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ON THE NATURE OF MOTOR PLANNING VARIABLES DURING ARM POINTING MOVEMENT: COMPOSITENESS AND SPEED DEPENDENCE

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Abstract—The purpose of this study was to investigate the nature of the variables and rules underlying the planning of unrestrained 3D arm reaching. To identify whether the brain uses kinematic, dynamic and energetic values in an isolated manner or combines them in a flexible way, we examined the effects of speed variations upon the chosen arm trajectories during free arm movements. Within the optimal control framework, we uncovered which (possibly composite) optimality criterion underlays at best the empirical data. Fifteen participants were asked to perform free-endpoint reaching movements from a specific arm configuration at slow, normal and fast speeds. Experimental results revealed that prominent features of observed motor behaviors were significantly speed-dependent, such as the chosen reach endpoint and the final arm posture. Nevertheless, participants exhibited different arm trajectories and various degrees of speed dependence of their reaching behavior. These inter-individual differences were addressed using a numerical inverse optimal control methodology. Simulation results revealed that a weighted combination of kinematic, energetic and dynamic cost functions was required to account for all the critical features of the participants' behavior. Furthermore, no evidence for the existence of a speed-dependent tuning of these weights was found, thereby suggesting subject-specific but speed-invariant weightings of kinematic, energetic and dynamic variables during the motor planning process of free arm movements. This suggested that the inter-individual difference of arm trajectories and speed dependence was not only due to anthropometric singularities but also to critical differences in the composition of the subjective cost function. © 2016 Published by Elsevier Ltd. on behalf of IBRO.

Key words: arm movement, speed-dependence, optimal control, composite cost, motor planning.

INTRODUCTION

Understanding how the brain controls 3D arm movement is a long-standing issue in motor neuroscience. The complexity of the musculoskeletal system is such that the accurate achievement of athletic tasks but also of the most basic daily life activity constitutes a challenging problem. In particular, the anisotropic distribution of mass, gravity, and interaction torques acting on all degrees of freedom make the upper-limb dynamics highly nonlinear but the brain seemingly overcomes those difficulties effortlessly. Coping with such a complexity requires efficient control strategies and, therefore, the central nervous system (CNS) might internally represent or monitor some critical variables to implicitly value skilled movements such as baseball pitching, overarm throwing or just placing a cup of coffee on a table. What is the exact nature of these variables and computational rules underlying the selection of one trajectory among the infinity of possible trajectories, and whether cells in the motor cortex encode dynamic, kinematic separately or a combination rule of such variables during movement planning remain questionable even though the issue was extensively investigated in neurophysiological studies (Georgopoulos et al., 1982; Mussa-Ivaldi, 1988; Kalaska et al., 1989). In general, tackling this problem is tricky because kinematic and kinetic quantities are tightly linked by the equations of motion and many sensorimotor transformations, through internal models (Kawato et al., 1987; Wolpert et al., 1995), may occur within the CNS before a goal-directed movement is eventually triggered. This question was nonetheless addressed in many behavioral and computational studies, but whether the control of upper-limb motion relies more upon geometrical properties pertaining to the position of body segments and joint angles (i.e. kinematic variables) or upon mechanical properties pertaining to the mass distribution and torques (i.e. dynamic variables) is still a matter of debate (Pagano and Turvey, 1995; Wolpert et al., 1995; Soechting and Flanders, 1998; Darling and Hondzinski, 1999). Isableu et al. (2009) showed that, during a cyclical upper-limb rotation task with a flexed arm (''L-shaped''), subjects exhibited spontaneous changes of rotation axis, switching from a geometrical one (Shoulder–Elbow axis, SE, a kinematic-related parameter) to an inertial one (minimum principal inertia axis, e3, a dynamic-related parameter) when executing the task at a larger speed. Hence, this suggested that the variables represented by the brain to control unrestrained 3D arm movement might combine both kinematic

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Abbreviations: CNS, central nervous system; DoF, degrees-of-freedom; IOC, inverse optimal control; NLP, nonlinear programming problem; OCP, Optimal control problem.

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and dynamic parameters and that, importantly, their interplay may depend on speed.

