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MOVING IN A MULTI-FORCE ENVIRONMENT PRODUCED BY ROTATION: A COMPLEX TASK IN A COMPLEX ENVIRONMENT

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INTRODUCTION

Accurate motor control allows human beings to produce goal-directed movements with great accuracy in a large variety of environmental conditions. In the last two decades, concomitant to the development of modern transportation, and the exploration of space, a great number of studies have analyzed motor control in altered force-field environment. In such particular situations, for example when seated in a car taking a bend, or simply when turning on our own feet around their vertical axis, individuals are exposed to inertial forces that could disturb the normal execution of reaching movements. In practical terms, when an unexpected mechanical perturbation deviates the hand from its intended straight-line trajectory, the reaching movement becomes suddenly inaccurate, leading to potential dramatic effects. It is then crucial to understand how the central nervous system apprehends these forces to keep an acceptable level of performance.

Most of the studies analyzing the way subjects encounter the induced perturbations were conducted in single force fields. The single force fields, named "single-force environments" by Kurtzer *et al.* (2005), were produced experimentally either through the use of a robotized manipulandum (which dynamics characteristics could be adjusted as required during the execution of the hand movements) or by the platform rotation paradigm (with subjects seated at the center of the rotating platform). Independently of the experimental device, results demonstrated that motor adaptation to the only movement-dependent force was easily reached in a few trials, on the basis of the proprioceptive inputs from the moving limb (*i.e.*; Shadmehr & Mussa-Ivaldi, 1994; Lackner & Dizio, 1994). This has been demonstrated in complete absence of visual feedback.

However, generalization to more complex force fields was not possible, and explanations remained limited to the range of single perturbations. Still, a few studies analyzing pointing movements performed in a multi-force environment (composed of simultaneous acting forces) showed that complete motor adaptation could not be reached in the absence of visual feedback (Bourdin *et al.*, 2001; Lackner & Dizio, 1998). These studies were conducted with force-fields which were singularly more complex than the previously described single-force fields. Subjects were not only submitted to the disturbing effect of one movement-related force, but at the same time, to the effect of the centrifugal force exerted on the whole body. As a result, the pattern of stimulation created by the rotation of the platform was considerably more complex than the one resulting in a single-force environment. For example, the background force of gravity produces vestibular stimulation as well as proprioceptive stimulation to the entire body, contrary to what is observed in experiments conducted in a single-force field where sensory stimulations are restrained to the moving limb. This complexity has not been clearly analyzed, and the understanding of motor control in such conditions remains largely partial. More specifically, it remains unknown why full motor adaptation could not be achieved without visual feedback. Many hypotheses have been evoked to explain this discrepancy, going from misperception (visual and proprioceptive) to production of inappropriate motor commands (Bock *et al.*, 1996). We present here a series of three experiments conducted in our laboratory to further explore some problems related to specific multi-force environments as compared to single-force environment on the production, the on-line control and the adaptation of perceptual and motor tasks. Finally, we will discuss more generally the way the central nervous system may represent these forces and integrate their disturbing effects in the specification of the motor commands.

METHODOLOGY

The experimental paradigm (platform rotation paradigm) was identical for the three experiments. Subjects seated on a platform, 70 cm away from the centre of rotation, either facing tangentially or facing radially to the rotation were asked to perform as accurately as possible different perceptive and motor tasks. Subjects performed the tasks with the platform still or rotating counter-clockwise at constant velocity (120°/sec). At this constant velocity, subjects were submitted to a centrifugal acceleration equivalent to 3.07 m.s⁻². The Gravitoinertial vector (Gi) was then tilted by 17.38° from the vertical with an intensity equal to 1.0478 G. In this way, subjects performing reaching movements were submitted to the simultaneously disturbing effects of the centrifugal force or/and of the Coriolis force (movement-related force). With subjects seated tangentially, both forces applied in the same direction (to the right of the main movement direction), whereas the direction of the forces were orthogonally directed when subjects were seated radially on the platform. When subjects were engaged, as in the second experiment, in a perceptive task (no movement required), they were submitted to the only effect of the centrifugal force.

