

A joint-centred model accounts for movement curvature and spatial variability

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Abstract

Hand reaching toward a visual target needs the central nervous system (CNS) to encode target location and initial limb posture. Once these sensory inputs are encoded within a common frame of reference, the motor system builds a motor command to drive the limb towards the target. In order to face the controversy concerning the variables (in task-space versus joint-space) the motor system may manipulate to build a motor command, we propose to compare recorded hand pointing movements to a task-space vector model and to a simplified joint-centred model. Subjects repeated large 3D free movements toward 12 different targets lying on a pointing table. Corresponding endpoint confidence ellipses were then computed. The main directions of these ellipses were finally compared to those predicted by the two models. The present work differs from earlier related studies in the fundamental approach data were recorded. Indeed, we put our emphasis on isolating the motor planning component from other online sensorimotor processes and higher level cognitive processes. In particular, we did not impose cognitively controlled movement features such as movement shape or planar constraint. Furthermore, a precise control of online feedbacks allowed us dissociating motor planning from online feedback processing. The obtained data better fitted the joint-centred model than the task-space vector model. Moreover, the recorded data exhibited curved trajectories very similar to the simulated values obtained from the joint-centred model.

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In a hand reaching task, the target location needs to be encoded according to various input signals such as retinal eccentricity, eye-in-head posture, head-on-trunk posture. Then the central nervous system (CNS) encodes both target and hand in a common frame of reference. At that level, the motor system builds a motor command devoted to move the limb toward the target. The question we address focuses on the potential variables the motor system may manipulate to build this motor command. Organisation of motor commands while pointing to a visual target for instance, has often been argued to depend on a separate and independent control of two main motor variables: movement direction and movement amplitude. The original idea comes from an approach of motor control developed by Morasso [21],

Abend et al. [1], Flash and Hogan [11], which tries to find a law minimizing the jerk of an endpoint movement trajectory in cartesian coordinates and thus leads to a linear trajectory in task space. This view has received a strong electrophysiological support when it has been discovered within the motor cortex individual cells and population vector cells aligned along the movement direction. It has been suggested that movement direction, i.e. the line connecting movement starting point to movement endpoint, is the main neural variable [12,14,20]. This view has been strengthened by the observation that small amplitude movements appear roughly straight, so that they can be easily described as vectors. Such a splitting of motor variables in direction of movement and its amplitude has been called the *vector coding hypothesis* by Vindras and Viviani [36].

Although there are frequent and recurrent controversies in the literature [2,6,22,31–33] recent studies continue to support this view [4,19,24,37]. However, a careful analysis of the methodologies reveals that all the studies supporting the *vector coding hypothesis* are based on movements planned in a

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single plane. Actually, in most of the pre-cited experiments in humans, subjects had to point to a target using a tool (stylus, mouse). This 2D constraint and the straight feature of movement paths may be derived from cognitively imposed skills. So, the measured features of movements in these studies could reflect the way higher brain variables such as symbolic representations interfere with the motor system [6,7], rather than the natural motor variables.

In the present study, we propose to retest the *vector coding hypothesis* and a joint-centred model in free movements, i.e. without any need to represent a tool to use and its limitations. These movements are also 3D free in order not to impose a straight line representation potentially elicited in a 2D task. Furthermore, the procedure removes all visual feedback (i.e. both hand and target disappear during movement execution), so that no online visual feedback loop can interfere with a motor command [13,23,27,26]. In a first step, the main directions of observed endpoint confident ellipses are compared to those predicted by the *vector coding hypothesis*. In a second step, the same main directions of observed endpoint variability ellipses are compared to those predicted by the joint-centred model. In general, a perceptual noise (except for visual depth perception) is considered as isotropic [35], and can influence the shape (or the size) of the endpoint confident ellipse, but not its orientation which is more specifically determined by the motor command noise. Comparing the data with the two models predictions should allow to infer the way raw motor commands are generated in the control of reaching movements.

Fourteen right handed healthy subjects with normal vision participated in the experiment. Their mean age was 34.5 ± 1.19 (mean \pm S.E.) and all gave their informed consent. The experiment was conducted in accordance with the Declaration of Helsinki and under the terms of local legislation.

