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Vision of the hand prior to movement onset allows full motor adaptation to a multi-force environment

C. Bourdin ^{*}, L. Bringoux, G.M. Gauthier, J.L. Vercher

UMR 6152 “Mouvement & Perception”, CNRS & Université de la Méditerranée, Faculté des Sciences du Sport,
163 av. de Luminy, CP 910, 13288 Marseille Cedex 09, France

Abstract

In everyday life, because of unexpected mechanical perturbation applied to the hand or to the whole body, hand movements may become suddenly inaccurate. With prolonged exposure to the perturbation, trajectories slowly recover their normal accuracy, which is the mark of motor adaptation. However, full development of this adaptive process in complete darkness has been recently challenged in a multi-force environment. Here, we report on the effectiveness of static hand position information as specified through vision prior to movement onset on the adaptive changes, over trials, of pointing movements performed in a gravito-inertial force field. For this, subjects seated off-center on a platform rotating at constant velocity, were either confined to complete darkness (No Vision Session, NV) or provided with vision of the hand resting on the starting position prior to movement onset (Hand Vision Prior to Movement Session, HVPM). Overall, our results showed that adaptation to the centrifugal force was very rapid, and allowed subjects to demonstrate appropriate motor control as early as of the very first trials performed during the rotation period, even in the NV condition. They also showed that the integration by the Central Nervous System (CNS) of visual and proprioceptive information prior to the execution of a reaching movement allows subjects to reach full motor adaptation in a multi-force environment. Furthermore, our data confirm the existence of differentiated motor adaptive mechanisms for centrifugal and Coriolis forces. Adaptation to the former may fully develop on the basis of an *a priori* coding of the characteristics of the background force level even without visual information, while the latter needs visual cues about hand position prior to movement onset to take place.

Keywords: Multi-force environment; Visuo-manual reaching; Vision; Proprioception; Motor adaptation; Internal model

1. Introduction

Accurate motor control allows human beings to produce goal-directed movements with great accuracy in a large variety of environmental conditions. In particular, a well-known characteristic of 2D reaching movements is a smooth, almost straight trajectory from the starting to the ending point [24]. When an unexpected mechanical perturbation displaces the hand from its intended straight-line trajectory, the reaching movement becomes suddenly inaccurate. However, if the perturbation remains, the resulting hand path errors are rapidly compensated over subsequent movements by an adaptive control mechanism (i.e. motor adaptation [20,29]), so that trajectories converge towards the unperturbed straight-line path. This is the mark

of motor adaptation which allows the system to anticipate or counteract the disturbing force and maintain or restore accurate performance. Over the past 20 years, the notion of an internal model,¹ a system which mimics the behavior of a natural process, has emerged as an important theoretical concept in motor control [17,36]. The related central idea is that the brain uses internal models of limb dynamics to compensate for feedback delays, to plan movements and specially to adapt to environmental conditions. The optimization of a motor performance is then based on the accuracy of the sensory representations of the initial conditions, on the ability to update the internal models to produce the adapted motor commands and on the accuracy of the online control system. The purpose of the present study concerns the sensory representations of the initial conditions. We ques-

¹ The term “internal model” is used to emphasize that the CNS is modelling the sensorimotor system, but not to design a model of the CNS.

tion the incidence of a combination of visual and proprioceptive information available before the triggering of a movement carried out in a multi-force environment on the adaptive processes to the perturbing forces.

Many studies have focused on the motor adaptation phenomenon, showing that adaptation can occur without visual feedback (i.e. with somatosensory feedback alone [5,8,18,26,32]). For example, in an experiment conducted with congenitally blind subjects, Dizio and Lackner [9] have shown that complete motor adaptation to the disturbing effects of the Coriolis force is based on the proprioceptive sensing of the limb position.

Most of the studies which have demonstrated the existence of motor adaptation to perturbing forces were conducted in a single-force environment, in which the unusual force was either movement-independent, as inertial forces, or dependent, such as the Coriolis force [9,29]. In this type of environment, motor adaptation is based on adaptive force representations encoded within a limb-based coordinate system dominated by proprioceptive input [9]. Results from previous studies carried out within a single-force environment [5,20] indicated that the compensation for the disturbing effects of the Coriolis force (or more generally for the effects of a velocity-dependent force) can be achieved through learning, by generating an internal model of the dynamics, that is, a neural representation of the relationship between motor command and movement [17]. In a single-force environment, this updating process has been shown to rely on proprioceptive information [9]. This robust and remarkable ability of the Central Nervous System (CNS) to compensate for and adapt to perturbing forces has been recently challenged using a multi-force environment, where subjects are submitted to the concomitant actions of the Coriolis and the centrifugal forces. The Coriolis force is related to the inertial dynamics of the limb, and by extension is a movement-related “dynamic” component of the complex environment [19]. In contrast, the centrifugal force is a gravity-related static component of the multi-force environment. The experiments of Lackner and Dizio [21] and Bourdin et al. [2] performed in a multi-force environment showed that afferent feedback from the limb proprioceptors did not seem to be sufficient for the reaching movements to recover straight, smooth and accurate characteristics over time. In other words, in the absence of visual cues, subjects were unable to adapt their reaching movements to the complex force field. However, previous experiments did not allow a full understanding of the reason for pointing movements performed with an unseen hand in a multi-force environment to remain inaccurate after several trials.

