

Visuomotor adaptation to a visual rotation is gravity dependent

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Submitted 20 May 2014; accepted in final form 9 December 2014

Toma S, Sciutti A, Papaxanthis C, Pozzo T. Visuomotor adaptation to a visual rotation is gravity dependent. *J Neurophysiol* 113: 1885–1895, 2015. First published December 10, 2014; doi:10.1152/jn.00369.2014.—Humans perform vertical and horizontal arm motions with different temporal patterns. The specific velocity profiles are chosen by the central nervous system by integrating the gravitational force field to minimize energy expenditure. However, what happens when a visuomotor rotation is applied, so that a motion performed in the horizontal plane is perceived as vertical? We investigated the dynamic of the adaptation of the spatial and temporal properties of a pointing motion during prolonged exposure to a 90° visuomotor rotation, where a horizontal movement was associated with a vertical visual feedback. We found that participants immediately adapted the spatial parameters of motion to the conflicting visual scene in order to keep their arm trajectory straight. In contrast, the initial symmetric velocity profiles specific for a horizontal motion were progressively modified during the conflict exposure, becoming more asymmetric and similar to those appropriate for a vertical motion. Importantly, this visual effect that increased with repetitions was not followed by a consistent aftereffect when the conflicting visual feedback was absent (catch and washout trials). In a control experiment we demonstrated that an intrinsic representation of the temporal structure of perceived vertical motions could provide the error signal allowing for this progressive adaptation of motion timing. These findings suggest that gravity strongly constrains motor learning and the reweighting process between visual and proprioceptive sensory inputs, leading to the selection of a motor plan that is suboptimal in terms of energy expenditure.

sensorimotor adaptation; visual verticality; motor planning; internal model of gravity

ADAPTATION TO A VISUAL CONTEXT that disconnects the visual space from the action space follows robust identified rules (Bock 2013; Bock and Burghoff 1997; Henriques and Cressman 2012; Krakauer et al. 2000). In general, during adaptation the neural system progressively learns the new association between the sensory states of the arm—its position and velocity—and the instantiated motor commands, in order to decrease as much as possible the effect of the visual perturbation. Typically, error in position due to a visual shift is compensated trial after trial on the basis of sensory feedback to recover the performance of the baseline condition (Krakauer et al. 1999; Shadmehr et al. 2010; Tseng et al. 2007; Wei 2010; Wei and Kording 2008). However, most of the visuomotor adaptation paradigms have been performed in the horizontal plane and

have mainly examined the adaptation of spatial features of the movement (e.g., path direction, curvature). In a recent work, the extent to which the visuomotor conflict task implies changes in the temporal structure of the motion was investigated (Sciutti et al. 2012). These authors found that a visuomotor rotation produces a significant change in the motor plan, i.e., changes to the symmetry of the velocity profile. Moreover, it was shown that the central nervous system (CNS) 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. Furthermore, Le Seac'h and McIntyre (2007) showed that when lying on their side with their eyes closed subjects performed head-to-toe movements of the arm with velocity profiles typical of vertical arm movements with and against gravity, suggesting that visual, gravitational, and idiosyncratic cues combine to define the vertical used to plan optimized movements of the limb.

These previous findings raised two open questions: First, when the task involves visuomotor transformations different from those classically described in the literature (that is, in both the vertical and the horizontal planes) do spatial and temporal features of arm motions adapt differently? Second, would the CNS, after a longer exposure to a visuomotor conflict involving vertical and horizontal movements, be able to completely disregard the influence of visual verticality on arm motion, thereby readopting an optimal movement kinematics?

The goal of the present study was to further investigate the role of gravity force field in the adaptation process during a visuomotor conflict involving the horizontal and vertical planes. In the main task we asked participants to make horizontal arm movements while receiving a vertical visual feedback of their movements. With respect to the first question, we hypothesize that during adaptation the internal representation of the relationship between the motor command and the resulting sensory signals (i.e., the forward model) is corrected by remapping only the visuomotor space, leaving unchanged the temporal pattern of arm motion, which was compatible with task achievement anyway. We particularly focused on the velocity profile because it constitutes an ideal parameter to examine the adaptation process along horizontal and vertical axes. Indeed, velocity profiles significantly differ between horizontal-symmetric (Gentili et al. 2007; Morasso 1981) and vertical-asymmetric (Atkeson and Hollerback 1985; Le Seac'h and McIntyre 2007; Papaxanthis et al. 1998b; Sciutti et al. 2012) arm movements.

A possible prediction about the second issue is that, during prolonged practice, the motor plan relies more on the visually

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perceived verticality than on the constant mechanical effect of gravity experienced by the arm during horizontal movement. Indeed, the input about verticality given by the visual context could significantly influence the motor plan and participants would progressively adopt the temporal pattern of a vertical movement while moving in the horizontal plane. This would require that participants adopt planning corresponding to the intended movement (against gravity) and not that corresponding to the actual movement (parallel to gravity). Although previous works (see Le Seac'h and McIntyre 2007 and Sciutti et al. 2012) support this hypothesis, none of them investigated the evolution in time of the reported effect. Alternatively, after a period of conflict exposure, participants might learn to disregard the conflicting vertical visual information and to produce horizontal arm movements similar to those without visual rotation, that is, with symmetric velocity profiles. This is in accordance with studies demonstrating that the asymmetric velocity profiles of vertical arm movements result from a minimization of the absolute work of the muscles involved in the motion (Berret et al. 2008; Papaxanthis et al. 2003). Thus, since moving horizontally following the kinematics of a vertical arm movement is energetically suboptimal, minimizing the effort of the motor system (as a general rule of human motor control) would lead to rapidly adopting a horizontal temporal pattern.

MATERIALS AND METHODS

Subjects

Seventeen right-handed volunteers participated in this study. Seven volunteers (all men, mean age = 29.1 ± 3.6 yr) participated in the main experiment. The remaining 10 subjects (6 men and 4 women, mean age 24.4 ± 3.3 yr) completed the control experiment. None of them had neuromuscular disorders, and all had normal or corrected-to-normal vision. 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).

Apparatus

The main experiment was performed in a dark room. Participants were comfortably seated on a chair (Fig. 1, *A* and *B*) in front of a large rear projection screen (projection area of $185 \text{ cm} \times 140 \text{ cm}$ at a viewing distance of $\sim 130 \text{ cm}$) where two target zones were displayed on a black background (Epson emp1815 LCD; $1,280 \times 1,024$ pixels with 75 Hz refresh rate). These zones were delimited by two white semicircles (60 cm apart) with radius of 42.5 cm that were positioned either at the two sides of the screen or at the top and the bottom of the screen (Fig. 1, *C* and *D*). Visual feedback (i.e., cursor) about the position of the participants' right arm end point was provided by a white dot (3-cm diameter; Fig. 1, *C* and *D*) that moved on the screen in real time with participants' movements. A VICON Motion Capture system with six infrared cameras (sampling rate at 100 Hz) detected the time-varying position of two passive reflective markers placed on the subject (right index fingertip and acromion). The time delay between the real motion of the finger and its projection on the screen was $< 30 \text{ ms}$. The scaling factor between arm movement amplitude and cursor displacement was 1; consequently, the distances covered by the fingertip and the cursor were similar (i.e., 70 cm corresponding to a shoulder rotation of $\sim 65^\circ$). Participants wore a mask that kept them from seeing their arm during the whole experiment. Moreover, the rear projection screen avoided any possible shadow of partici-

pants' arm. For the control experiments participants were comfortably seated on a chair in front of a vertical panel ($150 \text{ cm} \times 200 \text{ cm}$) at a 150-cm distance. A video projector (Epson emp1815 LCD; 70 Hz, $1,280 \times 800$ pixels) placed 2 m behind the screen retro-displayed the motion of a black dot (2-cm radius) along the upward direction. The position of the projected stimuli on the panel was adjusted to each participant's height so that his/her eyes were at the same level as the stimuli. Dot upward motion reproduced the movements of the finger extremity of the outstretched arm of other participants recorded in a previous study. More precisely, those subjects were measured in a set of 12 upward and 12 horizontal movements. Therefore, dot motion reproduced real subjects' movements performing a pointing task in the sagittal plane with a rotation around the shoulder joint with a total angular displacement equal to 65° .

