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NEURAL CONTROL OF ARM MOVEMENTS REVEALS A TENDENCY TO USE GRAVITY TO SIMPLIFY JOINT COORDINATION RATHER THAN TO DECREASE MUSCLE EFFORT

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Abstract—How gravity influences neural control of arm movements remains under debate. We tested three alternative interpretations suggested by previous research: (1) that muscular control includes two components, tonic which compensates for gravity and phasic which produces the movement; (2) that there is a tendency to exploit gravity to reduce muscle effort; and (3) that there is a tendency to use a trailing pattern of joint control during which either the shoulder or elbow is rotated actively and the other joint rotates predominantly passively, and to exploit gravity for control of the passively rotated joint. A free-stroke drawing task was performed that required production of center-out strokes within a circle while selecting stroke directions randomly. The circle was positioned in the horizontal, sagittal, and frontal plane. The arm joints freely rotated in space. In each plane, the distribution of the strokes across directions was non-uniform. Directional histograms were built and their peaks were used to identify preferred movement directions. The directional preferences were especially pronounced in the two vertical planes. The upward directions were most preferred. To test the three interpretations, we used a kinetic analysis that determined the role of gravitational torque in the production of movement in the preferred directions. The results supported the third interpretation and provided evidence against the first and second interpretation. The trailing pattern has been associated with reduced neural effort for joint coordination, and therefore, we conclude that the major tendency with respect to gravity is to exploit it for simplification of joint coordination.

Key words: 3D arm movements, optimal control, muscle energy, interaction torque, inter-segmental dynamics.

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Abbreviations: DOF, degrees of freedom; GT, gravitational torque; GTC, gravitational torque contribution to PT; IT, interaction torque; MT, muscle torque; MTC, muscle torque contribution to NT; NT, net torque; PT, passive torque; SDP, strength of directional preferences.

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INTRODUCTION

Human movements are performed in the gravitational field, and therefore, gravity needs to be taken into account during movement control. Evidence suggests that the central nervous system possesses a representation of the gravity effect which is used for movement planning and execution (Lackner and DiZio, 1996; Bock, 1998; Gentili et al., 2007; Crevecoeur et al., 2009a; Bringoux et al., 2012; Senot et al., 2012). However, it remains unclear how neural control of movements is adjusted to gravity. Previous research offers three distinct interpretations.

The first interpretation is that muscular control at each joint includes two components, tonic and phasic (Flanders and Herrmann, 1992; Flanders et al., 1994; d'Avella et al., 2008). The tonic component compensates for gravity and eliminates its effect on the limb, while the phasic component produces the required movement. Apparently, the elimination of the gravity effect through the tonic component predicts similar movement characteristics regardless of whether the limb moves in the direction of or against gravity. This prediction is however at odds with findings that kinematic characteristics, including trajectory curvature, magnitude of peak acceleration, time of acceleration, and others, differ between movements performed along with and against gravity (Atkenson and Hollerbach, 1985; Papaxanthis et al., 1998, 2003; Gaveau and Papaxanthis, 2011).

The second interpretation follows from a proposition that muscle effort is minimized during human movements (Hatze and Buys, 1977; Nelson, 1983; Soechting et al., 1995; Alexander, 1997; Prilutsky and Zatsiorsky, 2002; Shimansky et al., 2004; Diedrichsen et al., 2010). The propensity to reduce muscle effort logically suggests that gravity is used to partially substitute for muscle activity. In agreement with this interpretation, it has been proposed that the differences in kinematic characteristics between upward and downward arm movements are a result of minimization of muscle effort. This was supported by Crevecoeur et al. (2009b) with the use of 'control input' (representing total magnitude of all control signals to the muscles) as a cost function, although minimization of a linear combination of 'absolute work of muscle torques (MTs)' and 'integrated sum of squared joint accelerations' was used more consistently (Berret et al., 2008, 2011; Gaveau et al., 2011, 2014).

The third interpretation is that gravity is exploited together with other passive factors to simplify joint coordination. Studies of horizontal arm movements (which are not influenced by gravity) provided evidence that passive interaction torque (IT) caused by mechanical interactions among limb segments is used to organize a simplified pattern of joint coordination (Dounskaia et al., 1998; Dounskaia et al., 2002a,b; Levin et al., 2001; Galloway and Koshland, 2002; Kim et al., 2009) which we will address as a 'trailing joint control pattern'. This pattern includes rotation of a single, 'leading' joint predominantly by MT and the use of IT caused by the leading joint motion for rotation of the other, 'subordinate' or 'trailing' joint (see Dounskaia, 2005, 2010 for reviews). MT at the trailing joint can interfere and adjust its passive motion according to task requirements. However, there is a tendency to minimize this interference and allow the trailing joint to move predominantly passively whenever possible (Goble et al., 2007; Dounskaia and Goble, 2011). The trailing pattern was associated with simplicity of joint coordination. Dounskaia and Shimansky (2016) specified that this simplicity is represented by reduced neural effort for joint coordination which, in contrast to muscle effort, represents the amount of neural resources required for control of multi-joint movements. Using the mathematical theory of information (Shannon, 1948), they assessed the amount of information that needs to be processed to coordinate joint motions (*neurocomputational cost of joint coordination*) and showed that the trailing pattern reduces this cost.