To explain the low level of adaptation when visual feedback of the arm is prevented while reaching, some authors have hypothesized that proprioceptive information used to provide limb position information is altered or misinterpreted in a modified background force environment. This might be caused by a mediation effect of the centrifugal force, seen as an extrinsic modification of the environment or by a drift of the limb proprioception signal [3,35]. This degraded position sense could lead to an inaccurate determination of the position of the reaching hand at the initiation, execution and/or end of the movement. As

limb position sense is essential for the control of the movement, especially when vision is not available, its degradation may explain the weakness of motor adaptation. To test this hypothesis, we requested subjects to reach towards memorized targets within a multi-force environment. Visual feedback of hand and workspace was given prior to, but not during the movement. Giving accurate visual feedback of the limb only at the start position thus provides no information on any alterations in trajectory or final position caused by an external force. Nevertheless, we make the assumption that static visual information of the limb could improve the accuracy of the sensed position of the hand, allowing for motor adaptation to take place. This hypothesis comes from previous work showing that the hand can be localized in space through both vision and proprioception [15,16]. Converging coherent visual and proprioceptive signals in the CNS may allow for a more precise sensory representation [25,33]. Indeed in the cat, discharge rate of neurons of the superior colliculus that normally fire for visual or auditory stimuli increase when congruent auditory and visual stimuli are provided [23]. Other neurophysiological data from monkey studies show that the position of the arm is represented in the ventral premotor cortex through visual and proprioceptive cues converging onto the same neurons [15]. In conditions with combined visual and proprioceptive signals leading to an enhanced sensory representation, movement performance becomes optimal. Then, allowing subjects to see their starting hand position may have an enhancing effect on the accuracy of the estimation of the initial hand location in a multi-force environment. This may be a way to compensate for the hypothetical misinterpretation of limb position sense mentioned earlier. Previous experiments have already suggested that endpoint errors observed in visual open loop target pointing reflect, at least partly, the systematic bias in the kinesthetic estimation of the initial hand location [6,27,34]. In the same way, visual information prior to movement onset might be also used for improving the vectorial coding of the planned movement [25]. As a consequence, improving the estimation of the initial hand location through static visual cues may further improve performance in the reaching movements performed in a multi-force environment.

Hence, the main goal of the present study was to investigate the role of static hand position coding as concomitantly specified through vision and proprioception, prior to movement onset, on the adaptative changes of the trajectory and accuracy of pointing movements performed in a gravito-inertial force field. We hypothesize that the combination of visual and proprioceptive signals before the execution of a reaching movement will allow the CNS to reach full motor adaptation to a multi-force environment, even if the presented visual cues were not directly informative on the level of performance achieved. The term multi-force environment is used to describe an environment in which the subjects experience both inertial forces simultaneously. A further intent was to confirm the existence of two distinct mechanisms for motor adaptation in response to the centrifugal force and to the Coriolis force. Here we made the assumption that these mechanisms are based on different sensory inputs and do not share the same time course.

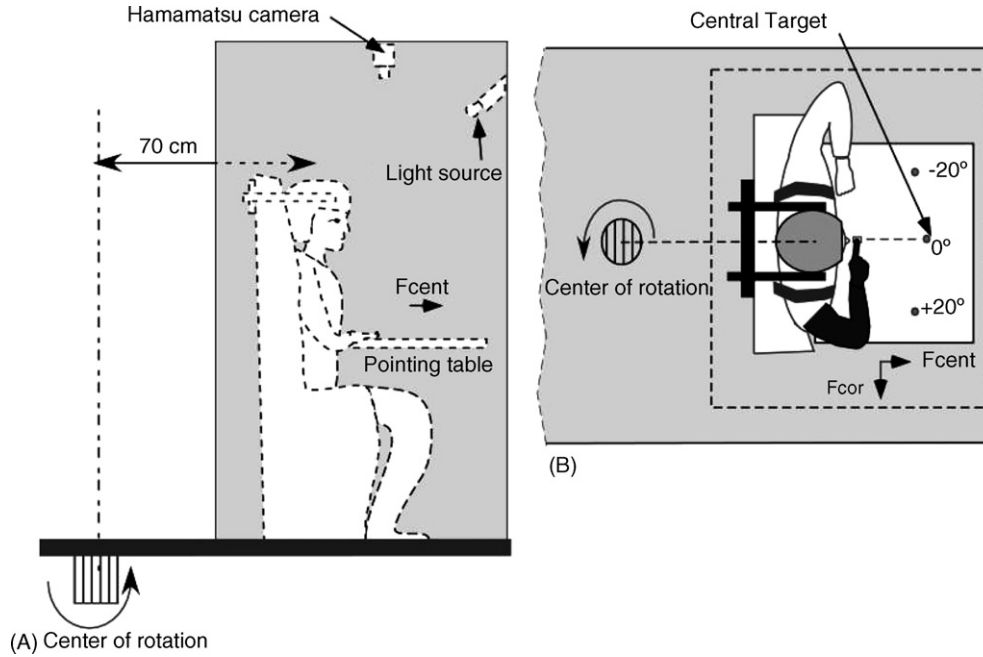


Fig. 1. Experimental set-up. Subjects were seated tangentially to the rotation direction of a platform. A cockpit-like structure prevented subjects from seeing the experimental room during rotation in the HVPM session. The subject's head was positioned in a crash helmet firmly fixed to the chair to prevent any head movement.

2. Methods

2.1. Subjects

Ten right-handed undergraduate students (six men and four women; mean age: 21.6 years) participated in this study. They gave their written informed consent and the study was approved by the local Ethics Committee. They were all naïve with respect to the scientific purpose of the study. All subjects had normal or corrected-to-normal vision, and were devoid of vestibular and known proprioceptive deficits.

2.2. Experimental set-up

A schematic representation of the general experimental set-up is presented in Fig. 1. Subjects were comfortably seated in a bucket seat positioned tangentially to the rotation direction of a rotating platform, at 70 cm from the center of rotation. The seat was in a cockpit-like structure which prevented viewing the walls of the experimental room (Fig. 1a). In this structure, a light source placed slightly above the subject was used to illuminate the workspace and the arm when required. The platform was rotated counterclockwise with a constant angular velocity of $120^\circ/\text{s}$ (20 rpm), reached in 110 s through a parabolic profile. The mean acceleration magnitude was $0.9^\circ/\text{s}^2$, linearly decreasing from $1.96^\circ/\text{s}^2$ at $t = 0-0^\circ/\text{s}^2$ at $t = 110$. This value was above vestibular canal thresholds reported in the literature [14]. At the constant speed of $120^\circ/\text{s}$, the direction of the gravito-inertial vector (G_i , Pythagorean sum of gravitational and centrifugal forces) was significantly changed (17.38°) but not the amplitude (1.05 G). A four-point safety belt was used to limit any trunk movement during the rotation phase. In addition, a crash helmet, firmly attached to the chair, was used to immobilize the subject's head in a comfortable position (the position of the helmet was adjusted to the height of the subject prior to the beginning of the experiment).

