Neuroscience 161 (2009) 589–598

FORWARD MODELS OF INERTIAL LOADS IN WEIGHTLESSNESS

F. CREVECOEUR,[a,b] J. L. THONNARD[b] AND P. LEFÈVRE[a,c*]

[a]*Center for Systems Engineering and Applied Mechanics, Université catholique de Louvain, 4 Avenue Georges Lemaître, 1348 Louvain-la-Neuve, Belgium*

[b]*Rehabilitation and Physical Medicine Unit, Université catholique de Louvain, 53 Avenue Mounier, 1200 Brussels, Belgium*

[c]*Laboratory of Neurophysiology, Université catholique de Louvain, 1200 Brussels, Belgium*

Abstract—In this experiment, we investigated whether the CNS uses internal forward models of inertial loads to maintain the stability of a precision grip when manipulating objects in the absence of gravity. The micro-gravity condition causes profound changes in the profile of tangential constraints at the finger–object interface. In order to assess the ability to predict the micro-gravity-specific variation of inertial loads, we analyzed the grip force adjustments that occurred when naive subjects held an object in a precision grip and performed point-to-point movements under the weightless condition induced by parabolic flight. Such movements typically presented static and dynamic phases, which permitted distinction between a static component of the grip force (measured before the movement) and a dynamic component of the grip force (measured during the movement). The static component tended to gradually decrease across the parabolas, whereas the dynamic component was rapidly modulated with the micro-gravity-specific inertial loads. In addition, the amplitude of the modulation significantly correlated with the amplitude of the tangential constraints for the dynamic component. These results strongly support the hypothesis that the internal representation of arm and object dynamics adapts to new gravitational contexts. In addition, the difference in time scales of adaptation of static and dynamic components suggests that they can be processed independently. The prediction of self-induced variation of inertial loads permits fine modulation of grip force, which ensures a stable grip during manipulation of an object in a new environment.

Key words: precision grip, adaptation, internal models, microgravity.

Motor actions are a fundamental mode of interaction between the human body and the external world. The mechanisms that underlie movement control are commonly described in terms of internal inverse and forward models (Wolpert and Kawato, 1998; Kawato, 1999; Wolpert and Ghahramani, 2000). Inverse models invert the dynamics of the limb in order to map a desired trajectory onto a motor command, whereas forward models predict the sensory consequences of a motor command (Miall and Wolpert, 1996; Davidson and Wolpert, 2005). The modulation of grasping forces with self-induced loads is an example of predictive control mechanisms based on forward models. When the object is held in a precision grip, i.e. between the thumb and the index finger, the grip force (GF) is synchronously modulated with variations in tangential constraints due to the sum of the object's weight and inertial forces (LF, load force). In this case, the absence of a delay in the response of GF to changes in LF is the signature of a predictive mechanism that is conceptualized as a forward model. Adaptation of motor control in general can be seen as an acquisition of appropriate internal models (Wolpert et al., 2001). To date, adaptation of forward models of inertial loads in the absence of gravity has not been demonstrated. Therefore, to address specifically the adaptation of forward models, this study focuses on the GF response to a variation of LF in a micro gravity condition ($0\times g$).

The tight coupling between GF and LF has been thoroughly studied on Earth in various paradigms, such as grip lift (Johansson and Westling, 1984; Westling and Johansson, 1984), horizontal and vertical point-to-point movements (Flanagan and Wing, 1993), and cyclic arm movements (Flanagan and Wing, 1995; Blank et al., 2001; Descoins et al., 2006). Modulation of GF with LF is also very efficient in other contexts such as multi digit grasp (Zatsiorsky and Latash, 2008), or when variations of LF are induced by locomotion (Gysin et al., 2003). In the context of precision grip, the coupling between GF and inertial, elastic and viscous loads induced by linear motors has provided evidence for a forward model of the manipulated object dynamics (Flanagan and Wing, 1997; Flanagan et al., 2003). Similarly, previous studies on the coupling between GF and LF in altered gravity have shed light on the adaptability of GF control in a new gravitational context. Stationary holding (Hermsdorfer et al., 1999) and cyclic arm movements (Hermsdorfer et al., 2000; Augurelle et al., 2003a; White et al., 2005) were performed under a $0\times g$ condition induced by parabolic flights. Under the normal gravity condition, a downward acceleration usually does not produce a negative peak of LF (except in very fast movements where the held load is accelerated faster than gravity); however, it does generate a decrease in tangential constraints resulting from the weight of the manipulated object. Consequently, there is no increase in GF in phase with the downward acceleration. In contrast, under the

*Correspondence to: P. Lefèvre, Center for Systems Engineering and Applied Mechanics, Université Catholique de Louvain, 4 Avenue Georges Lemaître, 1348 Louvain-la-Neuve, Belgium. Tel: +3210472382; fax: +3210472180.
E-mail address: philippe.lefevre@uclouvain.be (P. Lefèvre).
Abbreviations: D^+, positive peaks of load force measured in downward movements; D^-, negative peaks of load force measured in downward movements; GF, grip force; GF_I, increments of grip force; GF_S, static level of grip force; IRED, infrared emitting diode; LED, light emitting diode; LF, load force; U^+, positive peaks of load force measured in upward movements; U^-, negative peaks of load force measured in upward movements.

