm motion and its visual feedback were orthogonal. For example, the actual arm movement was horizontal and the visual feedback was vertical. More specifically, horizontal arm motion was associated with vertical visual feedback as follows: *1*) move horizontal (either outward or inward) while view up (H-u condition) and *2*) move horizontal (either outward or inward) while view down (H-d condition). In addition, vertical arm motion was associated with horizontal visual feedback as follows: *1*) move up while view horizontal (either outward or inward) (U-h condition) and *2*) move down while view horizontal (either outward or inward) (D-h condition). The initial position of the dot on the screen was at the top for downward visual feedback (associated with inward or outward actual arm motions) and at the bottom for upward visual feedback (associated with inward or outward actual arm motions). The dot was presented at the left of the screen for an outward visual feedback (associated with upward or downward actual arm motion) and at the right for an inward visual feedback (associated with upward or downward actual arm motions). The incongruent orientation conditions were tested in four sessions: *1*) 12 U-h (outward) movements alternated with 12 D-h (inward) movements, *2*) 12 U-h (inward) movements alternated with 12 D-h (outward) movements, *3*) 12 H (outward)-u movements alternated with 12 H (inward)-d movements, and *4*) 12 H (inward)-u movements alternated with 12 H (outward)-d movements. The order of the sessions was randomized. We did not perform a horizontal incongruent direction condition (i.e., "move left while view right," and vice versa), because it was not relevant for our study: horizontal movements in both directions share not only the same orientation with respect to gravity but also the same symmetric velocity profile.

Training Phase

The incongruence between the actual movement and the rotated visual feedback could induce a failure in movement execution. For instance, observing a vertical visual feedback while moving the arm horizontally could divert finger movement from horizontal. To be sure that subjects could perform movements in the requested directions in the presence of an incongruently oriented visual feedback, we started our protocol with a training phase. Before each incongruent condition, subjects were exposed to the corresponding visuomotor conflict. They carried out 12 movements by keeping their invisible wrist on soft physical haptic supports, which guided their movements in the vertical or horizontal direction, allowing only small deviations, on average $2.23 \pm 0.27°$, while they watched the white dot moving along horizontal or vertical axes. During this training session, the haptic guidance allowed subjects to learn to accomplish the required task. Indeed, immediately after the training phase, when the guides were removed, subjects showed on average a distortion of just $2.73 \pm 0.27°$ from the vertical or the horizontal directions with conflicting visual feedback. Thus the guidance guaranteed the fast reaching of a plateau in the learning of the mapping, as demonstrated by the fact that subjects learned to correctly perform movements in the desired direction even in presence of a conflicting visual feedback. We adopted this solution to speed up the learning process, because our focus was understanding the influence of incongruent visual information on arm motor planning, a process that is revealed only after visuomotor adaptation has occurred.

Effects of Incongruent Visual Conditions on Arm Motor Planning

In the current study, we investigated whether subjects change their motor planning when they receive incongruent visual feedback with respect to the actual motion of their arm. To evaluate the effect of the visual context, we needed a kinematic parameter that could discriminate arm movements in different directions and could allow us to make straightforward predictions. This parameter was the timing of the fingertip velocity profiles. Previous studies (Papaxanthis et al. 1998a, 1998b, 1998c, 2003a, 2003b) have consistently shown that acceleration duration is shorter than deceleration duration for upward movements, equivalent for horizontal (left or right) movements, and longer for downward movements. Consider the following scenario: a subject usually executes downward vertical arm movements with a velocity profile characterized by an acceleration phase longer than deceleration and upward arm movements with an acceleration phase shorter than deceleration (as described in Gentili et al. 2007). This subject is then exposed to the following visuomotor conflict: he performs a downward arm movement but sees his own motion rotated by 180°; that is, as if it was an upward movement. If the incongruent visual information has an influence on motor planning, then one could expect that the subject, after a sufficient exposure to this visuomotor conflict, will perform downward arm movements with the velocity profile that corresponds to an upward movement (i.e., with a shorter acceleration phase). If the incongruent visual information has no influence on motor planning, then the subject will continue to perform downward arm movements as usual (i.e., with a longer acceleration phase). A partial influence of the visual input will produce downward movements characterized by a velocity profile in between the one typical of a downward movement and the one expected for an upward one.

Control Experiment

To evaluate whether alterations on arm kinematics in the incongruent conditions were due to an actual change in motor planning or were just a consequence of movement correction caused by the presence of a conflicting simultaneous visual feedback, we performed a control experiment. Six new subjects were presented with a set of congruent conditions in the horizontal outward direction (15 movements), followed by one incongruent (orientation conflict) condition. More specifically, outward horizontal arm motion was associated with vertical upward visual feedback (H-u condition). Each subject realized a total of 12 rightward movements associated with an upward visual feedback, followed by 1 "catch trial" in which the visual feedback was suddenly turned off immediately before the beginning of the movement. If the effect of the conflict is mainly due to an online movement correction triggered by the incongruent simultaneous visual feedback, we expect the movement performed with no visual feedback to show again the classical symmetric velocity profile measured during the congruent horizontal condition. If instead the effect is mainly due to a change in motion planning due to the adaptation to the new visual context, the movement should show an asymmetric velocity profile, analogous to the one measured in presence of the conflicting visual feedback.

Data and Statistical Analysis

Kinematic parameters were computed from the three-dimensional fingertip position collected in successive frames taken at 10-ms intervals and low-pass filtered using a digital fifth-order zero-phase-lag Butterworth filter with a cutoff frequency of 5 Hz. Each movement was checked visually, and only movements showing a single-peaked velocity profile were taken into consideration. Overall, about 5% of all trials were rejected. In the first experimental phase, in the condition in which upward movements were associated with downward oriented visual feedback (U-d), two subjects were not able to produce natural one-shot movements. Therefore, they were removed from the population in the whole first experimental phase.

We computed the following temporal parameters: *1*) movement duration, defined as the time interval in which velocity was ≥5% of its peak value; *2*) movement amplitude, defined as the angular amplitude of the rotation around the shoulder joint; *3*) the ratio of acceleration duration to total movement duration (AD/MD), an index of the timing of movement velocity profiles, which has been shown to be significantly direction dependent (Berret et al. 2008; Crevecoeur et al. 2009; Gentili et al. 2007; Le Seac'h and McIntyre 2007). In the following, we refer to AD/MD as "acceleration phase duration." In addition, lateral deviation of each trajectory was computed as the angle (between 0° and 90°) formed by the straight line joining the beginning and the end of the trajectory with respect to a horizontal (or a vertical) line.

The AD/MD values showed normal distribution (Kolmogorov-Smirnov test) and therefore could be subjected to *t*-test analysis and to the analysis of variance (ANOVA). Velocity profiles observed in each incongruent condition were compared with those of the congruent condition sharing the same actual movement [e.g., "move up while view down" (U-d) was compared with the corresponding congruent condition "move up while view up"]. In particular, velocity profiles were considered different if the difference between AD/MD ratios reached significance level ($P < 0.05$). In addition, in each condition the adaptation was evaluated by performing linear regressions of AD/MD values over repetition number and computing a *t*-test on the slopes.