RESULTS

A: The presence of a constant centrifugal force induces head movements and inaccurate sensing of head position.

As already suggested, one of the main differences between experiments producing a single-force environment (Shadmehr & Mussa-Ivaldi, 1994; Lackner & Dizio, 1994) and experiments producing the multi-force environment (off-center rotation; Bourdin *et al.*, 2001; Lackner & Dizio, 1998) is the fact that in the second category, the sensory stimulation is applied on the whole body. In particular, the induced centrifugal force may act on the whole body segments and not only on the moving limb. Our first interest was to evaluate the behaviour of the head, considered as a limb, during rotation of the platform in the presence of constant inertial force. As head holds essential sensory organs, mainly the eyes and the vestibular apparatus, its behaviour may explain part of the

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ing a) and *t al.*, isory may was f the gans, f the reaching errors observed in previous studies (Bourdin et al., 2001). Indeed, visual perception and space perception depend on head orientation in space, and head position must be precisely coded for accurate perception and action in the environment. Therefore the decreased accuracy observed when performing reaching movements in a multi-force environment and the absence of complete motor adaptation could be at least caused by an inaccurate sensing of head position due to the presence of the centrifugal force combining with gravity. To test this prediction, we performed an experiment in which subjects were requested to align their head with their trunk, 30° to the left, 30° to the right or with the gravitoinertial vector, before (control), during (Per-rotation) and after (Post-rotation) offcenter rotation. A control experiment included tests on a tilted chair without rotation (to produce a dissociation between body longitudinal axis and gravity vector). Subjects were seated facing tangentially the rotation of the platform. Two visual conditions were proposed. In the dark condition, subjects were in complete darkness, whereas a visual frame aligned with the trunk axis was presented during the frame condition. Head movements in 6 degrees of freedom were recorded at a sampling frequency of 100 Hz by means of an electromagnetic movement sensor (Polhemus fastrack) placed on the top of the subjects' head. The data showed that, whereas subjects were able to reach the desired positions of the head with great accuracy in the control condition, they made great errors in positioning their head during the rotation of the platform and when they were seated on the tilted chair (Figure 1). As expected with regards to our hypothesis, this work showed that the control of head positioning was partly modified during passive body tilt or offcenter rotation. The data suggested a mismatch between the internal representation of the head positions to be reached and the sensory pattern related to the head positioning in the experimental conditions. This mismatch could find its origin in the presence of a gravitycombined force (here, the centrifugal force), producing a clear dissociation between the body longitudinal axis and the gravitoinertial vector.



Figure 1: Mean errors and SD of head adjustment with the gravitoinertial vector in the four different conditions in the dark on or with the visual frame (adapted from Sares et al., 2004).

Obviously, this discrepancy is no more effective in single-force environment with movement-related force such as the Coriolis force. As shown by several recent studies,

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the control of head positioning appears as a crucial element with regards to the performance, especially when working in a moving environment in normal gravity or in space station.

B: Performance in localizing visual memorized targets is altered in multi-force environment.

Making a reaching movement towards a memorized visual target in complete darkness necessitates to initially represent the spatial location of the target relative to an egocentric frame of reference. The accuracy of spatial location may be influenced by head position. Based on the previous results on head positioning sense, one may question the accuracy of visual target localization in a perturbed gravitoinertial force field with the head maintained aligned with the trunk or free to move. We were particularly interested in assessing the localization accuracy in a purely cognitive task. For this, ten subjects, tangentially seated on the rotating platform, were required to report verbally the spatial egocentric localization of visual targets flashed for 200 msec. Responses consisted in giving both the direction of the flashed targets (by reporting verbally "central", "to the left" or "to the right" of it) and the eccentricity of the presented target (that is the distance in centimetres separating the target from the subjective visual straight ahead). Two experimental sessions were conducted on different days. The head-fixed session was performed with the head kept aligned with the trunk by means of a rest. The head-free session was performed with the head unrestrained (no specific instructions were given to the subjects concerning their head position). The main variable computed to determine the influence of the inertial forces and head position on target spatial localization was the error in localizing the position of the presented targets (Figure 2).