Main Experiment Protocol

Participants were required to produce uncorrected (i.e., one shot) visually guided vertical and horizontal arm motions and blind (i.e., open loop) horizontal arm movements. In both visually guided and blind motions, subjects' hand was out of sight throughout the movement. Arm motions were performed with a rotation around the shoulder joint at a natural self-selected speed (Fig. 1, *A* and *B*). During baseline conditions where visual feedback was provided, participants had to produce 12 upward and 12 rightward arm motions in order to displace the cursor upward (BSL_up; Fig. 1*C*, *left*) and rightward (BSL_right; Fig. 1*C*, *center*), respectively. Thus the aim of the baseline motions with visual feedback was to move the cursor within the vertical (BSL_up) and horizontal (BSL_right) target zones. During baseline trials where visual feedback was turned off (blind movements), participants had to perform 12 rightward arm movements looking at the screen where the target zones were still displayed at both sides of the screen (BSL_noFb; Fig. 1*C*, *right*).

In conflicting trials (CONFL; Fig. 1*D*, *left*), visual feedback of participants' fingertip was 90° counterclockwise rotated and target zones were vertically displayed (i.e., lower and upper limit of the screen). Thus participants controlled upward cursor displacements by rightward arm motions. Such a conflict condition corresponded to the H-u orientation condition that in our previous work (Sciutti et al. 2012) produced the largest influence on participants' performance. As in BSL_up and BSL_right conditions, the movement goal during CONFL was to drive the cursor from one target zone to the other and participants had to produce rightward arm motions to move the cursor from the lower to the upper target zone. The conflict condition included four blocks of 27 trials where the cursor was rotated with respect to hand motion. At the end of each block the cursor was unexpectedly turned off during three consecutive trials (catch; Fig. 1*D*, *center*), after which the next conflicting block was started. Even though visual feedback was removed, during catch trials target zones remained vertically oriented and participants had to complete rightward arm motions looking at the screen. Once the last catch trial series, coming after the fourth conflicting block, were performed, participants executed another seven blind rightward motions again with the target zones displayed in the lower and upper parts of the screen (washout; Fig. 1*D*, *right*). Unlike previous studies, we decided not to randomize the order of catch trials to keep constant the number of conflicting presentations among each catch series duration. In total, subjects completed 127 rightward arm motions (108 for CONFL, 12 for catch, and 7 for washout trials). To avoid fatigue effects, subjects were free to relax the arm as soon as they felt fatigued. Before the conflict condition subjects had very few practice trials (never more than 3) to familiarize with the visual rotation and perform motions as straight as possible and at natural speed. Unlike Sciutti et al. (2012), here we chose not to submit subjects to a proper training phase in order to be able to observe the evolution of the visuomotor adaptation elicited by the conflicting visual context.

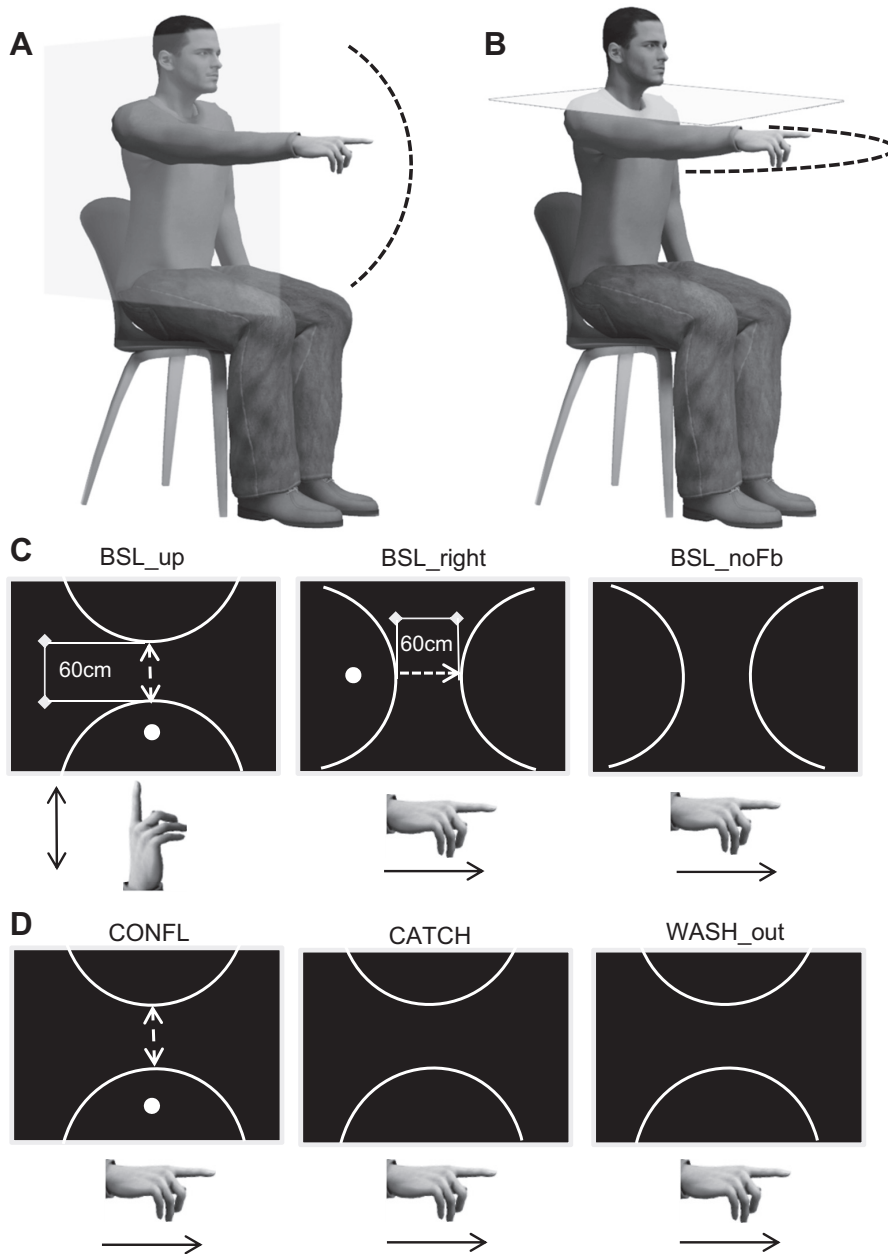


Fig. 1. Protocol schema. *A* and *B*: 12 vertical and horizontal movements were performed keeping the arm slightly on the right of the sagittal plane or under the transversal plane, respectively. *C*: for both movement directions visual feedback of the arm end point was provided (BSL_up and BSL_right) or removed throughout the motion (BSL_noFb). *D*: subjects participated in an experimental session of 4 blocks composed of 27 rightward movements associated with an upward rotated visual feedback (CONFL), 3 rightward movements without feedback (CATCH) at the end of each block, and 7 movements after the fourth catch trial series (WASH_out). White dashed and black solid arrows describe feedback and hand motion directions, respectively. Semicircles depict movement target areas, and the white dot visual represents the visual feedback of hand motion.