Measure of the Effect

The relative importance of the visual context in the planning of arm movements was evaluated by using a simple linear model. Each incongruent movement is characterized by two kinds of directional information: the direction of the movement specified by the visual context (or visual direction) and the direction of the movement that the subject actually performs with the arm (or nonvisual direction). As previously noted, each arm movement direction is associated with a specific velocity profile, characterized by a different duration of the acceleration phase (AD/MD). Precisely, the adopted kinematics would depend on an internal model of gravity, which, as a function of movement orientation and direction, determines the optimal features of the velocity profile (see also Papaxanthis et al. 1998c).

$$VP_{tot} = F(\mathrm{dir\_of\_motion}) \quad (1)$$

where VP_{tot} is the velocity profile of the movement and $F(\mathrm{dir})$ is a (possibly nonlinear) function associated to the internal model of gravity, which computes the optimal speed profile for a specific motion direction.

We assume that the CNS computes the direction of motion as a result of a combination of both the visual and nonvisual directional information to determine the velocity profile of the next movement. As the simplest approximation, we hypothesize a weighted linear combination of the direction suggested by the visual context and the nonvisual direction:

$$VP_{tot} = F\left[\alpha \times \mathrm{dir}_{vis} + (1-\alpha)\mathrm{dir}_{non\_vis}\right] \quad (2)$$

where α is a parameter representing the relative weight associated with the direction of the visual feedback.

If we further assume that the function which associates the optimal velocity profile to each given motion direction is linear, as a first-order approximation would give, we can write

$$VP_{tot} = \alpha F(\mathrm{dir}_{vis}) + (1-\alpha)F(\mathrm{dir}_{non\_vis}) \quad (3)$$

In the congruent condition $\mathrm{dir}_{vis} = \mathrm{dir}_{non\_vis}$; so the previous equation becomes

$$VP_{tot} = F(\mathrm{dir}_{vis}) = VP_{vis} \quad (4)$$

Therefore, for each incongruent condition, we could measure the components $VP_{vis} = F(\mathrm{dir}_{vis})$ during the congruent condition in which the motion is performed in dir_{vis} and $VP_{non\_vis} = F(\mathrm{dir}_{non\_vis})$ in the congruent condition in which the motion is performed in dir_{non_vis}. Thus, by measuring the velocity profile adopted in any incongruent condition, we may derive the weighting factor α, which is the relative role of the visual and non-visual motion direction in determining the motor plan of the next movement.

$$VP_{tot} = \alpha VP_{vis} + (1-\alpha)VP_{non\_vis} \quad (5)$$

This model holds, assuming that the pointing movements are generated under feedforward control. This assumption may be reasonable based on the following arguments: *1*) before each session of incongruent movements, subjects were trained and learned to not deviate from the movement direction (see MATERIALS AND METHODS and RESULTS); *2*) before the start of each incongruent trial, the position of the arm (felt through proprioception) and the corresponding position of the visual feedback (the dot on the screen) clearly informed participants about the visuomotor conflict; and *3*) most movements were performed with a one-shot speed profile, without any corrective submovement due to feedback intervention (see RESULTS). In fact, subjects presented smooth one-shot profiles as soon as they performed the first movement in any remapped condition. Further evidence in favor of the hypothesis that pointing movements are realized under feedforward control is also presented in RESULTS (see *Control Experiment*).

It is then possible to measure VP_{tot} as the velocity profile (in terms of acceleration phase duration or AD/MD) in a particular incongruent condition (e.g., H-u, where motion is performed on the horizontal plane but visual feedback is presented in the upward direction). VP_{vis} will be then the velocity profile typical of a congruent upward motion (because upward is the movement direction associated to the visual feedback), and $VP_{non\text{-}vis}$ will be the velocity profile measured during a congruent horizontal movement (because horizontal is the nonvisual movement direction). Given these three measures, we can use *Eq. 5* to estimate the parameter α, that is, the relative importance of the incongruent visual context in determining the kinematics of the executed movement.

Replicating *Eq. 5* for each *i*th subject and each *j*th incongruent condition, we can build a system of several equations of the form

$$VP_{tot(i,j)} = \alpha VP_{vis(i,j)} + (1-\alpha)VP_{non\_vis(i,j)} \quad i = 1,..,N; \quad j = 1,..,M \quad (6)$$

where N is the number of subjects and M is the number of different conditions considered. We can then evaluate the relative weighting between visual context and intended movement by finding the least-squares solution of the system of equations (*Eq. 6*).

RESULTS

General Features of Arm Movements

After the training phase, all subjects were able to perform arm movements without deviating from the sagittal or the lateral plane. In all incongruent conditions, the average directional accuracy, measured as the angular deviation from a straight path, was relatively small (on average 2.67 ± 0.1°) and did not differ significantly among conditions (1-way ANOVA, $P > 0.05$). Movement duration (Tables 1 and 2) was roughly constant within the experimental conditions (on average 652 ± 76 ms; 1-way ANOVA, $P > 0.05$). Similarly, movement amplitude (Tables 3 and 4) was comparable between the experimental conditions (on average 67.7° ± 4.7°; 1-way ANOVA, $P > 0.05$).

Table 1. *Movement duration: horizontal arm movements*

	Congruent	Upward	Downward
Inward	0.69 ± 0.09	0.69 ± 0.07	0.69 ± 0.06
Outward	0.69 ± 0.11	0.69 ± 0.07	0.69 ± 0.05

Values are averages and SD of movement duration (in seconds) of horizontal arm movements for congruent and incongruent conditions in the main experiment.

Table 3. *Movement amplitude: horizontal arm movements*

	Congruent	Upward	Downward
Inward	71 ± 10	69 ± 8	68 ± 7
Outward	71 ± 10	68 ± 7	69 ± 7

Values are averages and SD of movement amplitude (in degrees) of horizontal arm movements for congruent and incongruent conditions in the main experiment.

Lastly, head movements remained small and stable across all conditions (average head rotation 1.7 ± 0.9°; 1-way ANOVA, $P > 0.05$).

Congruent Conditions

Figure 2 shows fingertip velocity profiles, normalized in space and time, for a typical subject during horizontal (*A*) and vertical (*B*) arm movements with congruent vision. When the visual feedback was consistent in orientation and direction with the performed movement, we observed the same acceleration phase durations (AD/MD) and the same pattern of asymmetries reported in the literature (Papaxanthis et al. 1998c, 2003b). In particular, both inward and outward movements were characterized by a rather symmetric velocity profile (Fig. 2*A*), whereas peak velocity occurred earlier for upward than downward movements (Fig. 2*B*). One-way repeated-measures ANOVA (4 movement directions) revealed a main effect of movement direction on AD/MD ($P < 0.01$). Post hoc analysis (Bonferroni) showed that acceleration duration for upward movement was significantly different from those of all the other directions ($P < 0.01$ for all comparisons). Acceleration phase durations (AD/MD) of outward, inward, and downward movements were not significantly different ($P > 0.05$).

