Published in final edited form as:

Neurosci Lett. 2015 May 19; 595: 104–107. doi:10.1016/j.neulet.2015.04.017.

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

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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.

Keywords

referent configuration; back-coupling; equifinality; positional errors

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

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(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 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 yrs; body mass = 71 ± 3 kg; body height = 1.76 ± 0.03 m, mean $\pm$ 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 towards 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 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 condition, six trials were collected consecutively for each participant. A short rest (15 s) was provided between trials. The entire experiment lasted for about an hour.

2.3. Data analysis

The handle coordinate along the x -axis was computed at the initial state (X_0 ; the average x coordinate within a 0.5-s time interval ending 0.5 s prior to the application of F_{PERT}), at the intermediate location (prior to F_{PERT} removal, X_{INT}), and at the final state (after the F_{PERT} removal, X_{FIN} ; the average x coordinate within a 0.5-s time interval starting 1 s after F_{PERT} dropped to zero) as illustrated in Fig. 1B,C. Positional errors were estimated as the difference between X_{FIN} and X_0 .

All values in the texts are presented as means $\pm$ standard errors. Repeated-measures ANOVA was used to analyze effects of the three factors, *Vision*, *P-Direction*, and *Dwell*, on the handle x -coordinate at different phases. Each factor had two levels as described above. The normality assumption was checked using the Kolmogorov-Smirnov test; DOFs were adjusted in cases of sphericity violations.

3. Results

The application of F_{PERT} led to hand deviation from the body or towards the body by about 10 cm. When F_{PERT} was removed, the hand moved towards the initial coordinate (X_0) but, on average, stopped anterior to X_0 across all conditions. The deviations from X_0 were larger

for F_{PERT} leading to anterior hand deviations and had a tendency to be the largest for the anterior hand perturbation with the 6-s time dwell time between F_{PERT} application and removal. Typical hand trajectories averaged across subjects as the functions of total robot force are illustrated in Fig. 1C. No error shades are presented to make the plot readable.

There were no effects of vision on any of the outcome variables ($p > 0.5$ across all comparisons). Hence, further analysis used the data averaged over 12 trials, 6 trials with eyes open and 6 trials with eyes closed, for each condition. The main results are illustrated in Fig. 2. The hand deviations produced by F_{PERT} application ($|X_{INT} - X_0|$) were of about the same magnitude across conditions (close to the nominal 10 cm; Fig. 2A), while positional errors at the final state ($X_{FIN} - X_0$; Fig. 2B) depended on the direction of F_{PERT} . On average, X_{FIN} shifted anterior of X_0 across conditions. The magnitude of the positional errors was significantly larger for the anterior perturbations compared to posterior perturbations (2.97 ± 0.57 cm vs. 0.47 ± 0.33 cm; $F_{(1,7)} = 14.1$; $p < 0.001$), while the effect of dwell time was not significant ($F_{(1,7)} = 0.6$; $p = 0.44$); there was no interaction.

4. Discussion

According to the idea of control with referent coordinates (RC), the initial state of the hand can be described with a value RC_0 located closer to the trunk as compared to the actual initial hand coordinate (X_0 ; Fig. 3). The difference between RC_0 and X_0 produced the hand force vector: $F_H = k(X_0 - RC_0) = -F_{BIAS}$, where k is a coefficient of apparent stiffness (cf. [16]). If neither k nor RC changes, any transient change in the external force is expected to lead to the same hand position when the external force returns to F_{BIAS} , because the system is in equilibrium with F_{BIAS} at X_0 only. The observed deviations of the final hand position (X_{FIN}) from X_0 suggest that RC shifted during the perturbation with or without a change in k . An important observation is the lack of the hand position drift in the intermediate position (X_{INT}) during the time interval between F_{PERT} application and removal during the trials with the dwell time of 6 s (see, for example, Fig. 1B). This observation confirms earlier reports [22,23] and suggests that a parallel drift of RC and k took place (note the different slopes of the straight lines connecting X_{INT} with X_0 and X_{FIN} for the anterior perturbation in Fig. 3).

Earlier studies considered a possibility that the positional errors following the transient perturbations could reflect muscle properties such as force depression after muscle shortening [3,17] and force enhancement following muscle stretch [4,18,19]. Note that perturbations in opposite directions in our study produced opposite changes in the length of agonist-antagonist muscle pairs. If the mentioned factors were primarily responsible for the difference between X_0 and X_{FIN} , one could expect that perturbations in opposite directions would produce deviations from X_0 also in opposite directions. This was not true, however. Hence, the current findings support the alternative hypothesis that the positional errors reflected changes within the central nervous system, namely changes in the hand referent coordinate [22,23].

