*Neuroscience* 135 (2005) 371–383

# KINEMATIC AND DYNAMIC PROCESSES FOR THE CONTROL OF POINTING MOVEMENTS IN HUMANS REVEALED BY SHORT-TERM EXPOSURE TO MICROGRAVITY

**C. PAPAXANTHIS,[a]* T. POZZO[a] AND J. McINTYRE[b]**

[a]*Plasticité et Motricité, INSERM ERIT-M 0207, U.F.R S.T.A.P.S, Campus Universitaire, Université de Bourgogne, B.P. 27877, 21004 Dijon, France*

[b]*Laboratoire de Physiologie de la Perception et de l'Action (LPPA) CNRS-Collège de France, 11 place Marcelin Berthelot, 75005 Paris, France*

**Abstract—The generation of accurate motor commands requires implicit knowledge of both limb and environmental dynamics. The action of gravity on moving limb segments must be taken into account within the motor command, and may affect the limb trajectory chosen to accomplish a given motor task. Exactly how the CNS deals with these gravitoinertial forces remains an open question. Does the CNS measure gravitational forces directly, or are they accommodated in the motor plan by way of internal models of physical laws? In this study five male subjects participated. We measured kinematic and dynamic parameters of upward and downward arm movements executed at two different speeds, in both normal Earth gravity and in the weightless conditions of parabolic flight. Exposure to microgravity affected velocity profiles for both directions and speeds. The shape of velocity profiles (the ratio of maximum to mean velocity) and movement duration both showed transient perturbations initially in microgravity, but returned to normal gravity values with practice in 0×*g*. Differences in relative time to peak velocity between upward versus downward movements, persisted for all trial performed in weightlessness. These differences in kinematic profiles and in the torque profiles used to produce them, diminished, however, with practice in 0×*g*. These findings lead to the conclusion that the CNS explicitly represents gravitational and inertial forces in the internal models used to generate and execute arm movements. Furthermore, the results suggest that the CNS adapts motor plans to novel environments on different time scales; dynamics adapt first to reproduce standard kinematics, and then kinematics patterns are adapted to optimize dynamics. © 2005 Published by Elsevier Ltd on behalf of IBRO.**

**Key words: motor planning, velocity profile, internal models, motor adaptation, gravity force.**

Examination of the kinematic features of the limb movements provides useful information about the control processes governing arm movements. Characteristics of hand trajectories that remain the same despite differing task constraints (speeds of movement, amplitudes or direction) or differing dynamic conditions (externally applied forces or changing inertial loads) can indicate what criteria are being applied by the motor system to choose from an infinite number of possible motor plans that could be used to perform a given movement. One such "invariant characteristic" is the stereotypical bell-shaped and symmetrical velocity profile observed for point-to-point movements of the hand. Tangential velocity profiles are approximately symmetric in time; the hand spends as much time accelerating as decelerating, independent of the speed and amplitude of the movement and independent of externally applied loads. Furthermore, the temporal shape of the velocity profile remains relatively constant; for instance, peak velocity (Vpeak) for a given average movement speed is more-or-less the same for a wide a range of movements. It has been proposed that point-to-point movements respect the minimum jerk principle, in which the relative time to peak velocity (TPV) is equal to to 0.5 (equal acceleration and deceleration time) and the ratio of peak to mean velocity (C) is equal to 1.875. The invariance of velocity profiles has been used to argue that hand trajectories are planned to maximize smoothness (minimize jerk; Flash and Hogan, 1985), or to minimize execution variability in the face of signal-dependent noise (Harris and Wolpert, 1998).

Despite the relative invariance of arm kinematics, specific parameters of hand trajectories may nevertheless be modified by changes in the physical constraints of a given movement. For instance, when an upward movement is performed, the hand tends to spend proportionally less of the total movement time accelerating as compared with a movement of equivalent distance and duration performed in the downward direction (i.e. $TPV_{up} < TPV_{down}$). Changing the inertial load on the limb or the speed of the movement, however, has little effect on TPV (Papaxanthis et al., 1998c, 2003). One can infer from this that upward and downward movements are based on intrinsically different motor plans and that movement direction with respect to gravity is therefore one of the criteria used by the CNS to plan and execute movements. In contrast, the C varies systematically with velocity over a range of movements durations (0.35 s to 0.70 s, see Discussion), but is largely insensitive to the direction of movement with respect to gravity (Papaxanthis et al., 2003). Thus, there is a disso-

---

*Corresponding author. Tel: +33-3-80396748; fax: +33-3-80396702. E-mail address: charalambos.papaxanthis@u-bourgogne.fr (C. Papaxanthis).

*Abbreviations:* AD, acceleration duration; C, ratio of peak to mean velocity; Dev, maximum path deviation from a straight line; DF, downward direction, fast movement; DN, downward direction, normally paced movement; I, path linearity; L, straight line; MD, movement duration; RMSD, root mean squared difference; RMSD el, elbow root mean squared difference; RMSD sh, shoulder root mean squared difference; TPV, time to peak velocity; UF, upward direction, fast movement; UN, upward direction, normally paced movement; Vpeak, peak velocity; 0×*g*, microgravity; 1×*g*, normal gravity.

0306-4522/05$30.00+0.00 © 2005 Published by Elsevier Ltd on behalf of IBRO.
doi:10.1016/j.neuroscience.2005.06.063

ciation of gravitational and inertial effects on the kinematic parameters of movements (TPV varies essentially with vertical direction but not speed, C essentially with speed but not vertical direction), suggesting that gravity is treated differently from inertial factors in the planning and execution of a motor command. Such a dissociation of inertial and gravity forces in planning performed by the CNS has also been proposed based on muscle activation patterns of vertical arm movements (Flanders and Herrmann, 1992).