Figure 2: Mean errors and SD in the localization task in both sessions (head-fixed and head-free) during each rotation condition (PRE, PER, POST) (adapted from Prieur et al., 2005).

The results showed that target mislocalization during modified gravitoinertial force background was observed in both head sessions. However, subjects made greater errors in localizing the targets in the head-free session than in the head-fixed session. As a consequence, the change in target position perception could not be only due to head movements in the head-free session. Therefore, mislocalization may also result from a possible Popov, based or the grav inputs), highligh whole b environ both cen **C**: The level the subjects pointing direction describe to demo inertial movema gravityplatforn

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ravitoinertial force de greater errors in xed session. As a only due to head also result from a possible shift of the egocentric reference frame. In line with previous studies (Smetanin & Popov, 1997), we suggested that egocentric localization in poor visual environment is based on an internal representation of the world elaborated on the perceived orientation of the gravitational force (the gravity-related force, through vestibular and proprioceptive inputs), that is from a combined egocentric and geocentric frame of reference. This result highlights the specific effect, at the perceptual level, of the centrifugal force applied to the whole body. This could have consequences on the motor performance in multi-force environment. This effect has been tested more specifically in the next experiment, where both centrifugal and Coriolis forces were clearly dissociated in direction.

C: Centrifugal and Coriolis forces are integrated in different ways.

The previous results did not evaluate the effect of the centrifugal force at the motor level that is during the execution of a motor task. Instead, in the present experiment, subjects seated radially head first on the rotating platform were required to execute pointing movements. This particular position on the platform was used to dissociate the direction of both inertial forces of the multi-force environment. The objective was to describe more precisely the distinct perturbing effects of the forces and more importantly to demonstrate the existence of separate mechanisms underlying adaptation to these inertial forces. Figure 3 represents the time-course of the lateral errors (related to the movement-related force, *i.e.* the Coriolis force) and the sagittal errors (in relation to the gravity-combined force, *i.e.* the centrifugal force) before, during and after rotation of the platform.





The ANOVA suggested that rotation of the platform, which induces a multi-force environment, leads to significant errors in the direction of the Coriolis force but not to errors in the direction of the centrifugal force. As the centrifugal and the Coriolis were not acting in the same direction, it becomes clear that both forces, which induce differentiated sensory stimulation, disturb differently goal-directed movements. By extension, it becomes clear that the central nervous system may encounter the disturbing effects of both forces separately. The centrifugal force was rapidly and completely integrated into the motor commands to allow the subjects to accurately perform goaldirected movements. This was not the case for the Coriolis force, which effects were never totally compensated for during the course of the trials. Moreover, subjects showed a clear (though not significant) reduction of their movement amplitude starting as early as the first rotation trial. Remarkably, a reduction of the movement amplitude means that subjects overcompensated for the disturbing effect of the centrifugal force whereas they were not able to compensate for the disturbing effect of the Coriolis force.

GENERAL DISCUSSION

The purpose of this paper was to review some specific problems encountered by subjects performing perceptive or motor tasks in a multi-force environment to highlight the great complexity of such tasks in this type of environment. Secondly, on the basis of the presented results, we aimed at proposing some new insights on the understanding of motor adaptation processes under specific environmental conditions.

Our hypothesis was that the forces acting in multi-force environment, and specifically the centrifugal and the Coriolis forces, have their own characteristics and applied differently on the human body, so that subjects have to integrate these forces and their disturbing effects in separate ways, probably by using different sensory signals. In a previous paper, we already suggested that motor adaptation to multi-force environment was certainly not based on a unique process but rather based on differentiated processes (Bourdin et al., 2001). The presented results confirm this point of view. Particularly, the last presented experiment suggests that the underlying processes were certainly based on different signals. It seems that the subjects rapidly compensated for the effect of the centrifugal force while they did not for the effect of the Coriolis force. In addition, the time-course of the errors showed that these processes did not share the same time table. It is now clear that a multi-force environment, which is frequently encountered in several everyday life situations, imposes more complex stimulations and new problems to the subjects than a movement-only related force. As a consequence, valid conclusions reached by previous studies analyzing motor control in a single-force environment may remain limited to this type of stimulation.