On average, X_{FIN} was always anterior to X_0 across all conditions, although non-significant for posterior F_{PERT} . Overall, the results of the trials with posterior F_{PERT} suggest equifinality as predicted by the classical EP-hypothesis [8,9]: No significant deviations of

the hand from the initial position were observed across vision and dwell time conditions. Two explanations can be offered for these findings. First, the results are consistent with a conclusion drawn in an earlier study [1] that subjects are able to show equifinality when perturbations lead to shortening of an activated muscle, not when an activated muscle is stretched. In our study, in the initial position, a degree of co-activation of major arm muscle agonist-antagonist pairs was likely. However, there had to be higher activation of muscles contributing to hand force production against F_{BIAS} . Hence, stretching those muscles was more likely to lead to violations of equifinality, as observed in the experiment. Second, earlier studies [22, 23] demonstrated violations of equifinality with the magnitude proportional to the difference between the actual and referent coordinates during the dwell time. In the current study, this difference was large during the perturbations moving the hand away from the body and very small during the perturbations moving the hand toward the body (reflected in the different hand force values during the dwell times, see Figure 1). As a result significant violations of equifinality were seen only when the hand was moved away from the body.

The lack of visible hand drift during the dwell time is a non-trivial observation. One hypothesis suggested in an earlier study [23] was that this phenomenon was conditioned by the presence of visual information and the instruction to the subject “allow the robot to move your hand”, which could be interpreted as “the hand should not move when the robot force does not change”. To test this hypothesis, we ran experiments with eyes open and closed. All the effects were similar under those two conditions suggesting that visual information was not crucial for any aspect of the observed behavior.

One of the effects observed in earlier studies was under the significance level in the current experiment, namely the increase in the positional error magnitude with dwell time. This could be due to the fact that, even with the nominal dwell time of 0 s, the actual perturbation time was about 1 s. In earlier studies, an exponential drift of the hand final position with dwell time was observed with the exponent time constant of 1 s [22,23]. So, the comparably long perturbation time could be responsible for the non-significant effects of dwell time (although, on average, they were in the expected direction for anterior perturbations, see Fig. 1C, 2B).

A number of earlier studies reported violations of equifinality under the action of destabilizing forces, such as the Coriolis force and the simulated negative damping [5, 11, 12]. In those studies, the authors claimed that the results were inconsistent with the equilibrium-point hypothesis. A detailed response explained how such phenomena could be interpreted within the equilibrium-point hypothesis based on the idea of unintentional RC shifts [9]. Our current experiment, as well as a few earlier studies [22, 23], shows that violations of equifinality are indeed very common, even under the action of relatively usual force perturbations. As described earlier in the Discussion, these observations can be naturally interpreted within the recent development of the equilibrium-point hypothesis in the form of the referent configuration hypothesis applied to natural multi-joint movements [14].

To conclude, this experiment provides so far the strongest argument in favor of the hypothesis that an unintentional drift in the referent configuration of an effector can be produced by a perturbation driving the actual configuration away from the referent one (RC-back-coupling hypothesis). It demonstrated a highly non-trivial, even counter-intuitive, result: No change in the direction of positional errors following transient perturbations in opposite directions.

Acknowledgments

The study was in part supported by an NIH grant NS-035032.

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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 coordinate.
- Coupling between referent and actual coordinates might lead to the errors.

Figure 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.

Figure 2.

Asymmetrical effects of transient perturbations on the final hand position. Movement amplitude induced by the perturbation, F_{PERT} : $|X_{INT} - X_0|$ (A), and deviations of the final hand position from the initial position, $(X_{FIN} - X_0)$ (B). Mean across subjects data are shown with standard error bars for each dwell time (0 s and 6 s).

Figure 3.

Results of the experiment illustrated using the framework of the referent configuration hypothesis. At the initial position, the combination of bias force (F_{BIAS}) and hand coordinate (X_0) corresponds to a referent coordinate (RC_0) and apparent stiffness (k). A change in the force (F_{PERT}) leads to a deviation of the hand position to a coordinate that can be anterior to X_0 ($X_{INT}(ant)$) or posterior to X_0 ($X_{INT}(post)$) depending on the F_{PERT} direction. After F_{PERT} has been removed, the hand moves back to X_0 but stops short of it for anterior perturbations and slightly anterior to X_0 (non-significant) for posterior perturbations (shown with arrows and as $X_{FIN}(ant,post)$). Note the change in the final referent coordinate (RC_{FIN}) and k for the anterior perturbation only.