First Experiment: Effect of Incongruent Visual Feedback on Arm Motion Planning

In this first experimental phase, performed and viewed arm movements were in the vertical plane but had opposite directions. Specifically, subjects moved upward and saw the dot moving downward (U-d condition), and vice versa (D-u condition). To test whether this visuomotor conflict influenced arm kinematics, we compared upward and downward fingertip velocity profiles recorded in this incongruent condition with upward and downward fingertip velocity profiles recorded in the congruent condition. The analysis showed that upward visual feedback shortened the acceleration phase of the actual downward movement, whereas downward visual feedback lengthened the acceleration phase of upward movements (Fig. 3*A*). One-tailed paired-sample *t*-tests confirmed the significance of these results ($P < 0.05$, $t = 2.62$ for U-d and $P < 0.05$, $t = -2.75$ for D-u). It appears that subjects, in the presence of the visuomotor conflict, adopted an intermediate motor planning; i.e., velocity profiles had acceleration phase durations (AD/MD) that were between those recorded during upward and downward congruent arm movements (Fig. 3*B*).

We used the system of *Eq. 6* (see MATERIALS AND METHODS, *Measure of the Effect*) to evaluate the relative weight given to the visual context and actual movement planning in the conflict conditions considered. The least-squares solution of *Eq. 6* applied to the results of this first experimental phase (direction conflict, conditions U-d and D-u) yielded $\alpha = 0.32$ (95% confidence interval: 0.273, 0.367; adjusted $R^2 = 0.63$) Thus the incongruent visual feedback has a conspicuous impact in determining motion planning, with a relative weight of about 30%.

Second Experiment: Is the Change in Motor Plan Gravity Dependent?

To understand whether the replanning due to visuomotor conflict occurs similarly for different rotations of the visual feedback, we tested two further incongruent conditions: horizontal motion associated with vertical visual feedback and vertical motion associated with horizontal visual feedback.

A first possibility could be that visual context has a fixed influence on motion planning. In this case, visual feedback should have the same relevance (about 30%) for all conflict conditions (see Fig. 4*A*). An alternative hypothesis, however, could be that the impact of vision on movement planning changes as a function of the rotation amplitude between actual motion and visual feedback. In this case, we would expect a different weight of visual context when motion and visual feedback are in opposite directions (180° rotation, as in the first experimental phase) compared with the conditions in which the rotation between the two is just 90° (horizontal motion associated with vertical visual feedback, and vice versa). The two latter conditions, presenting the same rotation amplitude, should instead be characterized by the same impact of visual context (see Fig. 4*B*). As a last option, one could attribute a different relevance to the visual context as a function of visual feedback orientation with respect to gravity. Because of the constant presence of the gravitational field, visuospatial information on the vertical axis should be of particular relevance for motion planning. If this hypothesis is correct, the condition in

Table 2. *Movement duration: vertical arm movements*

	Congruent	Inward	Outward	Opposite dir
Downward	0.64 ± 0.07	0.66 ± 0.06	0.65 ± 0.07	0.64 ± 0.07
Upward	0.64 ± 0.06	0.66 ± 0.09	0.67 ± 0.06	0.66 ± 0.09

Values are averages and SD of movement duration (in seconds) of vertical arm movements for congruent and incongruent conditions in the main experiment. The different columns refer to the different directions of the visual feedback.

Table 4. *Movement amplitude: vertical arm movements*

	Congruent	Inward	Outward	Opposite dir
Downward	66 ± 6	74 ± 12	72 ± 11	67 ± 7
Upward	68 ± 8	73 ± 11	75 ± 11	70 ± 5

Values are averages and SD of movement amplitude (in degrees) of vertical arm movements for congruent and incongruent conditions in the main experiment. The different columns refer to the different directions of the visual feedback.

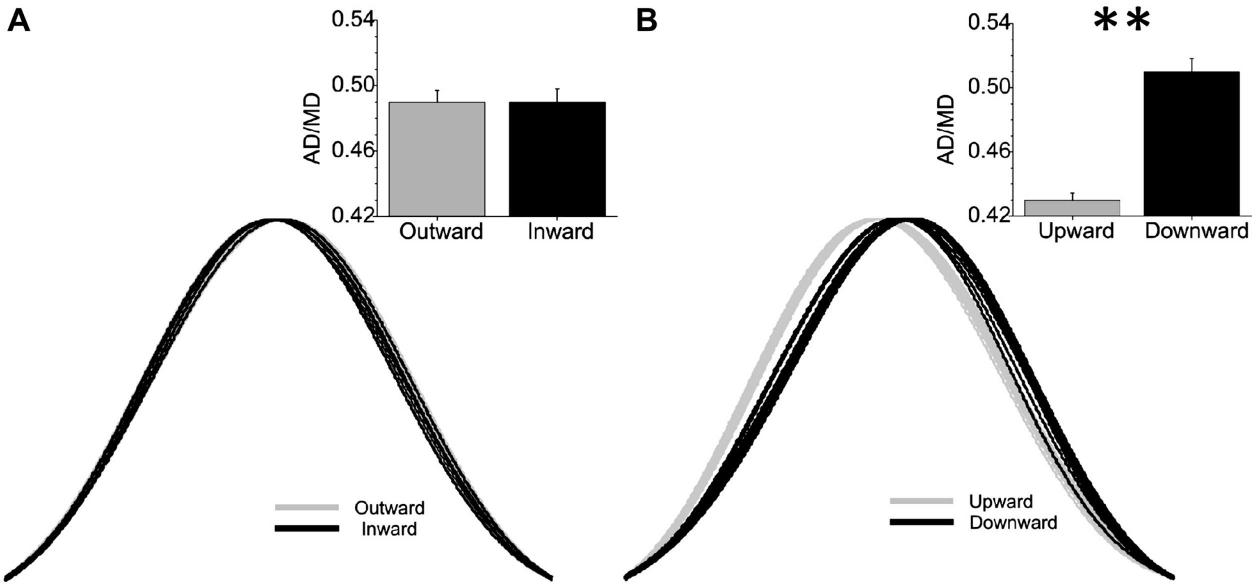

Fig. 2. Speed profiles in the congruent conditions. Normalized velocity profiles in time and velocity are shown for horizontal (*A*) and vertical (*B*) movements in the congruent conditions. Twelve trials in each direction are shown for 1 typical subject. *Insets* report the corresponding average values of movement timing (ratio of acceleration duration to total movement duration, AD/MD). Error bars represent population SE. $^{**}P < 0.01$.

which both intended movement and visual context orientations are vertical could represent a baseline weighting in which the verticality factor plays no role, because it is balanced between the two sources of information. Instead, when a vertical visual context is associated to a horizontal motion, we may expect an increase in the relevance of the visual weight, due to its orientation similar to that of gravity, to the cost of the weight of the nonvisual motion direction. The opposite would be expected when a horizontal visual feedback accompanies a vertical movement, with a reduction of the weight of the visual context in favor of a higher relevance of the vertical, actual movement orientation (see Fig. 4*C*).

