INTRODUCTION
During walking, humans select gait patterns that minimize their energetic cost of transport [2]. Subjects constrained to walk at a certain speed select the step frequency that minimizes their energetic cost and, similarly, subjects constrained to walk at a certain step frequency select the minimum cost speed [1]. Our recent research has found that when a physical perturbation is applied to walking subjects (such as a rapid change in treadmill speed), both a fast predictive and a slow optimization process are present in the selection of optimal step frequency [2]. The purpose of this study was to determine whether these two processes represent control mechanisms specific to speed constrained walking on a treadmill, or general control mechanisms for minimizing energetic cost in human walking. Our hypothesis is that both fast and slow processes are general control mechanisms.

METHODS
To test our hypothesis, we performed three different experiments. First, we repeated the constrained speed experiment by applying a series of rapid changes in treadmill speed to walking subjects while measuring the step frequency adjustments towards the subjects’ new preferred frequencies (Figure 1A). To allow for comparison of perturbations and responses of different directions and magnitudes we normalized all data to zero before the perturbation and one at steady state after the perturbation. We then used system identification techniques to test for the presence of fast and slow processes to obtain a model of the system dynamics. To test for the generality of these two processes, we tested the model against data collected from two validation experiments where very different contexts and perturbations were used.

In the first validation experiment we used non-physical perturbations. We asked subjects to synchronize their steps to a metronome frequency while walking on a constant speed treadmill. We played a metronome frequency that would result in a different step frequency than their preferred at that speed. We then replaced the metronome with white noise and measured the step frequency adjustments back towards their preferred frequency (Figure 1B).

In the second validation experiment we used a similar protocol to the original experiment but we switched the input and the output. This time we constrained subjects’ step frequency by asking them to synchronize their steps to a metronome while walking overground. We applied perturbations consisting of a series of rapid changes in metronome frequency and measured subjects’ speed adjustments towards their new preferred speeds (Figure 1C).

RESULTS
We found that for speed constrained treadmill walking with physical perturbations, there is a dominant fast process with a response time of 0.77±0.02 seconds, comprising approximately 85% of the overall amplitude change, and a slow process with a response time of 18.40±0.33 seconds comprising the remaining 15% of the overall amplitude change (R²=0.99, Figure 1D). These response times were fixed in a model which was then fitted to the validation responses. The good fit for the treadmill non-physical perturbation responses (R²=0.98, Figure 1E) and for the overground step frequency constrained responses (R²=0.99, Figure 1F) highlight the presence of the same dynamics in very different situations.

DISCUSSION & CONCLUSIONS
Our results indeed show that two processes are present in the selection of preferred gait patterns, regardless of whether speed or step frequency is constrained, whether subjects walk on a treadmill or overground and whether the perturbation applied is physical or non-physical. The presence of a fast and slow process in these various situations strongly suggests that prediction and optimization are general control mechanisms for selecting energetically optimal gaits.

REFERENCES