Maintaining position vs. maintaining timing: two timescales of walking control

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1 Introduction

Virtual scene motion has been used in treadmill walking experiments to provide insight into how visual information is used in human locomotion [1-2]. Recent studies have also made use of virtual visual environments to gain a better understanding of the neural control of human walking [3-4]. Thus, visual perturbations can be used to understand the control of walking as probes to control in addition to being used to understand the role of vision per se.

When walking on a treadmill surrounded by a fixed visual scene, subjects necessarily use vision to maintain their anterior-posterior position. As a result, small continuous visual scene motion can cause whole body translations of subjects [1,5]. In addition to altering step length, phase resetting due to shortening or lengthening the duration of a step is a potential strategy for maintaining position on the treadmill. Here we imposed experimental constraints on the nervous system to gain insight into the control strategy for positional maintenance. Walking was constrained in two ways. First, walking on a treadmill requires that subjects adjusted speed to stay on the treadmill. A second constraint used was dictating cadence on the treadmill with a metronome. By limiting the temporal variability in taking a step (step period), we predicted that: 1) the nervous system would not employ a phase-resetting strategy in response to perturbations; and 2) vision would be less important for the subtask of speed control.

2 Methods

Subjects (n=20) walked on a treadmill (5 km/h) placed within an immersive, 3-screen room with a virtual scene consisting of randomly oriented triangles with or without a metronome for six trials of 4 minutes in each condition. In all trials, a filtered white noise signal rotated the virtual scene about the subject's ankle in the sagittal plane. Across subjects, these driving signals had an average root mean square error (RMSE) of 4.08 deg and 6.89 deg/s. Full body kinematics and surface EMG of 16 muscles on the right side were recorded. The response variables were sagittal plane segment angles, anterior-posterior (A-P) displacements and rectified/filtered EMG activity. Whole-body sagittal plane displacement was approximated as the displacement of L1 in the sagittal plane. Phase-dependent impulse response functions (PD-IRFs) characterized the effect of visual scene motion on a kinematic or sEMG response variable and estimated the impulse response at the time the response and stimulus occurred with respect to the gait cycle (heel strike at 0/100%). PD-IRFs of changes in approximate phase ("phase PD-IRF") from visual scene motion were computed to investigate phase-resetting (phase advances/ delays). Permutation tests (1,000,[6]) based on the t-statistic between No Metronome and Metronome conditions at all combinations of stimulus phase and normalized response time were tested simultaneously and family-wise error rate (FWER) was controlled for each response variable ($\alpha = .05$).

3 Results

A subset (13 of 20) of subjects maintained error from the metronome within ±.5 metronome periods for the majority of the Metronome trials (e.g., 4 of 6). As these 13 subjects were able to follow the metronome during the Metronome condition, we focus on their data in the remaining analysis.

A positive phase PD-IRF response due to visual scene motion was initiated within the first cycle in both conditions, and plateaued at approximately 3-4 gait cycles from perturbation onset. As this was a positive impulse response, it shows that changes in step duration were in the same direction as changes in scene motion. When the visual scene moves forward subjects take a quicker step, resulting in a phase advance. Figure 1 shows both the phase PD-IRF and the A-P L1 PD-IRF at a repre-

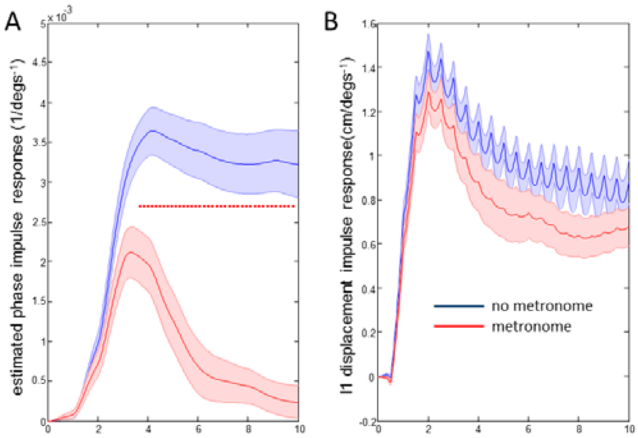

Figure 1. Impulse response functions of estimated phase and L1 displacement*. Impulse response functions of estimated phase (A) and L1 displacement (B) at the 14% stimulus phase in both conditions. Error bar is ± s.e.m. Asterisks denote normalized response times where a difference was observed between* Metronome and No Metronome condition (p<.05, see *Methods*).

sentative stimulus phase (14%). This positive phase PD-IRF response was suppressed in the Metronome condition beginning late in the 3rd gait cycle denoted by the diminishing of persistent phase-resetting. Responses of A-P L1 displacement were not different between the two conditions, however, indicating similar positional maintenance even though phase-resetting properties were clearly different.

4 Discussion

In this study we used constraints on the locomotive behavior of walking coupled with perturbations of virtual scene motion to investigate how the subtask of positional maintenance is controlled on the treadmill. As hypothesized, use of a metronome to dictate cadence diminished subjects' use of phase-resetting to maintain position on the treadmill. Interestingly, both change in position due to visual scene motion and phase-resetting due to visual scene motion were not initially different between conditions. As time progressed from the perturbation, the phase advance due to visual scene motion differed between the two conditions while the shift in the body's position did not. In sum, maintaining position on the treadmill was linked to phase resetting on a short time scale while being unlinked on a longer time scale.

The separation of phase-resetting and positional maintenance reveals two timescales of control for human locomotion: 1) a fast control initiated in the first cycle after the perturbation cycle that serves the subtask of speed control (i.e., positional maintenance on the treadmill) and 2) a slow control initiated several cycles after a perturbation to suppress phase shifts when maintaining a fixed cadence.

Understanding how the nervous system controls walking where relative position needs to be maintained simultaneously with other subtasks such as maintaining cadence is imperative for understanding situations such as how one maintains position and avoids collisions with others within a crowd while simultaneously navigating his or herself to a desired location.

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