Interestingly, the optimal control framework precisely makes hypotheses about the variables potentially represented by the brain during motor control (Todorov, 2004). Therefore, the question of which variables are the subject of motor planning can be rephrased in a normative way as follows: what is the nature of the optimality criterion underlying trajectory formation? (see Soechting and Flanders, 1998). In this context, some researchers have argued for kinematic-oriented motor planning (in either extrinsic or intrinsic space) where the nonlinearities of the motion dynamics are just compensated for or suppressed by the brain to preserve limb's stability (Hollerbach and Flash, 1982; Atkeson and Hollerbach, 1985; Sainburg et al., 1995, 1999; Bastian et al., 1996; Gribble and Ostry, 1999). The main advantage of using a kinematic-based motor control would be to simplify control and allow the brain (re)using a common motor pattern to perform movements at various speeds (i.e. "scaling law"). This approach found some experimental support in the literature (Atkeson and Hollerbach, 1985; Gribble et al., 1998). According to this view, speed-independent arm trajectories should be observed (and were actually observed to some extent in several arm reaching studies, e.g. Atkeson and Hollerbach, 1985; Gribble et al., 1998). Other authors have instead argued for dynamic-oriented motor planning where the mechanical limb properties are taken into account and exploited to the greatest extent possible (Dounskaia et al., 2002; Debicki et al., 2010, 2011; Hore et al., 2005, 2011). The advantage would be to utilize all the non-muscular torques originating from the nonlinearities of the limb's dynamics for producing least effort movements and somehow reducing the overall amount of muscle torque (or its mechanical work) to a minimum (Sainburg and Kalakanis, 2000; Dounskaia et al., 2002; Galloway and Koshland, 2002; Hirashima et al., 2007; Berret et al., 2008; Gaveau et al., 2011, 2014). In Wolpert et al. (1995), the authors directly addressed the issue about whether the brain controls movement in kinematic or dynamic coordinates for visually guided movements. They showed that the planning of constrained planar arm reaches was associated with the optimization of a kinematic cost function (i.e. Cartesian jerk) in order to perceive straight endpoint displacements on a screen. However it is known that unrestrained or 3D movements may have very different characteristics(Desmurget et al., 1997; Gielen, 2009) and whether the control of free arm movements also relies more upon kinematic rather than upon dynamic variables remained unclear. For 3D arm movements, evidence was found for a dynamic level of planning as the final arm posture was shown to depend on the initial arm posture in a way that could not be accounted for by any kinematic optimality criterion (Soechting et al., 1995). However, the effect of speed onto the final posture selection, which is a crucial assessment to distinguish between kinematic and dynamic strategies, has not been addressed in that study but experimental studies later revealed an invariance of the final whole-arm configuration with respect to motion velocity (Nishikawa et al., 1999) despite the fact that dynamic motor planning may potentially involve trajectory modifications with respect to speed because of the complex velocity and acceleration-dependent musculoskeletal dynamics.

To reconcile all these findings, the idea of composite cost functions relying upon kinematic, energetic and dynamic variables emerged as a possible avenue. Using inverse optimal control techniques for unveiling optimality criteria and/or rule from experimental trajectories (Mombaur et al., 2009; Berret et al., 2011a) and the free reach-endpoint paradigm for better discriminating between candidate cost functions (Berret et al., 2011a,b, 2014), it was shown that vertical movements starting from different initial positions and executed at a relatively fast pace could be accounted for by a composite cost mixing the angle jerk (i.e. a kinematic variable) and the absolute work (i.e. an energetic variable). However, it remained unclear whether these results would extend to 3D motion and whether a single composite cost could explain movements executed at different speeds. This question is also critical in regards to the understanding of self-paced movements where a cost of time may also combine with trajectory costs and the extent to which the latter varies according to speed instructions is a related open question (see Shadmehr, 2010; Shadmehr et al., 2010; Berret and Jean, in press).

Here we combined a specific motor task with an inverse optimal control methodology to address the above questions. First, we considered free 3D arm movements without a prescribed reach endpoint (the hand could freely move in 3D), which differs from classical point-to-point reaching paradigms; namely we considered a planar target. Thus, participants were free to choose any final finger position on the target plane while only caring about the vertical error (i.e. the task goal). Considering a 4-dof arm, the subjects were thus left with three angles to choose at the movement end. A real life example of this laboratory experiment would be that of placing a cup on an empty table or pushing a door for opening it. Furthermore, we varied the instructed speed to emphasize differences between kinematic versus dynamic control strategies or combination of them and used inverse optimal control techniques to identify the elementary components of the cost function among kinematic, energetic and dynamic quantities as well as their relative weights and speed dependence.

EXPERIMENTAL PROCEDURES

Experimental task

Participants. Fifteen healthy subjects (7 women and 8 men) voluntarily agreed to participate in the experiment. Written informed consent was obtained from each participant in the study as required by the Helsinki declaration and the EA 4042 local Ethics Committee. All of them were right-handed, free of sensory, perceptual and motor disorder, aged 27 ± 4 years, weighted 66

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