Control Experiment Protocol

In the control experiment participants were asked to estimate the motion duration of a dot moving upward whose trajectory was visible only during the first part of its motion (i.e., until the peak velocity). At each trial participants fixated a cross at the center of the screen and pressed the mouse button to initiate the display of the moving dot. After 1 s the cross disappeared and the dot appeared at the same position. After an additional 0.5 s the dot started moving upward and disappeared when it reached its maximum velocity, so only the acceleration phase was visible. Participants were instructed to press the mouse button again at the moment they estimated that the occluded dot motion had stopped. Therefore, the task of the participants was to estimate the total dot motion duration (motion duration = visible acceleration duration + occluded deceleration duration). Two kinds of upward kinematic profiles were displayed on the screen. The first consisted of a short visible acceleration phase (hereafter SHORT, 0.88 s), whose kinematics was extracted from an asymmetric velocity profile [acceleration duration (AD)/motion duration (MD) = 0.44

with MD = 2 s] recorded during natural upward movements. The second kind of profile was characterized by a longer acceleration phase (hereafter LONG, 0.98 s), whose kinematics was extracted from a symmetric velocity profile (AD/MD = 0.49 with MD = 2 s) recorded during natural horizontal movements. Both dot upward motion displays corresponded to an average value of other participants' vertical and horizontal movements, measured in a previous study (see *Apparatus and Control experiment*). We recorded participants' duration estimations from mouse clicks (time resolution 1 ms), and then we compared the estimations across the different kinematic profiles displayed.

Data and Statistical Analysis

Main experiment. For each trial, spatial and temporal parameters of participants' arm motion were analyzed separately. On the one hand, the spatial parameters we considered were the deviation from the sagittal and transversal planes to quantify arm orientation at starting position and arm maximum deviation from movement plane through-

out the motion. Then we evaluated whether subjects respected the task requirement of performing 1 degree of freedom arm motions. Specifically, we calculated whether their finger motion lay on the surface of a sphere centered in the shoulder and with arm length as radius (R^2 of the sphere fitting). The spatial error induced by the rotated visual feedback was quantified by an index of movement linearity, that is, the ratio between the shortest path joining initial with final hand position (L) and the actual fingertip path (D), minus 1. In accordance with such a value a perfect straight-arm motion would produce an index equal to 0. On the other hand, as temporal parameters we considered both velocity and acceleration profiles (i.e., first and second derivatives of hand position). From the velocity profile we extracted the ratio between acceleration duration (AD) and the total movement duration (MD), AD/MD. From the acceleration profile we calculated the relative time to peak acceleration as the ratio between peak acceleration (PA) and movement duration (MD), PA/MD (Gaveau and Papaxanthis 2011). Both ratios referred to the time of occurrence of the peaks normalized for the whole movement duration. As largely reported in the literature (Flash and Hogan 1985; Gaveau and Papaxanthis 2011; Gentili et al. 2007; Papaxanthis et al. 1998a, 1998b, 2003, 2005; Sciutti et al. 2012) a symmetric velocity profile, characterized by a peak velocity arising around half of the total movement duration (i.e., AD/MD \approx 0.5) is typical of horizontal movements. Conversely, a velocity profile characterized by an acceleration phase shorter than the deceleration (i.e., AD/MD < 0.5) is typical for vertical upward motions. Thus after averaging the AD/MD values across subjects we calculated the percentage of kinematic change at each block by means of the following ratio:

$$\frac{AD/MD_{hh} - AD/MD_{hu}}{AD/MD_{hh} - AD/MD_{uu}} \cdot 100$$

where $AD/MD_{hh} - AD/MD_{hu}$ is the difference between the AD/MD mean value measured during the horizontal baseline condition and the AD/MD average value measured at each conflicting block. This difference was then normalized with respect to $AD/MD_{hh} - AD/MD_{uu}$, which is the difference between the AD/MDs measured during horizontal and upward vertical baselines. Therefore a 100% AD/MD change would result if the difference in AD/MD values between conflicting and baseline horizontal trials was the same as the difference between baseline horizontal and upward baselines. Conversely, a zero percentage of change calculated during conflicting trials would indicate no modifications of AD/MD with respect to the horizontal baseline condition. In addition to the time to peak velocity, from individual acceleration profiles we also extracted the peak acceleration and normalized it in amplitude with respect to individual maximum acceleration, measured during baseline trials. Previous works investigating the timing and the magnitude of peak acceleration during horizontal and vertical motions showed a decrease of the time to peak and an increase of the peak during upward movements with respect to horizontal (Atkeson and Hollerbach 1985; Gaveau and Papaxanthis 2011; Gentili et al. 2007). In the light of these findings we predicted a reduction of the time to peak acceleration and an increase of the peak with respect to baseline values during horizontal motions associated with a vertical feedback. Conversely, we did not expect any changes in these parameters when vertical visual feedback was turned off (i.e., catch and washout trials). Since baseline conditions were composed of 12 trials and each block of the conflicting experiment was composed of 27 trials, we divided each conflicting block into 2 subblocks composed of the first and the last 12 trials.

All data collected during baselines and conflicting blocks, except the index of movement linearity, showed a normal distribution (Kolmogorov-Smirnov test). The main effect of visual feedback rotation among conditions was tested by means of a one-way repeated-measures ANOVA with block of trial as factor and nine levels (i.e., baseline and 8 conflicting subblock groups). Kinematic parameters measured within catch and washout trials were compared with both

BSL_noFb and each conflicting block value with two different one-way repeated-measures ANOVAs followed by Tukey's post hoc test (pairwise comparisons). The first comparisons tested whether conflict exposure might have influenced typical horizontal arm movements performed without any visual feedback, while the second comparisons were used to detect significant aftereffect. Since catch trials were composed of only three movements, we compared the associated kinematic measures (averaged across subjects) with those values extracted from the last three movements of baseline and each conflicting block. Greenhouse-Geisser correction was used to correct for nonsphericity of samples. Statistical analysis of the indexes of movement linearity values was performed by a Friedman ANOVA, as these measures did not follow normal distribution.

Control experiment. The main goal of the control experiment was to test whether participants used an internal representation of upward vertical motion to estimate the duration of dot motion. In fact, an intrinsic representation of the temporal structure of perceived vertical motions could provide the error signal, allowing for the progressive adaptation of motion timing we observed in the main experiment. Such a model of upward motion assumes the AD of dot motion to be shorter than its deceleration duration (DD), namely, predicting an AD/MD lower than 0.5. We refer to this assumption as the asymmetric hypothesis (AHyp). Alternatively, the lack of such an internal representation does not entail any differences between AD and DD. In this second assumption, hereafter the symmetric hypothesis (SHyp), an AD/MD equal to 0.5 is predicted. Since the acceleration phase of dot motion was the sole information available to participants, we suggest that they estimated the whole dot motion duration by dividing the visible acceleration duration of the dot with a predicted AD/MD either equal or lower than 0.5 (by assuming SHyp or AHyp, respectively). Thereby, in terms of motion duration estimation, the AHyp predicts higher duration, $MD = AD / < 0.5$, than those predicted by the SHyp, $MD = AD / \approx 0.5$. Figure 2 illustrates this point by depicting the visible AD and the predicted DDs for both dot velocity profiles presented (SHORT and LONG) and both hypotheses. The AHyp (Fig. 2A) always predicts a longer motion duration estimation with respect to that predicted for the same velocity profile by the SHyp (Fig. 2B). In particular, the AD/MD values used to predict dot motion duration were 0.49 and 0.44 for SHyp and AHyp, respectively. These values were extracted averaging the AD/MDs measured with other subjects in a previous experiment during both horizontal and vertical arm motions (see *Apparatus and Control Experiment Protocol* for details). As variables were normally distributed, we performed a two-tailed *t*-test analysis for dependent samples.