In the "horizontal motion, vertical visual feedback" conflict condition (Fig. 5, *A* and *B*, *left*), subjects performed horizontal arm movements, but their visual feedback was rotated by 90° so that they visually perceived a vertical arm movement (H-u and H-d conditions). Compared with the congruent condition, acceleration phase duration was shorter when horizontal (both inward and outward) arm movements were viewed as upward movements (H-u condition). This means that the acceleration phase in the incongruent visual condition was shorter compared with the one observed in the congruent vision condition. One-tailed paired-sample *t*-tests confirmed this observation ($t = -3.45$, $P < 0.01$ for outward movements and $t = -3.36$, $P < 0.01$ for inward movements). As in the first experimental phase, subjects adopted an intermediate motor planning; i.e., acceleration phase durations were a mixture of those recorded during horizontal and vertical congruent arm movements. Downward visual feedback associated with horizontal arm movements (H-d conditions) induced a slight, but

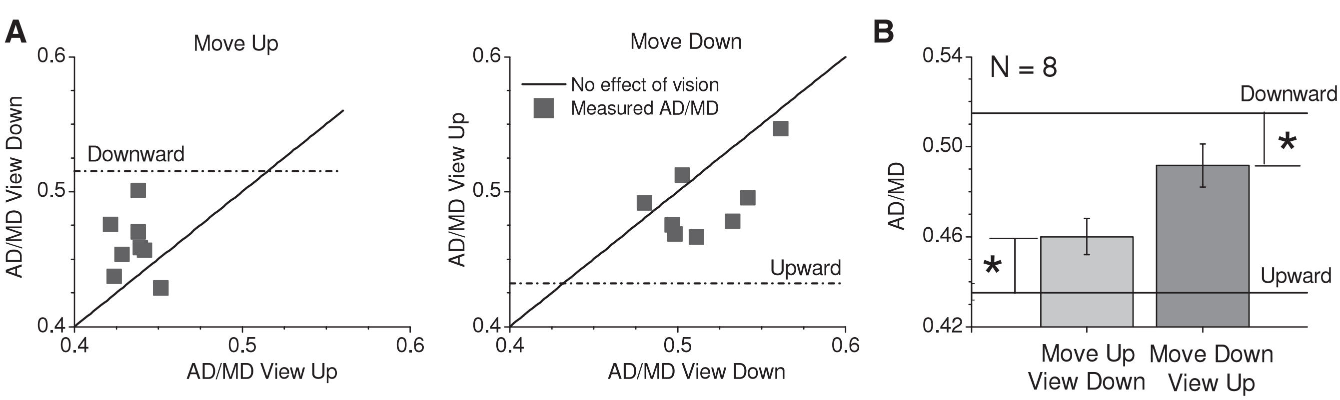

Fig. 3. Replanning in the presence of a direction visuomotor conflict. *A*: individual AD/MD ratios (filled squares) measured in the presence of conflicting visual feedback plotted against the corresponding AD/MD ratio in the presence of congruent visual feedback. *Left*: results for the condition in which upward motion is associated to downward visual feedback. *Right*: results for the condition in which downward motion is associated to upward visual feedback. The continuous lines indicate where the squares should lie if the conflicting visual feedback had no effect on motion planning, that is, if the movement was performed as a normal upward (*left*) or downward movement (*right*). The dotted horizontal lines indicate instead where the squares should lie if visual context alone determined the planning of the movement, that is if the movement was performed in the direction individuated by the visual feedback (downward, *left*, or upward, *right*). Data from single subjects lie between the dotted and the continuous line, showing a partial effect of the conflicting visual context. *B*: average AD/MD ratios (8 subjects) for the 2 conflicting conditions "move up while view down" (U-d) and "move down while view up" (D-u). The horizontal lines represent the average AD/MD ratios for downward and upward motion with congruent visual feedback. Error bars represent population SE. The conflicting visual feedback on average significantly changed the AD/MD of the planned movement. $^{*}P < 0.05$.

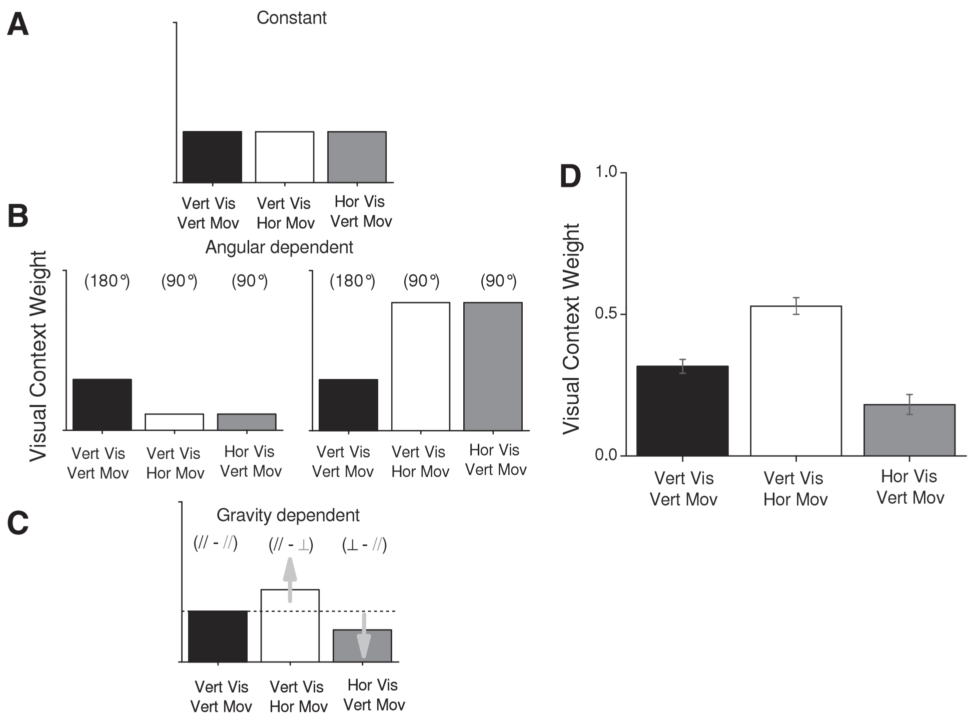

Fig. 4. Models of the effect of conflicting visual context. The possible influence of a conflicting visual context as a function of visual and nonvisual movement orientation was examined. The relevance of the visual information is evaluated as its relative weight (α) in determining motion kinematics, computed with *Eq. 6* (see MATERIALS AND METHODS, *Measure of the Effect*). *A*: results expected if the relevance of the visuomotor conflict did not depend on visual context orientation. *B*: 2 alternative results expected if the effect of the visuomotor conflict depended on the angular amplitude between the visual and nonvisual motion orientations (indicated above bars). *C*: results expected if the effect depended on the visual and nonvisual motion orientation with respect to gravity. (Symbols in parentheses: black symbols refer to visual context and gray symbols to nonvisual movement; double slashes indicate orientation parallel to gravity, and angles indicate orientation orthogonal to gravity.) *D*: actual results. Error bars represent population SE computed with a bootstrap procedure. The experimental results suggest the validity of the gravity-dependent model. Vert, vertical; Hor, horizontal; Vis, visual movement; Mov, nonvisual movement.