A table positioned horizontally in front of the subject, at navel level, was equipped with three red light emitting diodes (LEDs) used as targets (Fig. 1b). The LEDs were positioned along a 55 cm-radius circular arc from the subject's cyclopean eye. One LED was positioned in front of the subject, and the two others 20° to the left and to the right as seen from the subject's eye. The target LEDs were embedded into the pointing board and covered with a thin Plexiglas plate, preventing tactile feedback while pointing. A small switch defining the precise starting position for all subjects was placed on the table, 20 cm in front of the subject's navel.

Subjects were asked to reach from the starting position to one of the three visual targets with their right hand, as accurately as possible. Each target was flashed for 150 ms in complete darkness, i.e. subjects had no visual feedback during the execution of their movements. No explicit instructions regarding hand path were given. However, subjects were required to reach from the starting position to the final target position in less than 400 ms. Such instructions concerning duration of movements were provided in order to maintain movement time within a reasonably short and repeatable range since movement velocity determines Coriolis force amplitude. The experimenter had feedback on movement duration after each trial and was provided with a way to reject all trials with movement time longer than 400 ms. If rejected, the trial was repeated at the end of the running condition. Subsequent analyses confirmed indeed that subjects executed the task according to the instructions.

2.3. Experimental protocol

The subjects participated in two experimental sessions separated by at least 7 days. In one session named Hand Vision Prior to Movement (HVPM), the background light was turned on for 1 s before the presentation of the target to allow the subjects to have full vision of their hand resting on the starting position and of the workspace. In a second session named No Vision (NV) no light was available before and during pointing so that subjects performed the full task in complete darkness. The order of execution of the sessions was randomly selected for each subject.

Each experimental session consisted in three blocks of trials performed in three different conditions, for a total of 150 trials:

- *PRE-rotation condition*: Subjects executed 30 pointing movements (10 trials per target) without rotation of the platform providing pointing baseline in the normal gravity field.
- *PER-rotation condition*: Subjects performed 90 responses (30 trials per target) during platform rotation.
- *POST-rotation condition*: This condition was strictly identical to the PRE-rotation condition, and was used to evaluate the level of adaptation reached, as a result of the pointing movements executed during the rotation.

The three targets were randomly presented within each condition. Both the onset and offset of the platform rotation produced a rotatory nystagmus. Still, to eliminate its short-lasting effects, pointing movements in PER-rotation started

90 s after the platform had reached a constant velocity. For similar reasons, the last set of pointing movements (POST-rotation) was only initiated 90 s after the end of the rotation. Each experimental session lasted approximately 45 min, within which rotation phase of the platform lasted approximately 13 min.

The pointing index finger position was recorded at a sampling frequency of 200 Hz by means of a matrix of small infrared-emitting diodes positioned on top of the fingertip associated to an infrared-sensitive camera firmly attached to the platform, 1 m above the pointing table (Hamamatsu Motion Monitoring System). The analog output signal had a spatial resolution of 0.2 mm.

2.4. Data analysis

Task performance was quantified using measures that evaluated different aspects of hand path kinematics. We removed from the analysis the movement trials performed towards left and right targets used as lures to eliminate artifacts associated with the specific direction of the movements towards these targets relative to the main direction of the centrifugal force and the Coriolis force. Hence, only the reaching movements towards the central target were analyzed.

Firstly, velocity profiles were visually inspected to identify movement initiation and termination. Movement onset was defined as the time at which the tangential velocity reached 4 cm/s. Similarly, the first point in time for which the velocity dropped under 4 cm/s was considered as the end of the movement. We characterized each hand final position in terms of lateral and longitudinal errors. The standard deviation of both variables was used to characterize the evolution of its variability between sessions and conditions.

We computed the pointing movement path maximal deviation from straight line to the right and to the left and corresponding time of occurrence. This was achieved by connecting for each pointing movement starting and ending positions (irrespective of the accuracy of the endpoint position). Maximum deviation to the right and to the left, in cm, was used to characterize each pointing path curvature as we assumed that subjects intended to make straight-line reaching movements in the absence of explicit instructions [24]. Endpoint longitudinal and lateral errors were adjusted by using values obtained in the PRE-rotation condition as baseline for comparison with PER- and POST-rotation movements. Kinematic variables were submitted to a two sessions (HVP and NV) \times three conditions (PRE-rotation, PER-rotation and POST-rotation) analysis of variance (ANOVA) with repeated measures on all factors. Specific effects were evaluated by a Newman-Keuls post hoc comparison. Null hypotheses were rejected when probabilities were below the threshold of 0.05.

3. Results

The experimental results are summarized in Table 1.

