

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

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Received 5 April 2006; received in revised form 13 July 2006; accepted 11 August 2006
Available online 1 September 2006

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 adaptative 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.

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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-

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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.

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