not significant, effect (1-tailed paired-sample *t*-tests, $t = -0.97$, $P > 0.05$ for outward movements and $t = -0.37$, $P > 0.05$ for inward movements). This was not surprising because in the congruent condition, velocity profiles of downward, inward, and outward movements were not significantly different.

In the "vertical motion, horizontal visual feedback" horizontal condition, visual feedback did not affect the performance of upward and downward arm movements (Fig. 5, *C* and *D*, *right*). One-tailed paired-sample *t*-tests did not show any significant difference with respect to the congruent conditions [$t = 0.20$, $P > 0.05$ for U-h (outward); $t = -0.07$, $P > 0.05$ for D-h (inward); $t = -0.17$, $P > 0.05$ for U-h (inward); and $t = -0.46$, $P > 0.05$ for D-h (outward)].

To quantify the possible modulation of the visual context effect as a function of visual feedback orientation, we applied the system of *Eq. 6* to the results of the second experimental phase (orientation conflict). We estimated visual context relative weight (α) separately for the tasks in which motion was performed on the horizontal plane and the visual feedback was vertically oriented (conditions H-u and H-d) and for the tasks characterized by vertical motion and horizontal visual feedback (conditions U-h and D-h). Visual context weight amounted to about 53% ($\alpha = 0.529$, 95% confidence interval: 0.4704, 0.5876; adjusted $R^2 = 0.32$) when visual feedback was vertical but decreased to about 18% ($\alpha = 0.182$, 95% confidence interval: 0.1112, 0.2512; adjusted $R^2 = 0.13$) when it was horizontal. The results are summarized in Fig. 4*D*. These results show that the effect of visual context is dependent on the type of conflict between visual information and intended movement. In particular, visual context impact is not just a function of the amplitude of the angle between visual feedback and actual movement. In fact, for the same rotation between the two (90°), the effect is different when visual feedback or actual motion is vertical (see the difference between the open and shaded columns in Fig. 4*D* and the absence of overlap in the confidence intervals). Indeed, our results are consistent with the hypothesis of a particular relevance of the vertical direction (see the similarity between Fig. 4, *D* and *C*). The visual context acquires a higher impact when it describes the motion as oriented along the gravitational axis. Thus vision contributes differently to the planning of arm pointing movements depending on motion orientation with respect to gravity.

Stability of the Results in the Incongruent Conditions

It is important to note that after the training phase, changes in the symmetry of velocity profiles were permanent and that acceleration phase durations (AD/MD) did not vary between trials. To evaluate quantitatively whether an adaptation took place during the 12 repetitions of each condition, a linear regression of acceleration phase duration over repetition number was performed for each subject and condition. We did not find any evidence of an adaptation of motion kinematics occurring over trials. One-sample *t*-tests on the slopes confirmed that for all conditions, no significant adaptation occurred during the task ($P > 0.05$). Moreover, two-sample *t*-tests between the acceleration phase duration of the first and the last trial in each condition showed no significant changes during the experiment ($P > 0.05$ for all comparisons).

We also checked whether in any conflicting condition the observation of an incongruent motion during movement execution could have induced an increase in movement variance, as suggested by previous studies on oscillatory movements (Kilner et al. 2003; Stanley et al. 2007). In Fig. 6*A* we have represented the fingertip trajectories for a representative subject during the congruent (*top*) and incongruent (*bottom*) conditions projected on the *XY* plane (see Fig. 1*A* for the reference frame). The variance of the trajectories appears to be similar across conditions. To check this visual evalua-