RESULTS

Spatial Parameter Adaptation

During all conflict blocks participants did not show significant trajectory deviations of their motions with respect to baseline performances. Moreover, arm orientation at starting position presented only a slight deviation from motion plane ($3 \pm 1.1^\circ$ and $3.6 \pm 1.4^\circ$ from transversal and sagittal planes, respectively). The averaged R^2 measure used to quantify 1 degree of freedom motion was 0.92 ± 0.03 (see *Data and Statistical Analysis*).

Although the indexes of movement linearity never equaled 0 (i.e., straight movement), hand trajectory never deviated from a straight path >10% of the total length of the motion. Feedback rotation introduced a slight increase in the deviation from the straight path ($\sim 2\%$) that resulted not significantly different from baseline values, and it remained stable throughout conflicting trial cycles ($\chi^2 = 8.93$; $P = 0.34$). Moreover, the movements performed within all catch trials and washouts

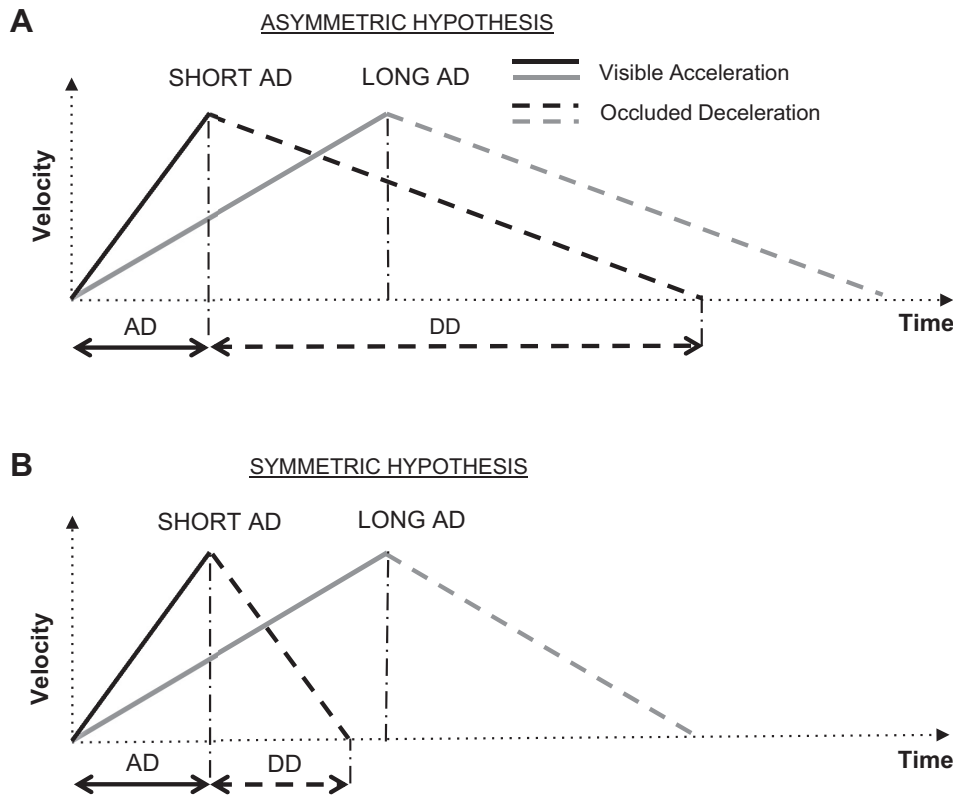


Fig. 2. Control experiment. Dot motion velocity profiles and predicted motion durations. Black and gray solid lines represent SHORT and LONG visible dot acceleration phases, respectively. Each dot motion was occluded at its peak velocity. Dashed lines represent predicted deceleration durations. *A*: if an internal representation of vertical motion is assumed [i.e., asymmetric velocity profile, acceleration duration (AD) < deceleration duration (DD), typical of vertical motion]. *B*: if a symmetric velocity profile is assumed (i.e., AD \sim DD, typical of horizontal motion).

were as straight as those in the baseline horizontal condition with feedback ($\chi^2 = 6.04$; $P = 0.3$). In sum, the introduction of visual feedback rotation did not induce spatial error in participants' motions.

Temporal Parameters

Conflict condition. In accordance with our previous observations (Sciutti et al. 2012), the presentation of an upward-rotated visual feedback while performing horizontal motions influenced the temporal structure of arm movements in a specific fashion. Indeed, participants progressively reduced their AD/MD, thereby showing a velocity profile similar to that typically used for upward movements (Fig. 3). Furthermore, analysis performed on individual measures showed that all but one subject tended to reduce their individual AD/MD values when exposed to upward-rotated visual feedback. In particular,

each participant showed a different amount of AD/MD reduction at different phases of the conflicting exposure, but in the last block six of seven subjects showed an AD/MD statistically lower than baseline (1-tailed, paired-samples *t*-test, BSL_{right} vs. last conflict block, all $P < 0.05$). Surprisingly, participants showed no tendency to reproduce the typical temporal structure of horizontal arm motions produced during the baseline session after the very first conflicting trials. Figure 3 and Table 1 report the modifications of the relative acceleration phase duration (AD/MD) with respect to conflict exposure. The AD/MD values measured during conflicting trials rapidly decreased across repetitions. The mean AD/MD value associated with the last subblock (i.e., last 12 conflicting trials of the fourth block; last three gray circles in Fig. 3) equaled 0.45 ± 0.03 , which was an intermediate value between those recorded for horizontal and upward baseline movements (i.e., 0.49 ± 0.02 and $0.42 \pm$

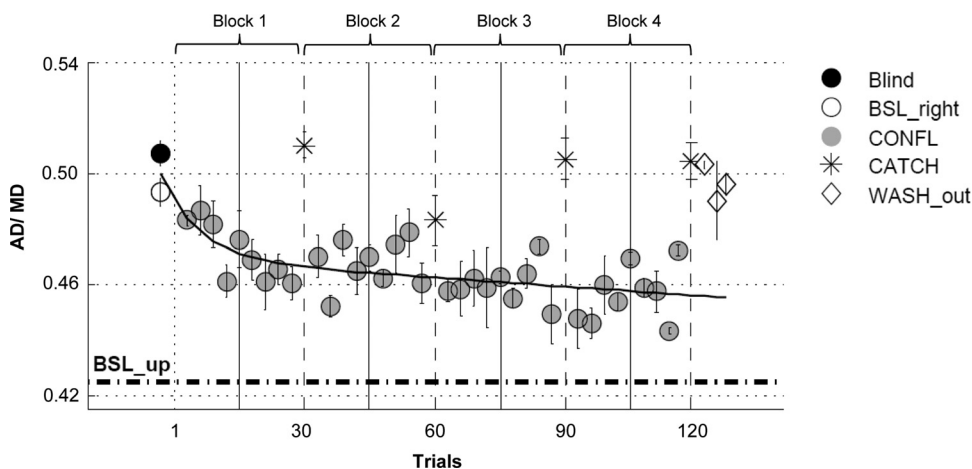


Fig. 3. Time course of adaptation to upward feedback rotation. Normalized acceleration duration (AD/MD) means and SE extracted from movements produced during horizontal baselines (white circle) and blind baseline (BSL_{noFb}, black circle). Conflicting trials (CONFL, gray circles), catch trials (asterisks), and washout trials (diamonds) are averaged (\pm SE) across subjects and over successive cycles of 3 movements. Dotted vertical line separates baseline values from the conflicting trials. Solid vertical lines divide subblocks. Dashed vertical lines represent catch trial set occurrences. Dashed horizontal line depicts the AD/MD mean value measured during upward baseline. Modification of the movement temporal pattern is shown by the progressive reduction of AD/MD values across repetitions. AD/MD reduction was fitted by a double-exponential function ($R^2 = 0.68$).