3.1. Movement time depends on the condition of rotation and on prior-to-movement visual information

Mean movement time was 355 ms. Moreover, movement time varied according to the experimental conditions. The ANOVA yielded a main effect of rotation ($F(2,18) = 7.1148$, $p < 0.005$). Movement time was statistically similar between PRE-rotation and POST-rotation (361 ms on average) but was significantly

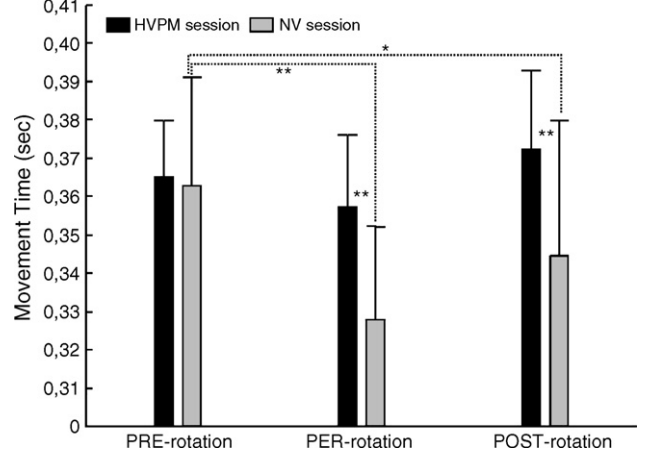


Fig. 2. Mean movement time and standard deviation (S.D.) as a function of experimental session and condition of rotation.

reduced during rotation (342 ms on average). Moreover, the ANOVA yielded a significant interaction between experimental session and condition of rotation ($F(2,18) = 4.5555$, $p < 0.05$; Fig. 2). When the platform was still (PRE-rotation), movement time was similar in HVP and NV sessions (mean movement time: 363 ms) ($p > 0.05$). In the PER-rotation condition, movement time was statistically shorter in NV (327 ms) than in HVP (362 ms) session ($p < 0.005$). Movement time was significantly greater in HVP session (372 ms) than in NV session during the POST-rotation condition (344 ms) ($p < 0.005$).

While pointing towards the central target during rotation, subjects were submitted to the concomitant actions of the centrifugal and the Coriolis forces. Because of the position on the platform relative to the center of rotation, the evolution of the subjects' endpoint longitudinal errors describes the way they counteract the perturbation induced by the centrifugal force, whereas the evolution of the endpoint directional errors is an indication as to the way they took into account over time and trials the perturbation induced by the Coriolis force.

3.2. Endpoint longitudinal error

Since the direction of the centrifugal force is parallel to the main direction of the pointing movements towards the aimed (central) target, the changes in the endpoint longitudinal error over the different experimental sessions and conditions illustrate the way subjects integrated the centrifugal force in their pointing movements. Close analysis showed no significant longitudinal

Table 1

Averages and standard deviations of movement times, endpoint lateral errors, maximal rightward deviations, maximal leftward deviations in each condition and session

	HVP session			NV session		
	PRE-rotation	PER-rotation	POST-rotation	PRE-rotation	PER-rotation	POST-rotation
Movement time (ms)	363 \pm 47	356 \pm 46	372 \pm 47	360 \pm 55	327 \pm 48	345 \pm 60
Endpoint lateral error (mm)	0.076 \pm 0.81	0.90 \pm 2.34	-1.98 \pm 2.72	-0.06 \pm 1.42	2.73 \pm 3.1	-0.89 \pm 3.15
Maximal rightward deviation (mm)	0.76 \pm 0.59	0.42 \pm 0.58	1.24 \pm 0.90	0.84 \pm 0.72	0.43 \pm 0.46	0.94 \pm 0.8
Maximal leftward deviation (mm)	0.62 \pm 0.59	1.70 \pm 0.87	0.57 \pm 0.66	0.63 \pm 0.6	1.33 \pm 1.12	0.57 \pm 0.69

error as a result of rotation. Indeed ANOVA performed on the longitudinal errors showed no significant effect of condition and session and no significant interaction ($p > 0.05$). Whatever the experimental session and the condition of rotation, the averaged endpoint longitudinal error remained small and constant over the trials (on average, -0.07 cm).

3.3. Endpoint lateral error depends on the visual condition

While pointing towards the central target during rotation, subjects were submitted to the concomitant actions of the centrifugal and the Coriolis forces. Because of the position on the seat relative to the center of rotation, the evolution of the subjects' endpoint lateral error is an indication as to the way they took into account, over time and trials, the perturbation induced by the Coriolis force. Indeed, because the Coriolis force develops perpendicularly to the direction of the reaching movements in the movement plane, we expected the finger endpoint trajectories to be deviated to the right of the target position. A decrease of this error over the course of the trials can be regarded as a proof for adaptation.

The ANOVA performed on this error yielded a significant effect of condition ($F(2,18) = 22.44$, $p < 0.001$). Post hoc comparison showed that the error made was statistically different between each condition of rotation. Accuracy observed in the PRE-rotation condition decreased strongly in the PER-rotation condition ($p < 0.05$). Indeed, as expected during rotation, large deviations of the final pointing positions were observed to the right (1.79 cm on average), that is, in the direction of the Coriolis force. After rotation, subjects exhibited post-effects, characterized by pointing movements deviated to the left of the aimed target (on average -1.45 cm to the left of the target). These results confirm previous results obtained in similar experimental conditions [2,21] and establish the effect of the perturbation induced by the inertial forces.

The ANOVA also unveiled a significant interaction between experimental session and condition ($F(2,18) = 4.2014$, $p < 0.05$; Fig. 3) on the endpoint lateral error. The significant difference in

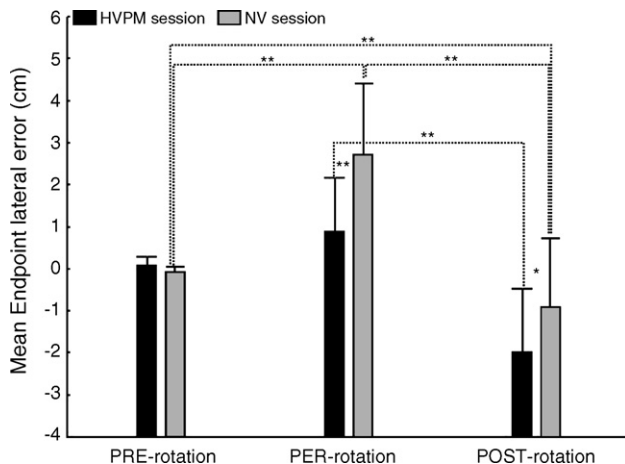


Fig. 3. Mean endpoint lateral error and S.D. as a function of experimental session and condition of rotation.