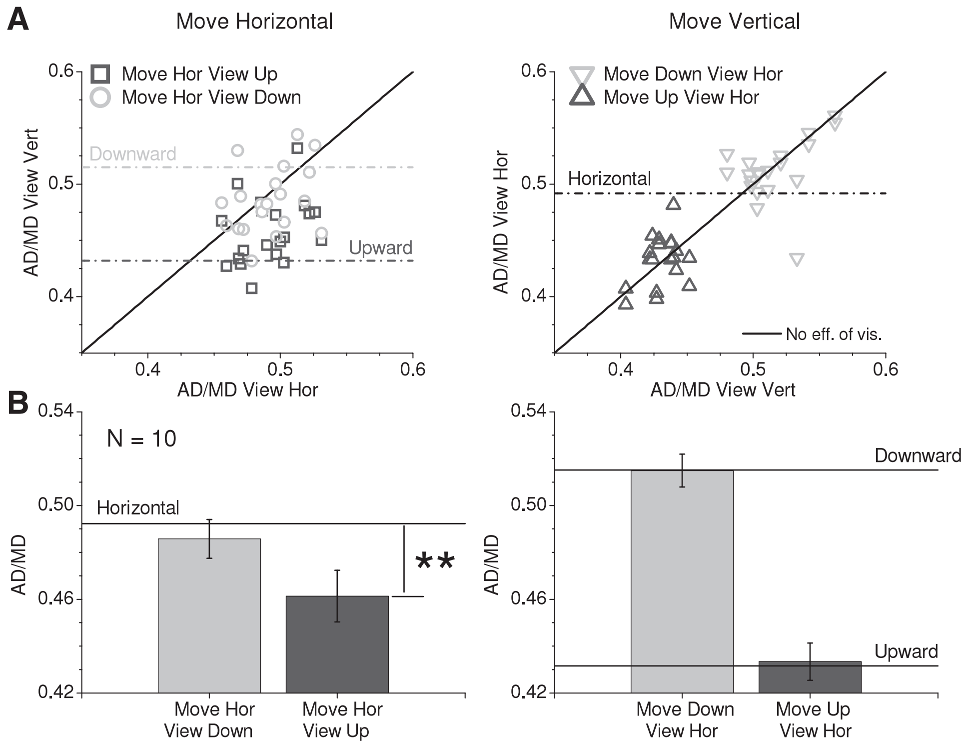

Fig. 5. Replanning in the presence of 2 different kinds of orientation visuomotor conflicts. *A*: individual AD/MD ratios measured in the presence of conflicting visual feedback plotted against the corresponding AD/MD measured when the visual feedback was congruent with actual movement. The results for horizontal arm movements associated with vertical visual feedback are presented at *left*, and those for vertical arm movements associated with horizontal visual feedback are shown at *right*. For example, each dark gray open square at *left* indicates the AD/MD ratio measured in the "move horizontal while view up" condition (H-u) plotted against the AD/MD ratio measured for the same subject in the corresponding congruent condition (move horizontal while view horizontal). The continuous line indicates where the data points should lie if the conflicting visual feedback had no effect on motion planning, that is, if the movement maintained the same velocity profile as with congruent visual feedback. The dotted horizontal lines indicate instead where the data points should lie if visual context alone determined the planning of the movement, that is, if the movement were performed in the direction individuated by the visual feedback. *B*: average values of AD/MD ratios for all 10 subjects. Horizontal arm movements associated with vertical visual feedback are shown at *left*, and vertical arm movements associated with horizontal visual feedback are shown at *right*. The horizontal lines represent the average AD/MD ratios for congruent visual feedback during horizontal, downward, and upward motion. Error bars represent population SE. The effect of the visual context was much more pronounced when the visual feedback was vertically oriented (*left*) than when it was horizontal (*right*). $^{**}P < 0.01$.

tion, we replicated the analysis performed by Kilner et al. (2003), measuring for each congruent and conflicting condition the movement variance in the direction orthogonal to that of the performed movement. Although an increase in the variability of the movement was observed in the incongruent conditions with respect to the congruent ones (Fig. 6*B*), this change was smaller than the one measured by Kilner (compare Fig. 6*B* with Kilner et al.'s Fig. 3) and did not reach significance (1-way repeated-measures ANOVA, Greenhouse-Geisser corrected, $P > 0.05$). In addition, we computed the curvature of the motion in three dimensions, measured as the maximum path deviation from a straight line connecting the initial and final finger positions divided by the distance between these positions (Fig. 6*C*). Also, in this case no significant change across conditions was observed (1-way Repeated-measures ANOVA, Greenhouse-Geisser corrected, $P > 0.05$). We believe that the absence of a significant increase in movement variance during incongruent movement observation could be due, among other reasons, to the fact that, differently from Kilner et al. (2003), we haptically trained subjects to perform movements in presence of a conflicting visual feedback before the experimental phase. The training, which was aimed at limiting the movement distortions provoked by the puzzling visual feedback, could have diminished substantially the interference effect due to observation. In addition, the adoption of discrete rather than oscillatory movements also could have contributed to reduce the directional distortion due to the conflicting visual information.

Control Experiment: Is the Asymmetry Change Due to a Modification in the Motor Plan or Just to an Online Movement Correction Driven by the Simultaneous Conflicting Visual Feedback?

The change in velocity profile measured in the incongruent conditions could in theory have two alternative explanations. Indeed, it could be caused by online movement corrections triggered by the simultaneous presence of the conflicting visual feedback, or, as we suggest, it could be the consequence of a change in the movement plan. In the latter case, the CNS should take into account before the initiation of the motion not only motion direction in the real space but also movement direction in the visual context. To verify which of these two possibilities was correct, subjects have been exposed to a block of 15 trials of conflicting visual context [as in the H (outward)-u condition described in the second experiment] and arm kinematics have been evaluated when movement visual feedback was suddenly removed before motion initiation. The new six subjects maintained constant movement duration (on aver-

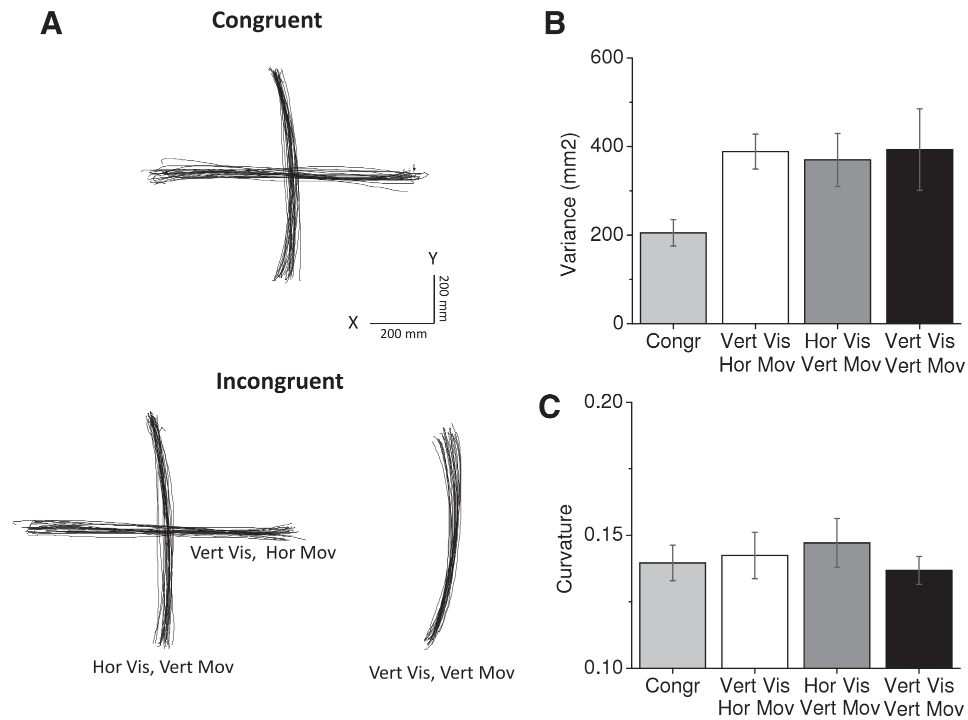

Fig. 6. Analysis of the spatial features of the movements. *A*: fingertip trajectories for a representative subject during the congruent (*top*) and conflicting conditions (*bottom*) projected on the *XY* plane (see Fig 1*A* for the reference frame). For clarity, all of the movements have been normalized so that their mean in the *X*- and *Y*-axes is equal to zero. The scale of all plots is illustrated at *top*. *B*: mean variances in executed movement in the nondominant direction. The variance was calculated in the dimension orthogonal to the dominant movement dimension, following the methods of Kilner et al. (2003). For instance, when subjects performed horizontal movements, the variance was computed on the vertical dimension, and vice versa. The mean of the movement variances was calculated across all trials for each condition. Error bars represent population SE. *C*: average movement curvature in 3 dimensions for all conditions, measured as the maximum path deviation from a straight line connecting the initial and final finger positions, divided by the distance between these positions. Error bars represent population SE. No significant change was observed in any of these parameters across conditions. Congr, congruent condition.