Table 1. Temporal parameters

	Horiz. Baseline	Block 1	Block 2	Block 3	Block 4	Catch	Washout
AD/MD	0.49 ± 0.02	0.47 ± 0.01	0.47 ± 0.01	0.46 ± 0.01	0.45 ± 0.01	0.50 ± 0.01	0.49 ± 0.02
Peak Acc	0.73 ± 0.02	0.71 ± 0.01	0.85 ± 0.01	0.81 ± 0.01	0.83 ± 0.01	0.78 ± 0.03	0.78 ± 0.02
Peak Acc/MD	0.20 ± 0.03	0.18 ± 0.02	0.18 ± 0.02	0.19 ± 0.01	0.19 ± 0.01	0.20 ± 0.04	0.21 ± 0.05

Values are average ± SD time to peak velocity [acceleration duration (AD)/total movement duration (MD)], normalized peak acceleration, and time to peak acceleration (Peak Acc/MD) across subjects and trial repetitions for each experimental condition.

0.02, respectively). A one-way repeated-measures ANOVA revealed a main effect of the visual feedback among levels [$F(8,664) = 7.97$, $P < 0.01$]. In particular, Tukey's test pairwise comparisons showed significant differences between baseline level and conflicting *subblock 2* [$t(664) = 6.49$, $P < 0.001$], between baseline and both *subblocks 3 and 4* [$t(664) = 6.04$, $P < 0.001$ and $t(664) = 5.31$, $P = 0.005$, respectively], between baseline and both *subblocks 5 and 6* [$t(664) = 7.56$, $P < 0.001$ and $t(664) = 7.28$, $P < 0.001$, respectively], and between baseline and both *subblocks 7 and 8* [$t(664) = 9.31$, $P < 0.001$ and $t(664) = 8.00$, $P < 0.001$, respectively]. Furthermore, a significant effect was observed between *subblock 1* and *subblock 7* [$t(664) = 6.15$, $P < 0.001$] as well as between *subblock 1* and *subblock 8* [$t(664) = 4.84$, $P = 0.018$]. The double-exponential learning curve (Krakauer et al. 1999) fitted to our data describes the overall behavior of AD/MD values across trials with a goodness of fit of ~70% (Fig. 3). By normalizing the reduction of AD/MD within each conflicting block with respect to the difference between horizontal and upward baselines (see *Data and Statistical Analysis* for details), we found that in the first conflicting block participants reduced their AD/MD values by ~32% of the total difference between horizontal and upward nominal profiles (Fig. 4A). Moreover, longer exposure to the upward rotation increased the similarity between the velocity profiles shown during conflicting trials and those shown during baseline upward motion. In fact, as depicted in Fig. 4A, at the end of the last conflicting block the averaged AD/MD value was reduced by ~60%. Although participants never produced a 100% AD/MD reduction [last *subblock* AD/MD values statistically differed from baseline upward, $t(664) = 7.55$, $P < 0.01$], the delta of its reduction across conflicting blocks showed a linear-like increase. We also investigated the modulation of both the peak of acceleration and the time of its occurrence in light of the literature showing that a careful analysis of the acceleration profile can yield important insight on how the CNS optimizes motor commands with respect to gravitational forces (Gaveau et al. 2014; Gaveau and Papaxanthis 2011). In accordance with previous findings on how these two parameters change with respect to arm movement direction (Atkeson and Hollerbach 1985; Gaveau and Papaxanthis 2011; Gentili et al. 2007), we observed that the exposure to the upward-rotated visual feedback produced a significant increase of the magnitude of the peak acceleration and a reduction of the time of its occurrence. Figure 5A and Table 1 report peak acceleration values, averaged across subjects per block, calculated from acceleration profiles normalized in amplitude. The exposure to the upward-rotated feedback introduced a significant change of peak acceleration across conditions [$F(8,664) = 14.63$; $P <$

0.005]. Post hoc pairwise comparisons revealed statistical differences between baseline measures and all *subblocks* ($P < 0.005$) with the exception of *subblocks 1* and *2* ($P = 0.84$ and $P = 0.99$). The increment of peak acceleration during the last three conflicting blocks was quantified as, on average, 11% more than the peak size shown for horizontal baseline. In contrast, statistical analysis performed between the peak acceleration values measured during horizontal motion not associated with an upward visual feedback and horizontal baseline did not show any main effect [$F(2,54) = 68.72$; $P = 0.13$]. Likewise, the timing of the peak acceleration (Fig. 5B and Table 1) appeared to be modulated by the direction of the feedback. Statistical analysis on the time to peak accel-

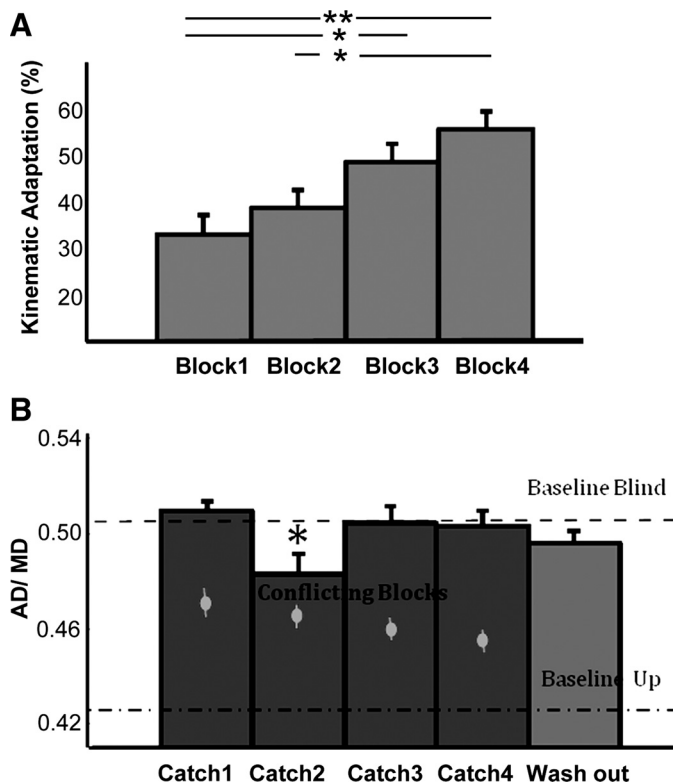


Fig. 4. Percentage of adaptation and catch trial analysis. A: % of kinematic adaptation, extracted by normalizing the reduction of AD/MD within each conflicting block with respect to the difference between horizontal and upward baselines (see *Data and Statistical Analysis* for details). A value of 100% indicates that AD/MD during conflicting trials decreased the same amount of the difference between horizontal and upward baseline values; 0% indicates no AD/MD changes. * $P < 0.05$, ** $P < 0.01$. B: catch trial analysis. AD/MD mean and SE of the 4 catch trial sets (dark gray) and washout (light gray) motion conditions. Dots represent AD/MD mean values and SE measured at each conflicting block. Horizontal dashed and dashed-dot lines indicate the AD/MD value of the horizontal blind and upward congruent baselines, respectively. *Significant reduction of the AD/MD during the second set of catch trials.