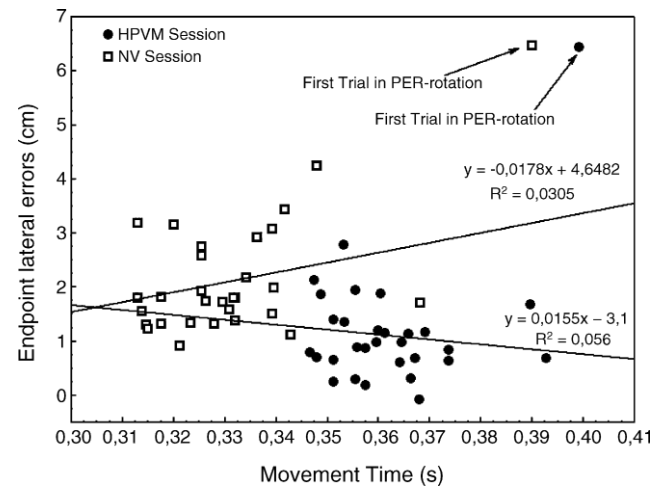


Fig. 4. Mean endpoint lateral error as a linear function of movement time. Computation of the regression linear functions was made without including the first trial of the PER-rotation condition.

endpoint directional accuracy between PRE- and PER-rotation conditions was not observed in the HVPM session. Post hoc revealed that subjects, who were provided with static visual information (HVPM session), exhibited similar endpoint lateral error in PRE (0.08 cm) and PER conditions (0.87 cm) ($p > 0.05$), whereas subjects performed large error to the right of the target during rotation in NV session (2.73 cm) ($p < 0.005$). Post hoc comparison also revealed that error made during rotation of the platform was significantly greater during NV session than during HVPM session ($p < 0.005$). Fig. 3 shows the average changes in endpoint lateral error in the PER- and POST-rotation conditions as compared to the PRE-condition readings, in the two sessions. After rotation, subjects exhibited a post-effect characterized by an error directed to the left of the target. The post-effect was larger in the HVPM (-1.99 cm) than in the NV session (-0.91 cm) ($p < 0.05$).

Results present in Figs. 2 and 3 show simultaneous modifications of movement time and endpoint lateral error during PER-rotation condition for both experimental sessions. What is the relationship between both results? Is the level of accuracy directly determined by movement time, or are these two variables dependant from the same and more general process. To give a satisfactory response, we represented the endpoint lateral error as a linear function of movement time (Fig. 4). The regression analysis yielded a non-significant linear relationship between both variables. Values of R^2 for both experimental sessions suggest that there is no relationship of proportionality between movement time and endpoint lateral error. This result allows us to reject that the evolution of the accuracy was directly and only dependent on movement time. Rather, it seems that the evolution of both analyzed variables reflects in the same way the existence of some other processes.

To further understand the difference between both experimental sessions, we analyzed the time-course of endpoint lateral error. Fig. 5 illustrates the evolution of the averaged endpoint lateral error along the different stages of both experimental sessions. It clearly shows an abrupt increase of the lateral error in

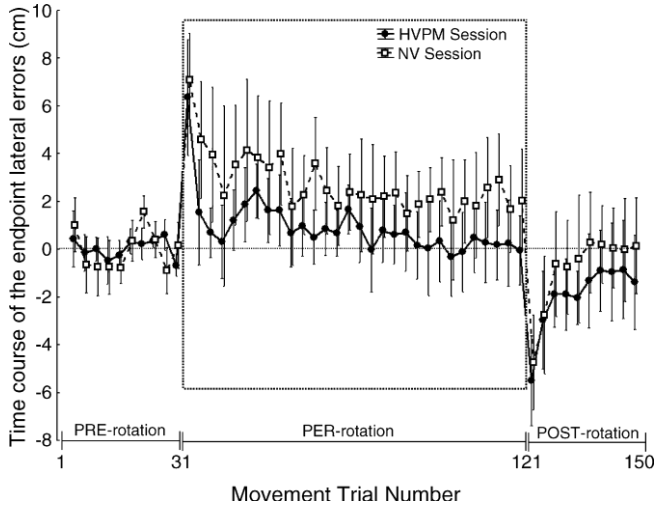


Fig. 5. Time course of endpoint lateral error as a function of trial number and experimental session averaged over subjects. Dotted rectangle delimits the PER-rotation phase.

the first trial performed during rotation (more than 6 cm to the right of the target), whatever the experimental session. Following this first trial, carried out in the newly experienced force field, the evolution of the lateral error becomes remarkably different between both sessions. When subjects were allowed to see the workspace and their immobile hand before producing the reaching movements (HVPM session), the endpoint lateral error progressively decreased during the rotation of the platform (PER-rotation condition) to rapidly recover the initial level of accuracy (PRE-rotation condition). During NV session, we observed a decrease of the endpoint lateral error during PER-rotation condition with no return to the initial (PRE) level of accuracy. Moreover, this difference in the evolution of the endpoint lateral error during PER-rotation condition between the two experimental sessions is also visible in the POST-rotation condition, in which post-errors decreased to recover the initial level of accuracy (PRE-rotation) in the NV session, whereas they never reached this initial level in the HVPM session.

Assuming that common hand pointing movements develop basically along straight lines (2D pointing movements), rightward deviation from straight line, regardless of endpoint accuracy, may be interpreted as the direct (non or insufficiently compensated) effect of the Coriolis force on the moving arm. To the contrary, leftward deviation from the straight line may be interpreted as an attempt to take into account and occasionally overcompensate the effect of the Coriolis force in order to reach the aimed target [22,28]. Hence, maximal rightward and leftward deviation values and the time at which peak deviations occur may be regarded as measures of the Coriolis effect (first trial) and the result of the subject's attempt to counteract the force (later trials), respectively. To characterize the trajectories in the above terms, we applied to each movement path, as developed in the methods section, an algorithm which extracted maximum rightward and leftward deviations (or either one when only one was present) and their respective time of occurrence.