The use of passive IT for simplification of joint coordination suggests that gravitational torque (GT) may be used for the same purpose. Dounskaia and Wang (2014) and Wang and Dounskaia (2015) made this assumption when they examined joint control during 3D arm movements by comparing contribution of MT and total passive torque (PT), PT = IT + GT, to net torque (NT) at each joint. The results supported the use of the trailing joint control pattern during 3D arm movements, thus being in favor of the third interpretation of the role of gravity. However, Ambike and Schmiedeler (2013) also demonstrated the trailing pattern during 3D movements, even though they assumed that the tonic component of MT compensates for GT, as described in our first interpretation. It therefore remains unclear how gravity is used during arm movements.

A possible reason why the results of the studies of 3D arm movements were inconclusive about the role of gravity is that the influence of gravity was not emphasized. Ambike and Schmiedeler (2013) analyzed reaching movements in different spatial directions none of which was strictly upward or downward. Similarly, vertical movements were not performed in the studies of Dounskaia and Wang (2014) and Wang and Dounskaia (2015). However, the experimental paradigm used in the latter two studies opens an opportunity to establish the role of gravity. A free-stroke drawing task was used that consisted in the production of a series of strokes from the center to the perimeter of a circle while selecting stroke directions in a random order. This task was initially tested for arm movements constrained to the horizontal

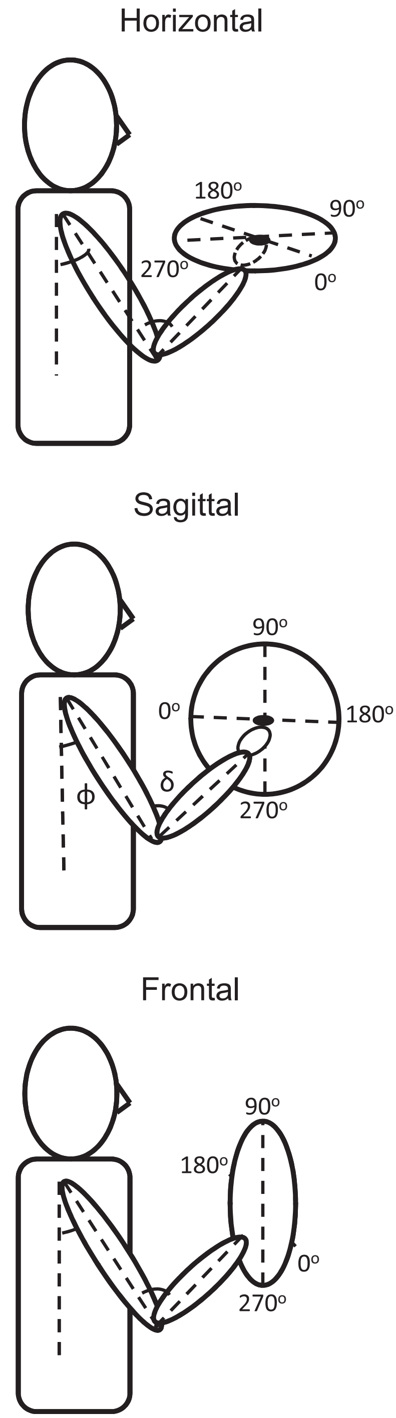

Fig. 1. A schematic representation of the experimental setup in the three planes. The depicted position of the arm is that used to determine the location of the circle center. For example, the hand is depicted with the dashed line in the Horizontal condition to indicate that it was underneath the circle when the position of the circle center was determined. During task performance, the strokes were produced on the surface of the circle visible to subjects (the top, left, and front surface in the Horizontal, Sagittal, and Frontal condition, respectively). The 0° direction was assigned to strokes to the right in the horizontal and frontal planes, and to the posterior in the sagittal plane. The 90° direction was associated with the anterior direction in the horizontal plane, and upward direction in the two vertical planes. This definition of directions provided subjects the same 'view' of the directions within the circle across the three circle orientations.