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Research article

Positional errors introduced by transient perturbations applied to a multi-joint limb

Mu Qiao, Tao Zhou, Mark L. Latash*

Department of Kinesiology, The Pennsylvania State University, University Park, PA 16802, USA

HIGHLIGHTS

- Transient perturbations to the hand lead to positional errors.
- Effects of perturbations in opposite directions are strongly asymmetrical.
- These effects persist under both eyes open and eyes closed conditions.
- The observations point at an unintentional drift in the hand referent configuration.
- Coupling between referent and actual coordinates might lead to the errors.

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ABSTRACT

We explored a recently discovered phenomenon that smooth transient perturbations applied to the hand can lead to violations of equifinality. Healthy subjects occupied an initial hand position against a bias force and tried not to interfere with hand displacements produced by changes in the force. The force changes were smooth and transient (ending up with the same bias force value), with or without a time interval (dwell time) between the force change application and removal. They could lead to an increase or a decrease in the bias force. The subjects performed the task with eyes open and closed. After the force change was over, the hand stopped consistently short of the initial position only when the initial force change increased the bias force. No consistent positional errors were seen for the opposite force change direction. These results were consistent across trials with and without dwell time performed with and without vision. We conclude that the positional errors were not due to muscle properties but reflected a drift in the hand referent coordinate within the central nervous system triggered by the perturbation and driven by the difference between the actual and referent hand coordinates during the dwell time.

1. Introduction

The equilibrium-point (EP) hypothesis [8] assumes that movements are controlled with neural variables that define referent coordinates (RC) for salient performance variables and lead to equilibrium states of the system consisting of the moving effector, its reflex connections, and external force field [14]. A transient change in external force (transient perturbation) is not expected to lead to changes in those equilibrium states assuming that the person is not reacting to the perturbation, i.e., not changing RC. Such phenomena of equifinality have been documented in several studies [2,15,20]. Violations of equifinality (positional errors) have also been reported [5,11,12]. In particular, recent studies have shown that a transient change in the external force applied to the hand can lead to deviations of the hand from the initial position at the new steady state despite the fact that the force field at the final steady state is the same as in the initial state and the subject is instructed and trained not to react to the perturbation [22,23]. Those positional errors increased in magnitude with the time interval between the perturbation application and removal.

An interpretation has been suggested that the positional errors reflected an unintentional drift of hand RC triggered by the perturbation and driven by the discrepancy between the RC and hand actual coordinate (AC), referred to as RC-back-coupling. The RC-back-coupling hypothesis allows making a non-trivial prediction: When a hand acts against a bias force, transient perturbations in opposite directions along the force line are expected to lead to positional errors in the same direction since (AC–RC) always has the

* Corresponding author at: Department of Kinesiology, Rec. Hall-267, The Pennsylvania State University, University Park, PA 16802, USA. Tel.: +1 814 863 5374; fax: +1 814 863 4424.
E-mail address: mll11@psu.edu (M.L. Latash).

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same sign. When application of the transient perturbation increases bias force, (AC–RC) increases. In contrast, when application of the transient perturbation decreases bias force, (AC–RC) drops. Hence, the second prediction is that positional error magnitude should be larger in the former case. The purpose of this study was to test these predictions.

2. Methods

2.1. Subjects

Eight male volunteers (age = 29 ± 1 years; body mass = 71 ± 3 kg; body height = 1.76 ± 0.03 m, mean ± standard errors), all self-reported right-handers, took part in the experiment. All participants were free of any neural or musculoskeletal disorders. They provided informed consent according to the procedures approved by the Office for Research Protection of the Pennsylvania State University.

2.2. Experimental setup and procedures

The HapticMASTER (MOOG, the Netherlands) admittance-controlled robot was used to generate bias force (F_{BIAS}) and its changes (perturbation, F_{PERT}). Participants sat upright and held the handle with three rotational degrees-of-freedom attached to the end-effector of the robot. The robot arm was aligned such that the participant's hand moved primarily in the parasagittal plane (Fig. 1A). The initial position of the handle was set as the origin of global coordinate system. The *x*-axis was a horizontal axis in a sagittal plane pointing in the anterior direction. The hand with the handle could move at least 10 cm freely along positive (*x*+) and negative (*x*−) directions.

We placed reflective markers on the following locations: suprasternal notch, 2 cm below the acromion process, medial/lateral epicondyles of the humerus, and ulnar/radial styloid processes. The marker coordinates were measured by a 3D motion analysis system (Qualisys AB, model ProReflex MCU240, 5 cameras, Sweden) and used to provide visual feedback on the initial joint configuration (using a 20" monitor placed 0.8 m in front of the subject). A self-selected comfortable joint configuration was set as the initial joint configuration, presented on the monitor, and reproduced across trials. During each trial, the position of and force to the handle were recorded at 60 Hz.