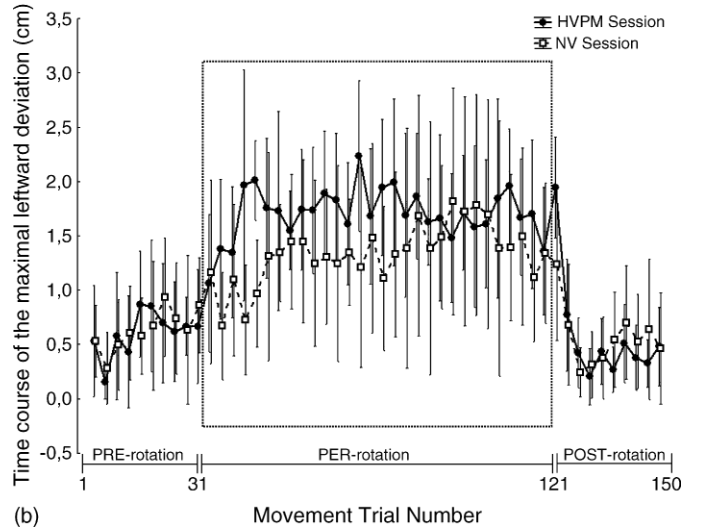
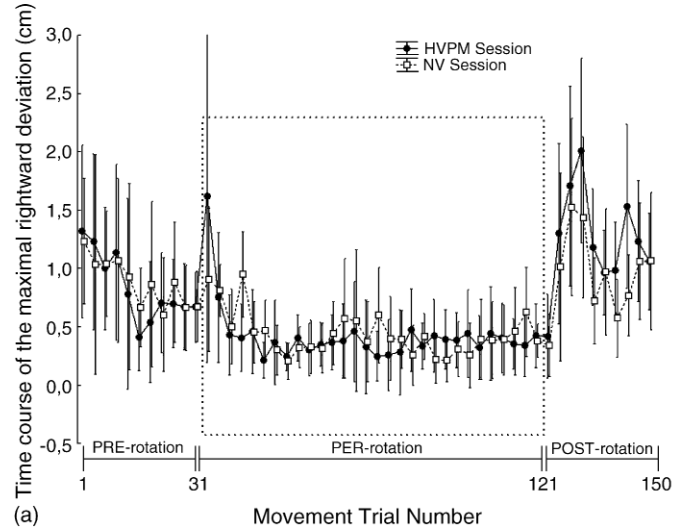


Fig. 6. (a) Time course of the maximal rightward deviation from the straight line as a function of trial order and experimental session averaged over subjects. Dotted rectangle delimits the PER-rotation phase. (b) Time course of the maximal leftward deviation from the straight line as a function of trial order and experimental session averaged over subjects. Dotted rectangle delimits the PER-rotation phase.

3.4. Movement path maximal rightward deviation from straight line and time of occurrence

Fig. 6a shows the maximal rightward deviation changes over trials and conditions. Two major features are worth quoting, one occurring at the beginning of the rotation in the HVPM session, and the other at the end (both sessions). Indeed, while the rightward deviation was of 0.75 cm in the PRE-rotation condition in both NV and HVPM sessions, the deviation increased to 1.6 cm in the first HVPM session during rotation. Later, in HVPM as well as in NV session, the deviation to the right tended to decrease over the first five trials to stabilize around 0.4 cm. The major change of rightward deviation occurred at the end of the rotation period, where the rightward deviation increased to peak at the fourth trial and later returns near the PRE-rotation value. The ANOVA applied to maximal deviation to the right

of the straight line (irrespective of endpoint accuracy) showed a main effect of Condition ($F(2,18) = 19.340, p < 0.01$). Post hoc comparison revealed that the maximal deviation to the right was smaller in the PER- (0.43 cm) as compared to PRE- (0.81 cm) and POST-rotation (1.09 cm) conditions.

The maximal rightward deviation occurred around middle of the second half of the movement (259 ms on average) for a total movement time around 355 ms.

Overall, these data concerning rightward deviation from straight-line (irrespective of the final position) reflect the online corrections near the end of the pointing movements. These suggest that during the first trial in PER-rotation of the HVPM session, subjects exhibited greater online corrections of their movements than in the NV session. This is also true for both sessions after the rotation of the platform.

3.5. Movement path maximal leftward deviation from straight line and time of occurrence

Fig. 6b shows the changes of maximal leftward deviation over the conditions in the two sessions. Maximal leftward deviation increased in both sessions as a result of rotation, though the increase was slower in the NV than in the HVPM session. During the POST-rotation condition, the first trial maximal leftward deviation remained at the PER-rotation level in both sessions. Over the following three trials, the deviation returned to the PRE-rotation condition value. These observations were confirmed by the statistical analysis. The ANOVA yielded a main effect of condition ($F(2,18) = 33.763, p < 0.005$) on the maximal leftward deviation. Post hoc comparison revealed that maximal leftward deviation from the straight line was greater during the PER-rotation (1.52 cm) than during the PRE- (0.62 cm) and POST-rotation conditions (0.57 cm). Subjects, submitted to the action of the inertial forces, exhibited a movement path which was more curved to the left than when no external inertial forces (no-rotation) were acting. The ANOVA also revealed a significant interaction between experimental sessions and condition of rotation ($F(2,18) = 4.7669, p < 0.05$) on the maximal leftward deviation. The post hoc test revealed no difference between experimental sessions in PRE- and POST-conditions. During PER-rotation, maximal leftward deviation was, in average, greater during HVPM session than during NV session.