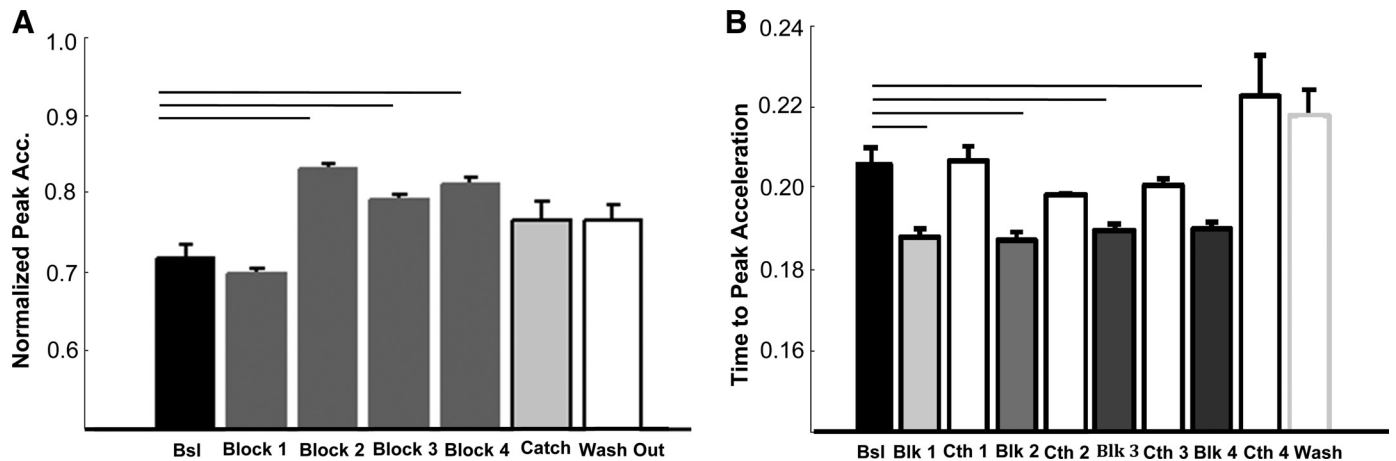


Fig. 5. Adaptation of peak acceleration and time-to-peak acceleration. *A*: normalized peak acceleration during conflict, baseline, and catch trial presentation. Mean normalized peak acceleration value and SE were calculated by averaging subjects' acceleration profiles normalized in amplitude with respect to their individual baseline maximum values. Black bar indicates average value of the normalized individual peak acceleration across subjects, produced during the horizontal feedback condition (BSL_right). Dark gray bars indicate average peak acceleration for each conflicting block. Light gray bar indicates average peak acceleration of movements performed during all catch trials. White bar indicates average peak acceleration associated with washout. Repeated-measures (RM) ANOVAs followed by Tukey post hoc comparisons were set at $P < 0.01$ significance level. *B*: time to peak acceleration for baseline, conflict blocks, and catch and washout trials. Time to peak mean values and SE were calculated from acceleration profiles of each movement normalized in duration and amplitude. Black bar indicates average time to peak acceleration of movements associated with horizontal congruent feedback, while light to dark gray bars indicate average time to peak acceleration for the conflicting blocks. White bars indicate average time to peak acceleration values of movements performed within each catch trial set. White bar with gray border indicates average value associated with movement executions during washout trials. RM ANOVAs followed by Tukey post hoc comparisons were set at $P < 0.01$ significance level.

ation measured during baseline and conflicting subblocks showed a main effect [$F(8,664) = 3.55$; $P < 0.005$]. Figure 5*B* shows clearly how peak acceleration occurs earlier in the movement during conflicting trials but comes back to baseline values every time the upward-rotated feedback is removed. Indeed, when subjects produced horizontal arm motions without any visual feedback they presented time to peak acceleration values statistically no different from baseline values [$F(4,80) = 1.48$; $P = 0.23$]. These findings give evidence that horizontal movements associated with upward visual feedback led participants to produce acceleration profiles that were similar to those of an upward arm movement, that is, with an augmented acceleration peak and an anticipation of its occurrence (Atkeson and Hollerbach 1985; Gaveau and Papaxanthis 2011; Gentili et al. 2007).

Catch Trials

Figure 4*B* depicts trends of AD/MDs observed both when the upward-rotated visual feedback was presented (i.e., conflicting trials) and when it was turned off (i.e., catch and washout trials). Throughout the four blocks, participants showed a specific modulation of AD/MD with respect to the visual context (i.e., presence or lack of the upward-rotated feedback). In fact, participants' AD/MDs of the last bin (3 last movements) of conflicting blocks 1, 2, and 4 were always shorter than the AD/MD measured within the next catch trial sets [pairwise comparisons, respectively, $t(16) = 4.1$, $P = 0.02$; $t(16) = 3.6$, $P = 0.03$; $t(16) = 3.6$, $P = 0.03$]. Moreover, no statistical differences from horizontal blind baseline were observed for all catch trial sets [respectively $t(10) = 0.55$, $P = 1$ for catch 1; $t(10) = 2.44$, $P = 0.54$ for catch 2; $t(10) = 0.3$, $P = 1$ for catch 3; $t(10) = 0.11$, $P = 1$ for catch 4; and $t(10) = 2.22$, $P = 0.63$ for washout]. Nevertheless, during the second catch trial series, averaged AD/MD was reduced even though the conflicting feedback was absent since the onset of motion. The

AD/MD value observed in this case was approximately in between the horizontal blind baseline values and the conflicting trial averaged values for the second block (Fig. 4*B*). Note that such an aftereffect occurred only in the middle of the learning phase (i.e., second block) and it affected significantly only velocity profiles, leaving acceleration temporal pattern untouched (compare the trend of AD/MD values in Fig. 3 with the trend of PA/MD in Fig. 5*B* during catch trials).

Control Experiment

The goal of the control experiment was to test whether participants use a visual representation of upward vertical motion to estimate the duration of dot motion. Our prediction about control experiment results was that if motion time estimation was carried out in accordance with the AHyp, which assumes an AD/MD of 0.44 (see *Data and Statistical Analysis and Control Experiment Protocol*), we should record duration estimations of 2 s (i.e., AD/0.44; 0.88/0.44) for SHORT profiles and 2.22 s (0.98/0.44) for LONG profiles [Fig. 6, *A* (averaged values) and *B* (individual values)]. On the other hand, if subjects' responses were explained by the SHyp (which assumes an AD/MD of 0.49), participants should show motion duration estimation as 1.79 s (0.88/0.49) for SHORT and 2 s (0.98/0.49) for LONG conditions (Fig. 6). Our results showed that subjects' estimation values, during the SHORT condition, were well predicted by the AHyp. A one-sample *t*-test revealed a significant difference between empirical data and SHyp prediction [1.98 ± 0.02 s vs. 1.76 s, $t(9) = 8.98$, $P < 0.01$] but not between empirical and AHyp expected values [1.98 ± 0.02 s vs. 2 s, $t(9) = -0.68$, $P = 0.51$]. In the LONG condition (Fig. 6*A*) averaged estimation values were significantly higher than the SHyp prediction [2.08 ± 0.02 s vs. 2 s, $t(9) = 4.48$, $P = 0.001$], but they were significantly lower than the AHyp prediction [2.08 ± 0.02 s vs. 2.22 s, $t(9) = -7.53$, $P < 0.01$]. Although our results are qualitatively in agreement with the