Subjects simply had to perform right hand pointing movements to visual targets. Their head and chest were fixed. The pointing table was tilted 17.5° for subjects' comfort, and for movements to be planned as naturally as possible. Before each trial, a fixation LED appeared in front of the subjects. The starting point, near from subjects' chest, was materialized by a tactile cue on the table. The limb was fully visible prior to movements for a better accurate motor planning [25]. Then, a peripheral target appeared in the right visual field. In order to respect natural eye–hand coordination, subjects had to synchronously initiate an orienting saccade and point to this target.

The task was performed in a completely dark room. Targets appeared at 12 locations along a 3-by-4 regularly spaced array covering the entire reaching space. Extreme (X , Y) target coordinates (cm) were (17.7, 13.5) and (40.8, 28.9) in a cartesian reference frame originated at hand starting point. Each subject performed 10 blocks of 12 movements each. The 12 targets in a block were randomly presented. Although not reaching biomechanical limitations, movement amplitudes were large enough to clearly differentiate curved from straight movements by contrast with other studies [2,6,22,24,31–33,36,37].

Real-time control of the presented stimuli allowed switching off the peripheral target at eye saccade onset, and switching off limb vision at limb movement onset. This “double open loop”

condition was used to completely preclude the online feedback processing evidenced in earlier studies [5,15,23,26]. Thus, analysis of motor planning variables remained unbiased.

During this very simple task, limb and eye movements were monitored online to allow real-time control of visual feedbacks. 3D limb movements were recorded using an OPTOTRAK (3020) camera at a 200 Hz sampling rate. Limb data were recorded for further analysis. The OPTOTRAK infrared LED was placed on the subjects' fingertip. Horizontal gaze direction was recorded using a calibrated DC EOG method [26] at a 1000 Hz sampling rate. These signals were used in real-time to control target LEDs and limb vision via an AD-WIN system (Keithley-Metrabyte).

Online detection of saccade onset was determined by an eye velocity threshold using a two-point central difference algorithm [3] with a 10 ms binwidth. This threshold was individually adjusted at one-third of the maximum eye velocity observed during calibration. Online detection of hand pointing movement onset was determined by a fixed 80 mm/s velocity threshold using the same method as for the eye (10 ms binwidth).

Only 2D limb movement projections on the pointing table were analysed to allow a comparison with simplified 2D models. The present study particularly emphasises the direction of endpoint variability ellipses of hand pointing movements. Data from the 14 subjects were normalized and pooled; this way we obtained 140 movements toward each target. For each target, a confidence ellipse of movement endpoints was drawn, and its main direction was determined. These results were compared to those obtained from the simulations.

Considering the *vector coding hypothesis*, for each target we predict that the directions of endpoint confident ellipses will be aligned with the average movement direction [14].

Considering a joint-centred hypothesis for motor planning, we compute the final posture of the hand through an inverse kinematics transform. Then, trajectory is derived from a linear co-variation of the two angular joint displacements during movement execution, i.e. the movement is considered as a straight line in joint coordinates. For each simulated trial we add an independent random noise on both joints. As movement variability increases as a function of movement length [29], the shoulder and elbow noises are introduced as a dynamic component, i.e. proportional to displacements in the corresponding joints. We also include a 1° gaussian static noise component at each joint to represent the noise in stabilizing a joint that does not have to displace. The levels of both shoulder and elbow dynamic noises are adjusted to get the closest trade-off between a null offset and a unity slope of the regression equation between recorded and predicted directions of variability ellipses. The shoulder location in the model is computed as the 2D projection of the mean shoulder location measured on subjects during experiments. The arm and forearm (including hand and finger) lengths in the model are computed as the 2D projection of the mean arm and forearm lengths measured on subjects.

For each model, the 12 predicted directions (for the 12 targets) are compared to those from the recorded data in a simple regression analysis. We expect a regression equation of $Y = X$ for a perfect model, where X and Y are, respectively, the direction of

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