Maximal leftward deviation occurred around mid-movement. On average, and for all conditions and sessions, maximal leftward deviation occurred 157 ms after the initiation of the movement, hence in the first part of the movement, since the mean movement time was 355 ms. Moreover, this maximal deviation, which occurred in the direction opposite to the Coriolis force developed very close to the peak of the pointing movement velocity (mean moment of occurrence of peak velocity: 169 ms) that is close to the maximal intensity of the Coriolis force.

4. Discussion

The aim of this study was to investigate the role of static hand position specified through vision prior to movement on the adaptive changes over time of the trajectory and accuracy of

pointing movements performed in a gravito-inertial force field. For this, subjects seated off-center on a platform were requested to perform accurate pointing movements towards memorized targets before, during and after rotation in two conditions: (1) without vision of the hand before, during and after the reaching movements (NV session) and (2) with vision of the hand only at starting position (vision allowed prior to, but not during and after, the pointing movement) (HVPM session).

Before specifically analyzing the effects of static visual information, providing hand position coding, on the adaptive process, it is essential to describe the specific effects of both centrifugal and Coriolis forces (when they apply simultaneously) on the reaching movements and to deduce the way the CNS takes into account these perturbing forces in the NV session. Overall, our results showed that the Coriolis force resulted in large lateral error in the early pointing trials executed after platform rotation onset, while the centrifugal force, the direction of which in our experiment was perpendicular to the Coriolis force, did not result in any endpoint longitudinal error. This result suggests that subjects do not compensate in the same way for the effects of the two inertial forces. This clear differentiation confirms previous results [21], suggesting distinct mechanisms for motor adaptation to the two forces. Our data also confirm recent data obtained by Kurtzer et al. [19] suggesting that “static” gravity-related and “dynamic” movement-related components are separately represented within the CNS. This partitioned organization suggests that at least two different motor adaptation mechanisms react in modifying the motor commands to compensate for the altering effects of the inertial forces.

4.1. Compensation for the effect of the centrifugal force does not need visual information

Our results showed that the altering effects of the centrifugal force were instantaneously compensated so that maximal accuracy in amplitude resulted as early as the first movement executed during rotation, even when no visual cues were available. The central question is how high accuracy was maintained in this condition. To produce accurate behaviors, subjects must have accurately coded the external world. In our conditions, they had to clearly identify the characteristics of the current gravito-inertial force field. Indeed, a new force field developed as soon as the platform was set into rotation. Therefore, before initiating any movements, subjects may have coded the characteristics of this environment through several sensory inputs likely to provide information on the direction and amplitude of the gravito-inertial vector. Vestibular as well as proprioceptive and visceral information allow the subject to sense the external world. Accurate sensing will result in accurate hand movements in all directions as the effect of the centrifugal force is applied uniformly over the whole body (providing the rotation radius is large compared to body size) and not dependent on the velocity of the limb. This form of generalization could represent a very low-cost mechanism to compensate for the effect of the centrifugal force.

In a recent study conducted in a single-force environment, Franklin et al. [11] suggested that adaptation to a novel force field was characterized by an initial increase in the activation

of all muscles, at the same time as the formation or updating of an internal model of the moving limb. They advanced the hypothesis that the motor system may use an impedance controller [4] to generate stability. According to these authors, the impedance controller modifies the impedance (resistance to imposed motion) of the limb by co-contraction of agonist and antagonist muscles without changing net torque. This result was obtained in an experiment in which a manipulandum was used to produce the perturbations. The pattern of stimulation was then quite different from the one we used, because Burdet et al.'s experiment [4] did not include vestibular or graviceptive information. In our experiment, the stimulation was applied to the whole body. It is then even more likely that this complex stimulation will induce a similar increase in stiffness in relation to the constant inertial force field, to limit the disturbing effect of the centrifugal force (but not of the Coriolis force) whatever the direction and the amplitude of the movements to be produced. The centrifugal force applied to the whole body "automatically" triggered an increase of stiffness that preceded the execution of any movements in any direction as early as the first movement executed in the novel force field. This was indeed achieved in the absence of visual cues as demonstrated in our study. According to Franklin et al. [11], the increased activity may have included reflex activity arising from muscle stretch, voluntarily activation during the movement and predictive activation. This speculative argument has to be further tested.

Our results suggest that subjects were able to quickly compensate for and adapt to the disturbing effect of the centrifugal force even in the absence of visual cues. Appropriate sensing of the stimulation prior to any movement allowed the subjects to anticipate for the perturbation. This compensation does not extend to the transient Coriolis force, which applies locally on the moving limb.

4.2. Coriolis force leads to endpoint lateral error in the open loop condition

The results from the NV session confirmed that without any visual information, subjects produced large endpoint lateral errors as a result of Coriolis force and were unable to fully compensate over the trials for its disturbing effect. The partial compensation did not yield PRE-rotation accuracy by far. This result confirms earlier observations by Lackner and Dizio [21] and Bourdin et al. [2]. This transient force relates mainly to the proper dynamics of the moving limb. In fact, during rotation, this force may change the dynamics of the limb which results in a discrepancy between the motor commands and the resulting movements. The persistency of endpoint lateral error does suggest that the motor commands remain maladapted to the dynamical changes of the limb during rotation.

4.3. Subjects need visual information to counteract the altering effects of the Coriolis force

When vision of the hand was allowed before pointing towards the central target, we observed that subjects were able to completely counteract the perturbing effect of the Coriolis force to

retrieve a great level of accuracy. Moreover, the presence of after-effects, manifesting as a pointing error directed in the direction opposite to the direction of the Coriolis force, in movements executed after the rotation, demonstrates that subjects were adapted to the effect of the Coriolis force. This is the first time that full adaptation to the disturbing effect of the Coriolis force in a multi-force environment is observed when subjects have no direct visual information about their movement. Indeed, here visual information was not directly related to pointing position accuracy. Still, presenting visual cues before the movement allowed accurate updating of the internal model of the limb.