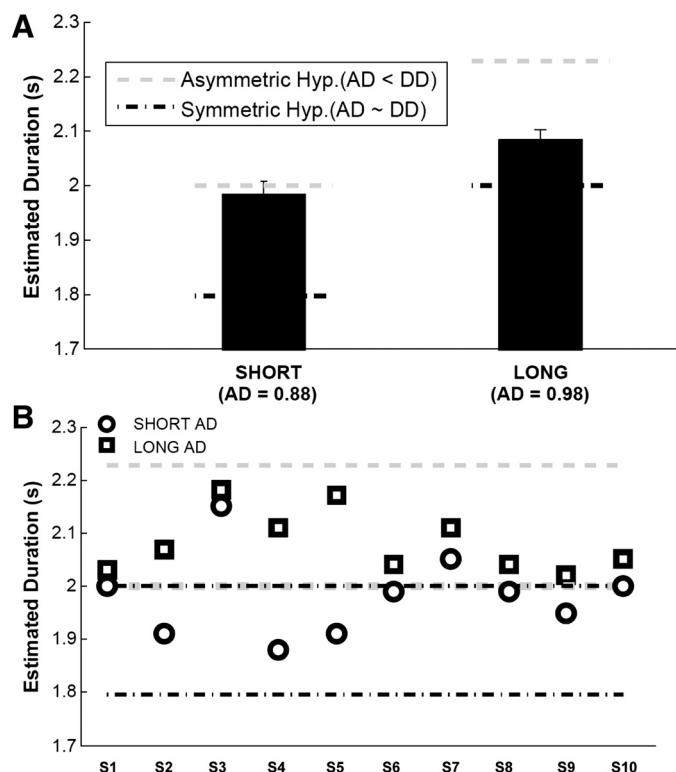


Fig. 6. Estimation of dot motion durations. *A*: average estimations of dot motion duration for the SHORT ($AD = 0.88$ s) and LONG ($AD = 0.98$ s) conditions. Black dashed horizontal lines represent predicted estimates if a symmetric velocity profile is assumed; gray dashed horizontal lines indicate predicted estimates if an asymmetric velocity profile is considered ($AD < DD$, with AD corresponding to 44% of motion duration). *B*: individual subjects' estimates for the SHORT (circles) and LONG (squares) stimuli. Horizontal lines, as in *A*, represent predicted durations according to the subject's assumption of a symmetric or asymmetric dot motion velocity profile.

overestimation predicted by the AHyp in the LONG condition, the estimated durations are quantitatively lower than the predicted durations. In other words, during LONG trials the SHyp and the AHyp seem to be combined, thereby producing intermediate time estimation. In summary, these findings give two important pieces of evidence: first, participants were able to reconstruct the temporal pattern of an upward movement by inferring the duration of the deceleration phase; second, participants showed a hard-wired temporal representation of vertical movements that is used to estimate the movement offset.

DISCUSSION

The present study shows that when the visual feedback of a horizontal movement is rotated by 90° , participants can adapt rapidly to the conflicting visuomotor context and reach the rotated target accurately. However, the horizontal movement is persistently performed with suboptimal kinematics, as movement timing (AD/MD) is close to that of a vertical motion. Throughout the conflict exposure (>100 trials) the temporal pattern of the horizontal movement remains influenced by the visual feedback, thereby showing velocity and acceleration profiles progressively more similar to an upward arm motion. Importantly, this visual effect, which increases with repetitions, is not followed by a consistent aftereffect. As soon as visual conflict was removed and subjects had to perform the same horizontal arm motions without rotated visual feedback

(catch and washout trials), they immediately adopted the proper horizontal velocity.

These findings raise two main comments. First, in the context of adapting three-dimensional movements perturbed by a 90° visual rotation, while spatial error is corrected after few repeated trials, the temporal features of arm reaching do not return to baseline values. Second, the present dissociated adaptation of the spatial-temporal parameters of the movement is not in agreement with a pure energetic optimization principle; rather, it gives evidence of a reweighting of the visual and kinesthetic input reliability guided by strong prior assumptions about the mechanical effect of gravity on ascending arm movement. In the following paragraphs we discuss these two points.

Temporal and Spatial Features of Arm Motion Follow Different Adaptation Processes

The spatial error induced by the visual rotation was rapidly corrected (see *Spatial Parameter Adaptation*). The large discrepancy between limb trajectory (rotated hand feedback), coded in visual space, and actual arm movement direction, coded in kinesthetic reference frame, may explain such immediate re-mapping. In line with this result is the reduced aftereffect that follows an abrupt rather than gradual introduction of a perturbation (Kagerer et al. 1997; Kluzik et al. 2008). Moreover, the visual kinesthetic input decoupling we displayed, which appears complex in Euclidean terms (i.e., 3-dimensional rotations), becomes much simpler if both sensory inputs are transformed in a common, body-centered frame of reference: a motion performed in one body plane (e.g., transversal) is presented as performed in another body plane (e.g., sagittal). It has been largely observed that the brain can exploit a common reference frame, centered on the body (Le Seac'h and McIntyre 2007) to optimally combine multisensory inputs. It is therefore plausible that our subjects expressed each available input in a common, body-centered, reference system, to compare the information about hand and dot motion provided by kinesthetic and visual signals. A similar transformation could then justify the rapidity of the spatial adaptation and the lack of aftereffects (Cohen and Andersen 2002).

In contrast, the temporal structure of arm movement adapted differently to the conflicting visual rotation. Velocity profiles of horizontal motion under conflict conditions approached progressively that of a vertical motion. This result is in discrepancy with the generally accepted idea that the nervous system, trial after trial, learns to predict and cancel effects of a novel environment. Nevertheless, the lack of any tendency to recover the baseline timing behavior we observed in our study, after the very first conflicting trials and during a quite long perturbation exposure, is difficult to compare with previous studies investigating adaptation process (Krakauer et al. 1999, 2000; Tseng et al. 2007; Wei 2010). In fact, those authors mainly used a coefficient calculated on the basis of a spatial error (i.e., the distance between hand position and the position of the target to reach) while in the present study we measured also the temporal features of hand trajectory. The persistence of an inadequate movement timing is, however, quite unexpected. Indeed, in Le Seac'h and McIntyre (2007) changes in arm movement timing performed in a lying position occurred immediately. While a systematic analysis of the adaptation

process was not performed in that study (which perhaps would have revealed a progressive recovery toward a horizontal symmetric timing of the horizontal/foot-to-head movement), one may speculate that when the signal about gravity direction coming from the otolith is irrelevant, graviceptors in the human trunk (the so-called idiotropic vector; see Mittelstaedt 1996) strongly bias spatial orientation judgment (Bringoux et al. 2003). In the present experimental setup we were able to manipulate the visual information while vestibular and somesthetic input remained relevant with respect to gravity. This difference can explain the present progressive motor effect of the visuomotor conflict.