age 916 ± 48 ms; paired-sample *t*-test, $t = -0.74$, $P > 0.05$) and movement amplitude (on average 64 ± 1°; paired-sample *t*-test, $t = -1.06$, $P > 0.05$) in both conditions. Although movement duration was slightly longer than in the main experiment, the relative duration of the acceleration phase in the congruent horizontal outward condition was similar to that observed in the main experiment and in literature (AD/MD = 0.498 ± 0.007). As in the main experiment, the association of an upward visual feedback to a horizontal movement produced a significant reduction in the relative duration of the acceleration phase of the movement (AD/MD = 0.471 ± 0.007; 1-tailed paired-sample *t*-test, $t = 3.24$, $P < 0.05$). Most interestingly, after the adaptation to the conflict, when the feedback was suddenly removed before movement initiation, subjects still presented a velocity profile similar to the one measured in the presence of the continuous visual feedback and significantly different from the velocity profile typical of a horizontal movement (1-way repeated-measures ANOVA on the AD/MD, $P < 0.05$). A Bonferroni post hoc test individuated a significant difference between the baseline and the conflicting condition, both in the presence of the continuous visual feedback and when it was turned off, although these latter two conditions did not yield significantly results (see Fig. 7). This finding indicates that the effect of the conflicting visual context on movement planning does not depend on online movement corrections caused by the presence of a continuous visual feedback, but rather on a change in the motor planning.

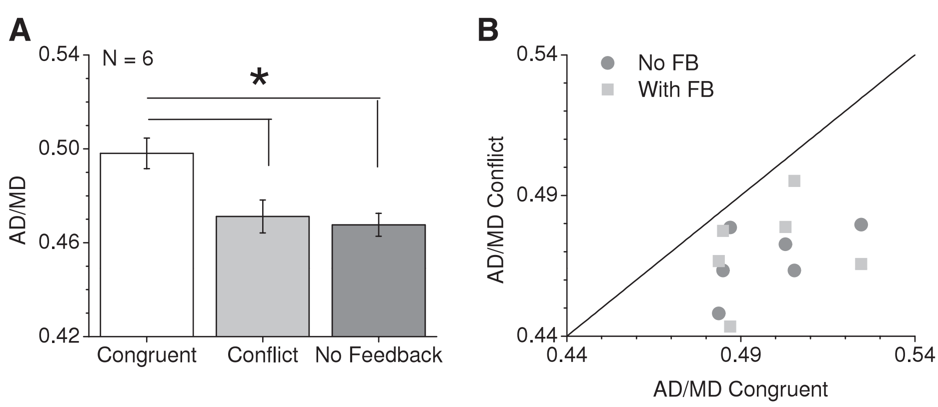

Fig. 7. Control experiment: the asymmetries depend on feedforward motor control rather than concurrent visual feedback. *A*: average AD/MD ratios (6 subjects) for the congruent horizontal outward condition, for the conflicting condition {move horizontal (outward) while view up [H (outward)-u]}, and for the "catch trial" in which the movement visual feedback was suddenly turned off before motion initiation (no feedback). Error bars represent population SE. *$P < 0.05$. *B*: individual subject's AD/MD ratios measured in the presence of conflicting visual context plotted against the corresponding AD/MD measured when the visual feedback was congruent with actual movement. Light gray squares represent the average AD/MD value measured for each subject during the incongruent condition with concurrent visual feedback. Dark gray circles indicate the AD/MD ratio measured in the catch trial, when motion visual feedback was absent. The continuous line indicates where the data points should lie if the conflicting visual context had no effect on motion planning, that is, if the movement was performed as a normal horizontal movement. The visual context significantly changed the AD/MD of the planned movement also in the absence of concurrent visual feedback of the movement.

DISCUSSION

In this study, we analyzed how the planning of vertical and horizontal arm pointing movements is affected by a conflicting visual feedback about the end effector. We tested the idea that when visual information on hand trajectory is artificially rotated, one might reach the target by using the same or a new motor plan generated in the new spatial context. Our results indicate that visual context influences arm kinematics. More specifically, we found a significant change of the temporal pattern (velocity profile) when visual information about the vertical (and not about the horizontal) is provided, suggesting that the visual vertical strongly constrained the planning process of arm pointing movements. Moreover, we verified that, after sufficient exposure, the effect of the conflicting visual information on the movement is not due to movement corrections triggered by online visual feedback, but rather to a change in the motor plan, which also takes into account the visual context direction before movement execution.

This finding is in line with previous data showing that the asymmetry in the velocity profiles is an effect at the planning phase, rather than a consequence of the sensory inflow. In particular, recent results from our group (Gaveau and Papaxanthis 2011) have demonstrated that asymmetries appear early in movement execution (before peak acceleration, i.e., before 100 ms) and persist until the end of the movement. This robust feature of vertical movements excludes the possibility that asymmetries are the outcome of a feedback control process and reinforces the idea of a feedforward control that takes into account gravity force.

In the following we discuss the effect of vision on hand trajectory planning for this particular case of visuomotor conflicts. Afterward, we focus on the possible role played by an internal model of gravity in the remapping between motor planning and the spatial goal.

Role of Vision in Trajectory Planning

In the first experimental phase, subjects had to perform arm movements in the vertical plane while they viewed the arm motion in the opposite directions (U-d and D-u conditions). The task required a novel mapping between end-effector displacement (the dot) and joint rotation: up on the screen corresponding to down with the arm, and vice versa. Unlike most other previous studies investigating the effect of a conflicting visual feedback by considering small shifts of the visual field (e.g., Hay and Pick 1966; Sober and Sabes 2003), we chose to introduce a large discrepancy between limb trajectory in visual space and movement direction in arm space. As a consequence, the visuomotor conflict was explicit, meaning that already before moving their arm, subjects were aware that arm movement and resulting visual feedback would be incongruent.

Hand velocity profile analysis revealed a strong effect of the visual context on a primary variable computed during movement planning. This agrees with several previous experiments demonstrating that constraints on motion planning are primarily perceptual in nature (Flanagan and Rao 1995; van Beers et al. 2002). However, the present changes in acceleration/deceleration ratio, not investigated in these previous experiments, were not evident. Indeed, the visuomotor conflict could induce a priori two possible behaviors. The discrepancy between visual feedback and actual arm movement orientation could have led to neglecting one of the two inputs, thus producing planning based on just a single source. For instance, neglecting vision would have led to remapping of arm movements without regard to the false/inverted visual feedback of the hand, and to keeping the same velocity profile. Alternatively, because the task was defined in visual terms, subjects could have been fully contaminated by the visual input, thus inducing a systematic change of arm kinematics in the direction of the rotated visual feedback. It appeared that subjects adopted an intermediate solution with acceleration phase durations that were between those recorded during upward and downward congruent arm movements.