To better understand the way that the brain differentiates between gravitational and inertial forces into the planning process, we studied the effects of weightlessness on the kinematic and dynamic features of vertical arm movements. Previous studies have examined arm movement execution and adaptation during transient perturbations of coriolis (Lackner and DiZio, 1994, 1998) and viscous forces (Shadmehr and Mussa-Ivaldi, 1994; Flanagan and Wing, 1997). As a whole, these studies indicate that the human motor system can learn to compensate for externally applied forces in a predictive, feedforward manner. Based on a number of studies in normal and microgravity conditions (Augurelle et al., 2003; Fisk et al., 1993; Sangals et al., 1999; McIntyre et al., 1998, 2001; Papaxanthis et al., 1998a,b,c; Pozzo et al., 1998; Zago et al., 2004), we hypothesize that gravitational forces might also be explicitly included in the criteria that the CNS uses when planning and executing arm movements. This implies the existence of a *dynamic* (rather than purely *kinematic*) planning process that takes into account the forces acting on the limb. Under this hypothesis, temporal features of the trajectory may differ as a function of movement direction with respect to gravity because the CNS optimizes the movement with respect to the forces acting on the limb. In this case, one would expect limb trajectories between the same two points in space to be altered over time when performed in microgravity, because a new motor plan would be constructed for the new environmental context.

As an alternative hypothesis, the CNS may use motor planning criteria that are independent of external forces. This could be manifested by a dynamic motor plan that optimizes only the inertial forces required by a given movement, ignoring the static forces imposed by gravity. Alternatively, the criteria used to plan the hand trajectory may be purely kinematic in nature, without regard to the forces and torques that must be generated to displace the hand. In either case, the brain must nevertheless account for the effects of gravitational force when generating the motor command used to obtain the intended movement. Accordingly, when suddenly faced with the total absence of gravity, movement trajectories should be temporarily modified until the "internal models" used to generate the desired trajectory can be updated to correspond to the novel environment.

To test these hypotheses we asked human subjects to execute vertical point-to-point arm movements during the $0\times g$ phase of parabolic flight. If kinematic factors are the only pertinent constraints that determine the motor plan selected by the CNS, one would expect that arm kinematics in $0\times g$ to eventually adapt to resemble those seen in normal $1\times g$ conditions, once the motor system has learned to deal with the absence of gravity-induced torque. On the other hand, if motor planning includes the consideration of external forces such as gravity, one would expect to see stable changes in the kinematic and dynamic profiles of upward and downward movements following extensive practice in the $0\times g$ environment. To this end we compared the kinematic and dynamic parameters of these arm movements between normal $1\times g$ conditions, initial exposure to $0\times g$ and after several minutes of practice in the $0\times g$ environment.

## EXPERIMENTAL PROCEDURES

Data presented in this study were taken from experiments made in a normal gravitational environment ($1\times g$) and in microgravity ($0\times g$); the latter achieved during parabolic flights. The experiments were performed on three flights executed on each of three successive flight days. Flights were composed of 30 parabolas, each consisting of three successive phases with respect to normal gravity: i) hypergravity ~$1.8\times g$, ii) microgravity, ~$0\times g$ and iii) hypergravity ~$1.8\times g$. Each phase lasted ~20–25 s, the parabolas were separated by a time interval of ~2 min and a whole flight lasted ~2 h. For a schematic illustration of a parabolic flight profile see Fisk et al., 1993.

### Subjects

Five males, 24–38 years old, participated in these experiments after giving informed consent. All were right-handed, had no previous neuromuscular disorders, and had passed medical tests to qualify for the parabolic flights. Four of them had never before participated in parabolic flights and thus had not previously been exposed to micro- or hyper-gravity conditions. The fifth subject had taken part in one parabolic flight one year prior to the current study. However, we did not detect any difference between his motor performance and that of the other subjects, for either normal or microgravity conditions, and therefore, we did not make a separate analysis for that particular subject.

### Apparatus and experimental setup

Two targets (reflective markers attached to wooden dowels) were fixed in front of subjects along the vertical axis, one 58 cm above the other and centered on the level of the shoulders. Subjects were asked to perform discrete, visually guided, point-to-point reaching movements using their preferred arm (all subjects used their right arm) in two different directions: upward (U) and downward (D) and at two different speeds: normally-paced (N) and fast (F). No instructions were given about the hand's path, arm postures or movement velocity. Movement accuracy was not the primary constraint on subjects during these experiments.

Movements in both normal gravity and microgravity conditions were recorded using an ELITE (BTS, Milan, Italy) optoelectronic system. Two TV-cameras (sampling frequency 100 Hz) were fixed on vertical rigid bars and placed 1 m apart with a 45° angle between them, 2 m from the pointing targets. After three-dimensional calibration (3-D), spatial resolution for measurements of movements in the present experiment was less than 0.5 mm. The motion of the arm was recorded by placing reflective markers (plastic spheres of 0.4 cm in diameter) on the shoulder (acromion), elbow (lateral epicondyle), wrist (in the middle of the wrist joint between the cubitus and radius styloid processes), hand (first metacarpophalangeal joint) and the nail of the index finger.

In order to record arm movements in the same context, experiments in normal gravity and microgravity were performed aboard the aircraft. Arm movements in normal gravity were re-