How is endpoint directional accuracy reached during rotation with prior-to-movement visual feedback (HVPM session)? Analyses of the changes in the endpoint lateral error and in the trajectories (maximal deviation to the left and to the right) over successive trials are very informative to understand the way subjects compensated for the perturbing effects of the Coriolis force. In fact, maximal deviation to the left, that is in the direction opposite to the direction of the Coriolis force, changed in the course of the first few trials carried out during rotation (after about nine trials including six trials towards the lure targets, see Fig. 6). Moreover, this maximal deviation developed relatively early in the course of individual pointing movements, that is before peak velocity (i.e. the peak of the Coriolis force). The relative early occurrence of the maximal leftward deviation suggests the existence of a compensatory (anticipatory?) strategy to oppose the disturbing effects of the Coriolis force. We make the assumption that this maximal deviation to the left reflects the modification of the motor commands, and consequently, of the internal model updating. Moreover, one striking result on the maximal leftward deviation concerns the first movement performed after the end of rotation of the platform (POST-rotation condition). As illustrated in Fig. 5, subjects initiated their first pointing movement to the left, as if the Coriolis force was still present. How could we explain this result? To our mind, this result simply reflects one of the main characteristics of the Coriolis force, which does not exist before initiating the movement. This suggests that subjects are not able to anticipate that the Coriolis force will be absent after the rotation of the platform. As a consequence, they continue to initiate their movements as if this force will perturb the movement path, leading to endpoint lateral errors to the left of the central target. After this first trial without rotation, subjects became rapidly aware that Coriolis force does not exist anymore and change accordingly the way to initiate their pointing movements.

However, the extent of the modification of the maximal deviation to the left was not sufficient to recover PRE-rotation accuracy. Changes in the maximal deviation to the right of the straight line, which may represent some corrective processes, are also of interest (see Fig. 6). In fact, the results showed that to reach a more accurate final position in HVPM session than in NV session, movement paths were first more deviated to the left (reflecting a predictive control) and then exhibited final corrections (reflecting online control). In other words, the increased maximal deviation to the left was accompanied by corrections of the trajectory at the end of the movement. Both modifications are essential to produce accurate pointing

movements. Therefore, visual information prior to movement seems to facilitate the change in the initial direction of the movement (early modification of the maximal deviation to the left) and to allow final corrections of the movement. This may confirm that presenting visual information related to the starting hand position induces modification in the way that the subjects control and produce their movements. Based on the work of Graziano and co-workers [15,16], we hypothesize that static visual information prior to movement onset may benefit to proprioceptive coding of the limb position. This proprioceptive coding is essential in an experiment in which subjects are required to point towards memorized targets without visual information on the moving limb. Many studies have shown that the initial limb position, what Desmurget et al. [6] called “prior knowledge of the effector physical configuration”, was used to improve movement accuracy through a better (more accurate) encoding of the initial state of the motor apparatus. It has been suggested that the kinematic plan for movement is “formed by combining the visually derived representation of intended final arm orientations with a ‘kinesthetically derived’ representation of initial arm orientations” [10]. In other words, knowledge of the initial arm configuration is necessary to set appropriately the feedforward motor commands (setting the internal model) for generating reaching movements [1,6,7,13,25,27,30].

In an experiment in which the vision of the static hand prior to movement was manipulated, Desmurget et al. [6] concluded that the knowledge of the initial upper limb configuration or position is necessary to accurately plan goal-directed movements. More interestingly, they also suggested that static proprioceptive receptors are partially ineffective in providing an accurate estimate of the limb posture. They hypothesized that static visual information improves the representation provided by the static proprioceptive channel. This visual-proprioceptive integration would lead to a better determination of the initial hand location. Sober and Sabes [31] already showed that the relative weighting of vision and proprioception in the visual-proprioceptive integration depends on both the sensory modality of the target and on the information conveyed by the visual feedback. Because our targets were visually presented, sensory integration was better in the HVPM session than in the NV session, because subjects rely more on the visual inputs concerning arm configuration. In addition, some single-unit recording studies have shown that limb position information influences the neural coding of movement parameters [12], suggesting that coding of movement is made in relation to both intrinsic and extrinsic representations of the initial hand position. Intrinsic representation is mainly based on proprioception and extrinsic representation is mainly based on vision. In our experimental conditions, the accurate initial arm configuration may be reached by integrating visual and proprioceptive information. The increased maximal deviation to the left observed in our experiment, which occurred early in the movement, may confirm this point. In fact, the visuo-proprioceptive integration could lead to a better sensed initial position of the limb (i.e. more accurate) and then to a determination of a more appropriate motor command. In addition and in line with this explanation, the complete motor adaptation may also be reached through a more accurate coding of the endpoint.

In complete darkness as in our experiment, this coding may only be reached via the proprioceptive inputs (targets were flashed hence not visible at the end of the pointing movements). The fact that late corrections (demonstrated by maximal deviation to the right of the straight line arising near the end of the movement) occurred in the HVPM session but not in the NV session may confirm this interpretation. Indeed, viewing the hand before starting a movement may help the subject to more accurately use the proprioceptive signal at the end of the movement to conduct trial-to-trial updating and on-line corrections.

In conclusion, we present evidence that the integration of visual and proprioceptive information before the execution of a reaching movement in a multi-force environment may yield full motor adaptation. It seems plausible that visual information about the hand starting position may allow a recalibration of the proprioceptive signal which constitutes the main signal used to activate the adaptive process. Moreover, our data confirm the existence of distinct adaptive mechanisms reacting to the centrifugal and to the Coriolis force. The former force may be taken into account on the basis of an *a priori* coding of the characteristics of the background force level even without visual information. The latter needs at least visual cues about hand position prior to movement onset to be progressively and fully compensated for.

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