0306-4522/09 $ - see front matter © 2009 IBRO. Published by Elsevier Ltd. All rights reserved.
doi:10.1016/j.neuroscience.2009.03.025

$0\times g$ condition, negative acceleration produces a negative LF since the weight of the held load equals zero. Therefore, the risk to lose grip stability associated to both positive and negative peaks of LF is specific to the $0\times g$ condition. In a preliminary study, Nowak et al. (2001) performed point-to-point movements in combination with other protocols in micro-gravity and emphasized a change in the pattern of GF in response to LF variations. This finding proves that an adaptation occurs in $0\times g$ condition, but the nature of the adaptive mechanism remains unknown. In particular, the ability to predict the positive and negative peaks of LF was not addressed and it remains unanswered whether the amplitude of the GF modulation is based on a prediction of the inertial loads. There is, to date, no formal proof that such changes in GF modulation in weightless condition rely on internal forward models of inertial loads adapted to the novel gravitational context. The aim of the present study was to provide a quantitative analysis of GF adjustments to variations of LF under the $0\times g$ condition in order to elucidate whether the adaptation is due to an internal forward model.

To this end, we varied the amplitude and direction of discrete point-to-point movements (see Hogan and Sternad (2007) for a definition) and investigated both the time course of GF responses to the variations of LF and the amplitude of the response with respect to the amplitude of LF. In the previous studies investigating oscillatory movements in changed gravity, the change in GF reflected a fine adaptive control, but sensory feedback continuously drove the GF modulation through the repeated cycles of identical amplitude. In addition, the mechanisms controlling rhythmic and discrete movements in altered gravity are different (White et al., 2008). In the context of point-to-point movements performed in $0\times g$, if the LF was predicted in a time-varying fashion and the GF was adjusted accordingly, we expect to uncover distinct GF responses to positive and negative peaks of LF leading to biphasic GF profiles with appropriate timing and amplitude for each individual movement.

EXPERIMENTAL PROCEDURES

Subjects

Eight healthy human subjects (24–37 years old), naive to the purpose of the study and to $0\times g$ conditions, participated in this experiment. All subjects gave their informed consent and received the approval to participate in parabolic flights from their National Center for Aerospace Medicine (class II medical examination). The experiment complied with the European Space Agency (ESA) ethical and biomedical requirements for experimentation on human subjects (ESA Medical Board Committee) and was approved by the local French CPP Committee (Comité pour la Protection des Personnes) in charge of reviewing the life science protocols in accordance with the French law.

Parabolic flight

These experiments were performed during the 43rd and 44th ESA Parabolic Flight Campaigns on board the A-300 0-G aircraft (starting from Bordeaux–Mérignac, France). A parabolic maneuver is composed of three distinct phases: 20 s of hypergravity ($1.8\times g$, pull-up phase) followed by 22 s of weightlessness ($0\times g$) before another period of around 20 s of hypergravity (pull-out phase). The beginning of each $0\times g$ phase is announced by the pilot as the injection point. The aircraft ran a sequence of 30 parabolas per flight organized in six groups of five parabolas separated by 5–8 min pauses. Each subject typically performed the task during 15 parabolas, but due to the unforeseeable nature of the experimental conditions, data could be collected during only eight parabolas for subject S6.

Experimental procedure

The task, illustrated in Fig. 1A, was performed only in the $0\times g$ phases. Four target light emitting diodes (LEDs) were placed along a structure that was vertically aligned with respect to the aircraft floor. The target LEDs were positioned every 15 cm. Data acquisition began at the injection point. The program generated a random sequence of targets at a frequency of 1 Hz. The target sequence was generated such that, at any time, the transition probability from the current target to any of the three remaining targets was equal to 1/3. The subjects were seated in front of the target axis and, during data acquisition, held a manipulandum in a precision grip (mass 800 g, grip aperture 4.5 cm). They were asked to align and stabilize the manipulandum with the current target as fast as possible until the next target was illuminated.

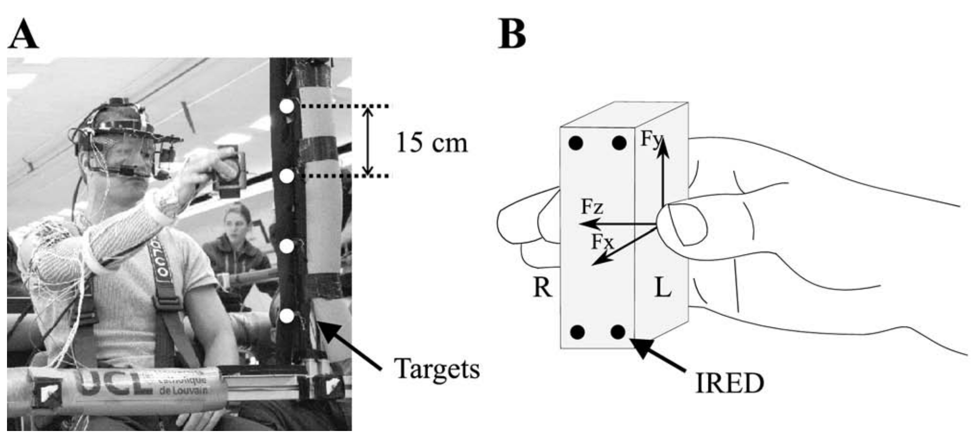

Fig. 1. (A) A subject performing the task. The white disks represent the position of the targets. (B) The subjects held the manipulandum in a precision grip between the thumb and the index finger. Fx, Fy, and Fz are the normal and tangential constraints between the fingers and the manipulandum measured by the left and right sensors (R and L). The four IREDs used to track the position and orientation of the manipulandum are represented by black disks.