Before data collection, participants performed familiarization trials. During those trials, the subjects held the handle against F_{BIAS} = 20 N pulling the handle away from the body along the *x* axis. A magnitude of perturbation force (F_{PERT}) added to or subtracted from F_{BIAS} was selected for each subject to produce handle motion over about 10 cm along either *x*+ or *x*− direction (Fig. 1B). As a result, the handle excursion was approximately matched while F_{PERT} varied across subjects. Note that at all times $|F_{PERT}| < |F_{BIAS}|$. Thus, the subjects only felt an increase or a decrease in F_{BIAS} while the total robot force did not change direction.

Each trial started with the subject holding the handle steadily in the initial position against F_{BIAS}. Further, the subjects were always instructed "not to intervene voluntarily" with the effects of force changes ("allow the robot to move your hand") [7,13]. After a random time interval (2–4 s), F_{PERT} was applied consisting of a ramp force change over 500 ms. This duration of F_{PERT} was chosen to avoid burst-like muscle reactions, so-called pre-programmed reactions [10,15,21], and no visible burst-like changes in muscle activation levels were seen in an earlier study using a similar procedure [6]. F_{PERT} either pulled the hand away from the body or toward the body by about 10 cm (Fig. 1B). After the handle velocity dropped under 10% of its peak value, F_{PERT} decrease could be initiated either

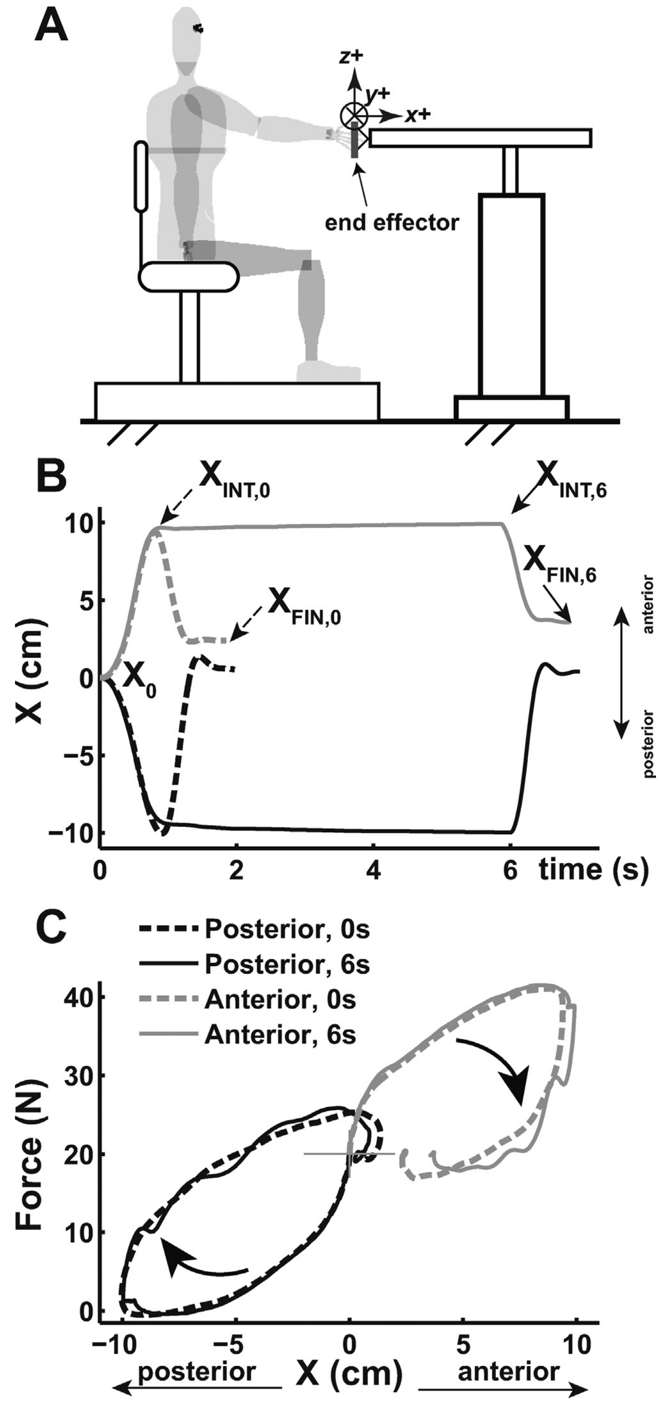

Fig. 1. (A) The experiment setup with the subject holding the handle of the robot (*x*+ means anterior to initial hand position); (B) hand *x* coordinate time series; and (C) hand position vs. hand force trajectories. In B and C, the trajectories are shown for both directions of the perturbation force (F_{PERT}, anterior and posterior) and for both dwell times (0 s and 6 s). X_0, X_{INT} and X_{FIN} show the hand positions in the initial state, the intermediate location (prior to F_{PERT} removal), and at the final state (after the F_{PERT} removal), respectively. Averaged across all subjects curves are presented.

immediately or after a 6-s dwell time (Fig. 1B). The hand moved to a final position, and the participants held the handle in the final position for 2–3 s. Each participant performed the trials with eyes open and with eyes closed after occupying the initial position.

There were eight conditions in the experiment with all possible combination of the three main factors, vision (present or absent), direction of perturbation (anterior or posterior), and dwell time (0 s or 6 s). The order of conditions was block randomized. Under each