Despite the explicit nature of the visuomotor conflict presented, subjects were not able to disregard the visual information (even with longer practice) and systematically adopted movement timing different from that adopted in the congruent condition. This finding is particularly unexpected in a task that requires interaction with the gravitational environment. Several authors have indeed demonstrated that, in general, sensory information does not always affect the motor program related to gravity (Zago et al. 2009). For instance, motor preparation to catch a virtual object falling at constant speed uses the timing needed to catch a gravitationally accelerated object, thus showing that movement planning is not affected by visual information (e.g., Zago et al. 2004). Even in microgravity (McIntyre et al. 2001; Papaxanthis et al. 2005), where proprioception and visceral inputs also communicate the absence of gravitational acceleration, anticipative motor mechanisms are still tuned to gravitational information. Moreover, we (Pozzo et al. 2006) have previously demonstrated that inference process allowing the reconstruction of arm trajectory performed along the vertical axis does not strongly rely on visual information. Therefore, showing that the use of gravitational acceleration in movement planning can be modulated by a simple rotation of the visual context is quite striking. We will come back to this point later in the DISCUSSION.

By considering a simple model that combines the visual and intended movement information, we derived from the measured speed profiles the relative weights of these two inputs used to determine the actual motor plan. Results showed that when an upward motion was associated with a downward visual feedback, and vice versa, the incongruent visual feedback had a conspicuous impact in determining motion planning, with a relative weight of about 30%. This result is in agreement with the idea that the sensory integration during reach planning is a dynamic process driven by the computational demands of the task (Sober and Sabes 2003, 2005). For instance, Sober and Sabes found that the movement vector and its transformation into a motor command rely on vision and proprioception, respectively. Presently, we found a great relevance of proprioception also in determining movement direction. In our task, however, subjects were asked to reach a target zone instead of a precise target point, thus possibly minimizing the role of the visual input in movement vector computation. Such a visual context in addition to the explicit discrepancy between vision and actual movement directions would emphasize the inverse dynamic process of the planning stage and could explain the present reduction in the weight of the visual input.

A peculiar aspect of the effect of the incongruent visual feedback in this study is that the adaptation to the conflict induces subjects to adopt a motion plan that is no more optimal in terms of the minimization of energy expenditure for the actually executed movement (Berret et al. 2008). This surprising result is, however, in accordance with a previous finding by Wolpert et al. (1995). During point-to-point arm movements, the authors altered the visual feedback of hand position so as to increase the perceived curvature of the movement. Cost functions specified by hand coordinate kinematics predicted an increase in hand movement curvature so as to reduce the visual curvature, whereas dynamically specified cost functions predicted no adaptation in the underlying trajectory planner. Their results showed that after adaptation the hand movement became curved, thereby reducing the visually perceived curvature. Wolpert et al. (1995) concluded that spatial perception, as mediated by vision, plays a fundamental role in trajectory planning. Here, the fact that subjects could not neglect the incongruent visual feedback even though their motor plan had to integrate the gravity force is in agreement with these results.

Vision and Internal Model of Gravity

The second experimental phase showed that when a horizontal motion was coupled with an upward vertical visual feedback, the resulting movement speed profile was no more symmetric, as it is for horizontal motion, but became more similar to those typical of vertical upward movements. On the contrary, when a vertical motion was performed, the presence of a horizontal visual feedback did not change motion kinematics. Thus motion kinematics were modulated by vision, but surprisingly only when visual input was oriented along the vertical.

The relevance of vision in motor planning has been widely demonstrated (Ghahramani et al. 1996; Guigon et al. 2007; Krakauer et al. 2000). However, in previous studies movements were performed on the horizontal plane, where gravity does not play a significant role in determining motion kinematics. This view has been recently extended to the elaboration of a gravity-dependent motor plan by Le Seac'h and McIntyre (2007), who investigated the role of intrinsic vs. extrinsic frame of references during arm pointing and showed that movement timing (i.e., speed profile) changes as a function not only of body orientation but also of availability of visual input. In this study we have moved a step forward, showing that the influence of vision on movement planning is orientation dependent.

An important question arises as to why the visual vertical had a stronger effect than the horizontal on the motor planning. Some experimental evidence suggests that mechanical effects of gravity on upper limbs are anticipated by the CNS (Le Seac'h and McIntyre 2007; Papaxanthis et al. 2005), allowing subjects, for instance, to start a smooth upward movement or to decelerate and stop a downward directed one in time. In other words, gravity would be encoded at different levels of the CNS, with the highest one representing gravity in the motor commands at the planning level (Papaxanthis et al. 2003b; Pozzo et al. 1998). Therefore the internal gravitational model would be used to account for the gravitational effects on the limb when planning arm movements. This might justify the higher weight attributed to vertical information, because vertical movements require a more complex gravity compensation than horizontal ones, as gravity-dependent torques change during motion as a function of arm position. Interestingly, this internal model of gravity would be involved not only in movement production (Lackner and DiZio 2005) but also in visual processes, to calculate the effects of gravity on seen objects (Indovina et al. 2005; see Zago et al. 2009 for a review). This visual gravitational model would be stored in the vestibular cortex, including a network of brain regions activated by both gravitational visual motion and vestibular stimulation, ranging from insular cortex (posterior insula and retroinsula), temporoparietal junction, ventral premotor area, supplementary motor area, middle cingulate cortex, and postcentral gyrus to posterior thalamus and putamen. Furthermore, Indovina et al. (2005) showed that the areas of somatosensory cortex and ventral premotor cortex activated by visual gravitational motion overlap with sensory and motor arm representations, thus confirming that the internal model of gravity is also used to account for gravitational effects on arm position when planning arm movements. Verticality then seems central in movement planning, significantly determining how different sources of information, and in particular vision, influence the motor plan.

Conclusion

Our results show that the use of visual information in three-dimensional arm motion planning is gravity dependent, because visual input along the vertical axis (but not the horizontal axis) significantly modified movement kinematics. One possibility to further confirm this result would be to record an increasing influence of incongruent visual feedback on movement execution when visual vertical relies on a richer and more structured environment, e.g., using virtual reality to accentuate the immersion in the visual context and the sense of verticality. On the contrary, introducing noise in the perception of verticality (e.g., galvanic or caloric stimulation of the vestibular system) or even just decoupling visual and vestibular vertical (e.g., in microgravity) could lessen the influence of verticality information on motion planning, thus cancelling the particular relevance of the visual vertical orientation in movement kinematics. Lastly, the present result raised an interesting question, which is whether after a longer adaptation to such a visuomotor conflict the CNS would be able to completely disregard the incongruent feedback, thus readopting an optimal movement kinematics after a process of reoptimization (Izawa et al. 2008).

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

Author contributions: A.S. and T.P. conception and design of research; A.S., L.D., and S.T. performed experiments; A.S., L.D., B.B., and S.T. analyzed data; A.S., L.D., B.B., S.T., C.P., and T.P. interpreted results of experiments; A.S. and L.D. prepared figures; A.S., L.D., and T.P. drafted manuscript; A.S., B.B., C.P., and T.P. edited and revised manuscript; B.B., G.S., C.P., and T.P. approved final version of manuscript.

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