Suggesting that differentiated processes underlie motor adaptation in a multi-force environment is a first step. But what are these processes? Let us propose some speculative arguments. As already suggested, the Coriolis force (or more generally the movement-related force) applied only on the moving limb. In addition, this force is a transient force because it does not exist before and after the completion of the limb movement. During the movement, this force modifies the dynamics of the limb, and by exten. the re notior has er Wolpe limb d enviro the into adaptat proprio environ the Cor model i percepti partially the prop complete limb seei be in tui egocentri inertial fo proprioce consequer environmc But, ' force appli

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in a multi-force s propose some ore generally the a, this force is a tion of the limb the limb, and by extension, if the motor command remains unchanged, the paths and the final positions of the reaching. But where are the dynamics represented? Over the past twenty years, the notion of an internal modelⁱ, a system which mimics the behaviour of a natural process, has emerged as an important theoretical concept in motor control (Kawato et al., 1987; Wolpert et al., 2001). The related central idea is that the brain uses internal models of limb dynamics to pass over the feedback delays, to plan movements, and to adapt to environmental conditions. Then, the Coriolis force could be integrated and represented in the internal model of the moving limb, which has to be updated to give rise to motor adaptation. In a single-force environment, this updating process, derived from proprioceptive information, is rapid. This is no more the case in a multi-force environment, in which subjects are not able to completely compensate for the effects of the Coriolis force. Proprioceptive inputs seem not to be sufficient to update the internal model in these situations. What could explain this result? The discrepancy on the perceptual level suggested by the two first reported experiments may represent, at least partially, a cause of the inability to accurately update the internal model on the basis of the proprioceptive inputs coming from the moving limb (the only usable signals in complete darkness to detect and correct errors). As these signals coming from the moving limb seem to be misinterpreted by the central nervous system, the related processes may be in turn also disrupted. This misinterpretation could be related to the shift of the egocentric frame of reference we described in the second experiment. In fact, the gravitoinertial force, which modifies the background force level, seems to alter the way proprioception may be used to update the internal model of the moving limb, and as a consequence, may perturb the motor adaptation previously demonstrated in a single-force environment.

But, where and how is the centrifugal force represented? Given that this specific force applies not only on the moving limb but on the entire body, and given that this force is present before any reaching movements, we could suggest that some other sensory signals may be used. Vestibular inputs but also inputs coming from graviceptors may play a major role in coping with such an environment. Their stimulation, as soon as the rotation of the platform begins, may induce a modification of the limb stiffness that could serve to reduce hand-path errors and provide additional stability. This could be achieved through an impedance controller as suggested by Franklin *et al.* (2003). An impedance controller modifies the impedance of the limb(s) by co-contraction of agonist and antagonist muscles without changing net joint torque. This speculative explanation has still to be tested. It can also be suggested that gravity-related force may not be coded in the internal model of the limbs but rather at a more general level of the central nervous system. Experiment analyzing transfer of adaptation could be conclusive on this point.

CONCLUSION

The presented results confirmed that constant inertial-related and "dynamic"/movement-related components are separately represented by the central

¹ The term « internal model » is used to emphasize that the CNS is modelling the sensorimotor system, and that these are not models of the CNS

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nervous system (Kurtzer *et al.*, 2005). It is plausible that the central nervous system could adaptively partition the net force of a multi-force environment into its underlying components. It confirms that performing a motor task in a multi-force environment is a very complex problem to the central nervous system. Some aspects of the problem have been described in this paper.

To conclude, it is worth noting that the nature and the characteristics of our multiforce environments are slightly different from those of the single multi-force environment used by Kurtzer *et al.* (2005). As these authors mentioned, their experimental set-up (which relied on a manipulandum to produce the new force field) was made to study how a <u>single</u> multi-force environment is represented. The term single is of importance. Even if they produced a constant force (as the centrifugal force) and a velocity-dependent force (as the Coriolis force), these forces applied only on the moving limb through the extremity of the manipulandum. The pattern of stimulation radically differs from those used in our experiment and the reached conclusions are certainly limited to the type of stimulation we produced. This complex stimulation pattern has to be more extensively studied to better understand the underlying processes.

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