In a previous report we demonstrated that the specific timing of vertical arm movements is due to a direction-dependent planning process that minimizes energy expenditure (Berret et al. 2008). One may expect a rapid recovery of the natural arm horizontal kinematics since horizontal reaching with a timing of a vertical motion is detrimental in terms of movement cost. In particular, the prolonged exposure to a nonoptimal motion and the consequent increasing effort should have pushed the nervous system to recover a more appropriate motor program. On the contrary, movement planning was clearly and gradually affected by the vertical visual feedback toward a less optimal (and more vertical) velocity profile. One explanation of the absence of motor correction from suboptimal to optimal arm movement timing could be that the adaptation to visuomotor conflict consists only in correcting the crucial variable of the task—i.e., the spatial error between the effector and the target position—neglecting the deleterious effect of a suboptimal movement. Since in our experiment task achievement required subjects just to reach the target, with no explicit constraints on movement kinematics, task completion would be achieved by remapping only the visuomotor space, leaving unchanged the temporal pattern of arm motion. This explanation, however, seems contradicted by our previous investigation (Sciutti et al. 2012), which showed an appropriate adoption of a vertical velocity profile when moving vertically and while seeing a horizontal feedback. In such a case the subject both remapped the visuomotor space and appropriately minimized the energy expenditure. The optimal feedback control (OFC) approach (Todorov and Jordan al. 2002) did not predict our results and leaves unanswered an important question: Why to optimize the control of an upward-rotated visual feedback do subjects need to modify their usual horizontal velocity profile? To address this issue we consider the possibility that the CNS, in order to reduce the deleterious effect of the divergent sensory predictions of hand feedback motion (i.e., rightward and upward for kinesthetic and visual inputs, respectively), reweights their combination during the sensory integration process.

This alternative agrees with the assumption that while undertaking sensory motor tasks weighting is used to privilege the most reliable (less variable) sensory information to estimate target and/or motion corrections (Sober and Sabes 2005; Wei 2010). Moreover, previous reports gave evidence of both visual and kinesthetic misperception due to the assignment of high reliability of one of the two sensory sources. For instance, Wolpert et al. (1995) showed that a high weight was assigned to vision during a reaching task where visual and kinesthetic information about curvature were mismatched. Under their perturbation, vision guided subjects' actions even if it produced a misperception of the actual kinesthetic signals (Wol-

pert et al. 1995). Mon-Williams et al. (1997) confirmed the high weight assigned to vision and, more interestingly, showed that the opposite effect is also possible (i.e., kinesthetic signals dominate action and produce visual misperception) as soon as visual information is sparse. Moreover, in our previous investigation (Sciutti et al. 2012) we analyzed how the planning of vertical and horizontal arm pointing movements is affected by a conflicting visual feedback about the end effector. We showed that vision dominates kinesthetic signals (i.e., leading to suboptimal motion) only if the visual feedback is vertical: the reliability of the two different sensory modalities involved in our visuomotor conflict strongly depended on which channel perceived the vertical direction. Accordingly, we speculate that the present sensory context, more specifically the visual vertical one, strongly constrained arm movement temporal structure and the underlying reweighting of visual and kinesthetic signals to guide action.

A Misadaptation Involving an Alignment on an Internal Representation of Gravity

Instead of baseline recovery, the visual effect on arm movement timing increased with repetitions. This progressive kinematic adjustment toward a suboptimal vertical motion implies nonetheless an adaptation process based on error feedback and motor corrections. Therefore, participants should experience trial after trial an error signal related to the relative duration of their acceleration phase (or AD/MD). In the present experimental condition we hypothesize that the error signal is the unsuitable (symmetric) horizontal temporal pattern of the dot displayed along the upward direction. More precisely, the discrepancy between the vertical visual feedback and an internal representation of the timing of a vertical motion would provide the error signal to modify the timing of the horizontal arm movement. In this way the timing of the actual horizontal arm movement (symmetric) would be compared and adjusted trial after trial to a stored upward temporal pattern (asymmetric). Actually, in our control experiment we found evidence in favor of such a comparison. On the basis of the visible acceleration phase of an upward motion participants were able to infer the duration of the missing deceleration phase that agreed with the kinematic of upward arm movement. More precisely, the inferred deceleration duration was always longer compared with the acceleration phase. Therefore, participants exhibited the capacity to recall kinematic details of vertical body movements in the temporal domain, a result in agreement with several previous investigations (Gavazzi et al. 2013; Pozzo et al. 2006; Saunier et al. 2007).

An Erroneous and Suboptimal Adaptation Without Memory

The progressive modification of the actual horizontal temporal pattern toward a vertical pattern was not followed by any consistent aftereffects, which usually highlight an adaptation process (Karniel et al. 2002; Shadmehr and Mussa-Ivaldi 1994). In other words, the spontaneous recovery when conflict was removed did not reflect the adaptation rate: the participants adapted slowly and deadadapted immediately. A shift from one dynamic model to another preexisting one might explain the lack of aftereffects. For instance, the MOSAIC model (Wolpert and Kawato 1998) proposed that the CNS composes and deals with multiple models selected with respect to task requirements

in order to facilitate rapid and effective switching between them. However, in the present case the horizontal kinematics was only partially assimilated to that of a vertical motion (60% adaptation), a value incompatible with a complete shift from one model to the other (as in Welch et al. 1993). A reweighting process with respect to the sensory context would rather explain the transient adoption of different arm movement timings. Such a possibility has been previously modeled according to the principles of maximum likelihood estimation (see Ernst and Bulthoff 2004 for a review), resting on the assumption that sensory signals that contain redundant information should be combined based on the expected variability of each channel to maximize the probability of the most reliable prediction about sensory feedback (Ernst and Banks 2002; Körding and Wolpert 2004; Welch et al. 1993). Moreover, in a previous investigation (see Papaxanthis et al. 2005) we found that exposure to microgravity transiently affected velocity profiles of upward and downward movement. However, after repeated practice the differences in kinematic and the torque profiles recorded during upward and downward movements decreased, suggesting that the CNS adapts motor plans to novel environments. In that case, the visual feedback was also vertical but the movement kinematic adapted to the new mechanical context in agreement with OFC, which predicts a symmetric velocity profile. However, in contrast with the present experimental setup, in weightlessness the vestibular organs (the only sensory organs giving a direct measurement of the gravity force field) detected the lack of gravity. In this context, our results suggest that subjects are particularly confident in the vertical nature of the motion (i.e., give to vertical visual input a higher weight), although their execution is performed on the horizontal plane.

The priority given to the visual vertical feedback when sensory inputs are conflicting may result from the continuous and predictable effect of gravity on the body and its hard-wired integration along evolution process. Specifically, like the passage from day to night, the gravitational field created by the mass of the Earth makes up one of the ethological constraints that permanently act upon living organisms (Pozzo et al. 1998). This impact is well illustrated by the widespread role of visual vertical/gravity on spatial and temporal aspects of human activity. For instance, a large body of evidence demonstrates that the gravitational component plays a fundamental role in human action production (Crevecoeur et al. 2009; Gaveau and Papaxanthis 2011; Papaxanthis et al. 1998a) and perception of living (Troje and Westhoff 2006) and nonliving (McIntyre et al. 2001; Senot et al. 2012; Zago et al. 2009; Zago and Lacquaniti 2005) object motion. Therefore, the probability to deal with gravity is strong even when its involvement is artificially created and also the processes of motor adaptations are shaped by an internal model of gravity.

GRANTS

This work was supported by the CAPES-COFECUB (project no. 819-14) and the Conseil Régional de Bourgogne (Projet Pari "Correlats Neuronaux").

DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

AUTHOR CONTRIBUTIONS

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

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