Physiological mechanisms underlying prediction and optimization of metabolic cost during walking

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Introduction: Of all the possible ways to walk, humans consistently prefer gait patterns that minimize metabolic cost. However, past methodology has been limited to description of this overall phenomenon without revealing the underlying neural mechanisms behind it. In other words, we have a good understanding of what gaits people prefer and why they prefer them, but a very limited understanding of how they are selected.

Energetically optimal gaits may be achieved with a process that directly senses metabolic rate and dynamically adjusts gait to minimize it. For example, chemoreceptors located in the carotid and aortic bodies are sensitive to changes in blood oxygen and carbon dioxide levels associated with metabolic demand, and play an important role in the control of ventilation [1]. Integrating signals from these receptors over a number of steps could provide the body with an estimate of metabolic cost. However, optimizing gait based on this and other metabolic sensory information would be expected to be relatively slow based on the response times of the direct metabolic sensors as well as the need to iteratively adjust gait and reassess metabolic rate in a closed-loop process [2].

Because walking conditions tend to change rapidly and most walking bouts are short-lived [3], it is possible that another mechanism may help to achieve efficient gaits over shorter periods. Visual feedback along with other body sensors could provide information that serves as a proxy for metabolic cost and would be rapidly available for adjusting gait on the fly. For example, prior knowledge of the association between speed and energy expenditure would allow one to predict the optimum gait adjustments immediately based on the currently sensed walking speed.

Our general hypothesis is that the nervous system relies on both an indirect predictive process and a direct optimization process to best select gaits that minimize energetic cost. In particular we tested whether this control makes use of a predictive mechanism that rapidly incorporates visual information in addition to a slower process that directly optimizes metabolic cost based on blood oxygen and carbon dioxide levels.

Methods: To test whether visual feedback is used for predicting economical adjustments to walking speed, we developed a treadmill based virtual reality system to suddenly perturb visually perceived speed of motion and measure the resulting adjustments in walking speed. We applied perturbations to visual flow rate through a wide field-of-view display while ten healthy subjects walked at their most comfortable speed on a self-paced treadmill. The visual field consisted of a virtual hallway tiled with randomly placed rectangles [4]. Rather than manipulating the speed of visual flow directly, we coupled it to the walking speed selected by the subject and then manipulated the ratio between these two speeds. During experimental trials, subjects walked with congruent visual information for 2 minutes and were then exposed to sudden changes in the visual flow rate lasting 3 minutes such that the visually perceived speed was 0.25, 0.50, 1.5, and 2.0 times the walking speed. We measured walking speed and used standard techniques from system identification to quantify the dynamics of speed adjustments in response to step changes in visual flow rate. To prepare the data for this analysis, we normalized the magnitude of each change in speed from 0 to 1 for each trial. We predicted that indirect prediction would cause subjects to rapidly change speed in response to a step input and a slower process, possible direct optimization, would gradually return subjects back to their preferred speed over time.

To test whether the blood gas levels of oxygen and carbon dioxide are important sensory inputs for directly optimizing metabolic cost, we have built a device that manipulates blood gases by controlling the expired levels of oxygen and carbon dioxide. The end-tidal partial pressures—gas pressures measured at the end of each breath—are reliable indicators of the levels of oxygen and carbon dioxide within the blood leaving the lungs [5]. The system consists of compressed gas sources (air, oxygen, nitrogen and carbon dioxide) connected via solenoid valves to a humidification chamber and an inspiratory reservoir bag from which the participant breathes [6]. A real-time control system compares actual end-tidal gas partial pressures with target pressures and mixes the gases on a breath-by-breath basis to minimize the differences. We will use respiratory gas control to change the levels of oxygen and carbon dioxide within the blood as a function of step frequency and test if subjects shift their preferred speed and step frequency to maximize blood oxygen and minimize carbon dioxide. We predict that when subjects are given a gas control function that increases oxygen (or decreases carbon dioxide) at high frequencies and decreases oxygen (or increases carbon dioxide) at low frequencies, they will shift their walking patterns towards higher frequencies even if it comes at a metabolic penalty. Conversely, a reversed control function that decreases blood oxygen (or increases carbon dioxide) levels at high frequencies will cause subjects to decrease preferred step frequency.

Results and discussion: In response to step changes in visual flow rate, subjects rapidly adjusted walking speed (Figure 1) with a response time of 1.4 +/- 0.3 seconds (mean +/- 95% CI). The directions of the speed changes were opposite of the visual perturbations and consistent with returning the visual speed toward the preferred walking speed - when visual speed was suddenly twice (half) the walking speed, subjects decreased (increased) their speed. Since people prefer walking speeds that minimize cost of transport, these results suggest that vision is used to rapidly predict energetically optimal speeds.

After the rapid response to the visual perturbations, subjects did not maintain the new speed but exhibited longer-term adjustments that gradually returned walking speed toward the steady state value before the perturbation. The time courses of these adjustments (response time of 365.5 +/- 10.8 seconds) are consistent with a process that optimizes energetic cost through direct sensing of metabolic rate. However, we cannot distinguish whether the observed slow adjustments are indeed acting as a separate optimization process or whether they result from a recalibration of self-motion perception. We are currently piloting the above mentioned experiment that manipulates blood gas levels to more explicitly test for the direct optimization of metabolic cost.

Conclusions: The timing and direction of the responses to visual perturbations strongly indicate that a rapid predictive process informed by visual feedback helps select preferred speed, perhaps to complement a slower optimization process that seeks to minimize energetic cost. Further testing is necessary to determine whether blood gas levels provide direct information about energy expenditure for optimizing gait economy.

Open Questions:

- Can we prove that people are optimizing metabolic cost when adapting gait based on blood gas levels?
- How else can we experimentally manipulate perceived energetic cost?

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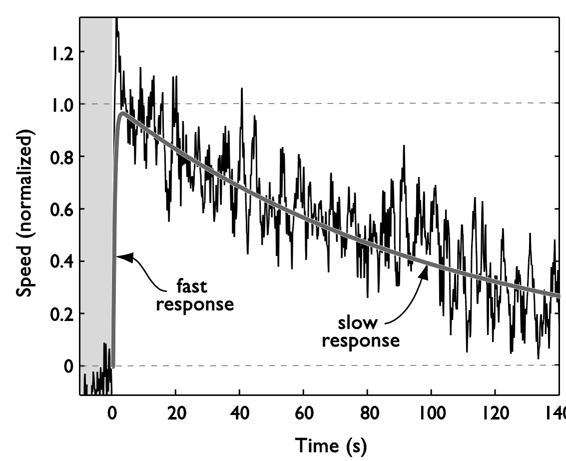

Figure 1: Subjects rapidly adjust walking speed (black line) in response to step perturbations of visual flow rate and then gradually returned toward their preferred speed (average response shown). This behavior is well described by a two-process model fit (grey line) with response times of approximately 1.4 and 365.5 seconds.