Tracking the adaptation of perceived speed asymmetry through hidden Markov models

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Introduction: Despite its central role in motor control, sensation has been less studied than motor output in sensorimotor adaptation paradigms. This might be because of the difficulty to measure sensation: while motor output has easily observable consequences, sensation is by definition an internal variable of the motor system. Perceptual studies offer the opportunity to investigate human sensation by asking subjects what they feel [Green and Swets, 1966], but it is critical to account for the probabilistic nature of people's responses [Ehrenstein and Ehrenstein, 1999]. Here we investigate how humans perceive speed differences between their legs and use a bayesian approach (hidden Markov models) to track the adaptation of this percept during split-belt walking (i.e., legs moving at different speeds), which is a well-established locomotor adaptation paradigm.

Methods: We used a two-alternative forced-choice task (2AFC) to first characterize the human ability to detect differences in belt speeds on a split-belt treadmill (Experiment 1, n=9; 24.6 ± 3.7 y.o.), and then used this information together with a Hidden Markov Model to track changes in subjects' perception of speed asymmetry during motor adaptation and de-adaptation (Experiment 2; n=10; 20.1 ± 0.99 y.o). In both experiments, perception of speed asymmetry was evaluated with 2AFC trials, which were interspersed during either regular treadmill walking or split-belt walking. Each 2AFC trial (Fig. 1, top left) started with an arbitrary speed difference $\Delta v = v_R - v_L$. Subjects walked at this speed difference for a full stride cycle (i.e., time duration between two foot landings of the same leg) after which they heard an audio cue signaling the beginning of the response window. Upon this audio cue, subjects pressed one of two keys (left or right) according to which belt felt to be moving slower. Once the response window was over, subjects would hear a second, different, audio cue indicating the end of the 2AFC trial, after which the belts returned to the same speeds as before the task started. In Experiment 1, the belt speed differences at the beginning of the perceptual tasks took one of 23 possible values ranging from -350mm/s to 350mm/s, which were pseudo-randomly presented. Subjects had up to 24 strides to respond to the task and they walked for bouts of 25 strides before a new 2AFC trial was introduced. Subject choices (i.e. left/right) and reaction times (i.e., time to respond after the start cue) were taken as outcome measures. Choices were characterized as a function of belt-speed difference through a logistic regression. The link between subject choices and reaction times was modeled through a drift-diffusion model to gain insights into the process gathering sensory information for making a choice. In Experiment 2, subjects performed the 2AFC trials in three consecutive experimental epochs: Baseline, Adaptation, and Washout. During Baseline and Washout inter-task walking bouts happened with no belt speed difference (same as Experiment 1). During Adaptation, inter-task walking bouts happened with the right belt moving 500 mm/s faster than the left. In this experiment subjects had only 6 stride cycles to respond to the task, and task presentations occurred in an irregular schedule and used only 6 possible belt speed difference values (Fig. 2, top). We used subject choices in this task to track the Point of Subjective Equality (PSE) which is defined as the belt speed difference at which subjects would perceive the belts to be moving at the same speed. In order to do this, we employed a Hidden Markov Model, where the PSE is modeled as a temporally evolving hidden variable (Eq. 1), and subject choices are related to the PSE through a logistic function (Eq. 2) consistent with the results of Experiment 1. In both experiments one belt speed up and the other one slowed down such that the averaged speed was maintained at 1.05m/s throughout the entire protocol.

Results: We found that subjects reached 75% accuracy in their perceived speed asymmetry when belt speed differences were at least 75 mm/s, corresponding to a Weber fraction of $\sim 7\%$. Moreover, the drift-diffusion model with fixed barriers was able to reproduce both accuracy and reaction time results (Fig. 1, bottom, middle and right), providing evidence that sensory information to determine speed asymmetry is gathered as specified by this framework. Our results also revealed that subjects adapt their perceived speed asymmetry (Fig. 2, middle and bottom). At its peak, the PSE reaches 300 mm/s, meaning that subjects perceived a belt speed difference of 300 mm/s as both belts moving at the same speed. This represents a 60% recalibration with respect to the 500 mm/s difference in belt speeds during split-belt walking, well above previous reports (60% vs. 36%, Leech et al. 2018; and 25%, Vazquez et al. 2015). Notably, PSE appears to adapt at two different timescales: very rapidly in the first ≈ 100 strides following the introduction of split-belt walking, and slowly for the remainder of it. Similarly, deadaptation occurs rapidly with PSE falling below 100 mm/s in less than 150 strides following the return to tied-belt walking.

Conclusions: We demonstrate the usefulness of a bayesian framework to measure changes in perception during motor adaptation through short, minimally invasive perceptual probes. Consistent with previous studies, we show recalibration of speed that accompanies locomotor adaptation, but to a larger extent than previously thought. This approach opens an avenue for investigating perceptual deficits and its relation to motor impairments in clinical populations.

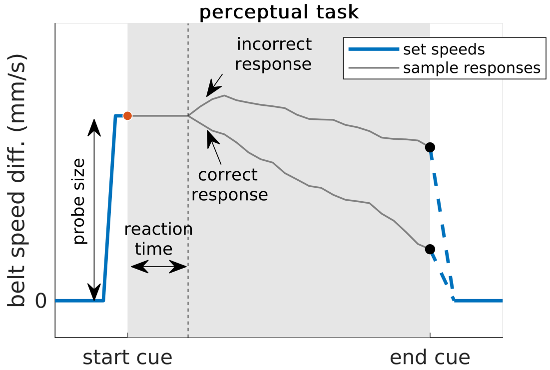
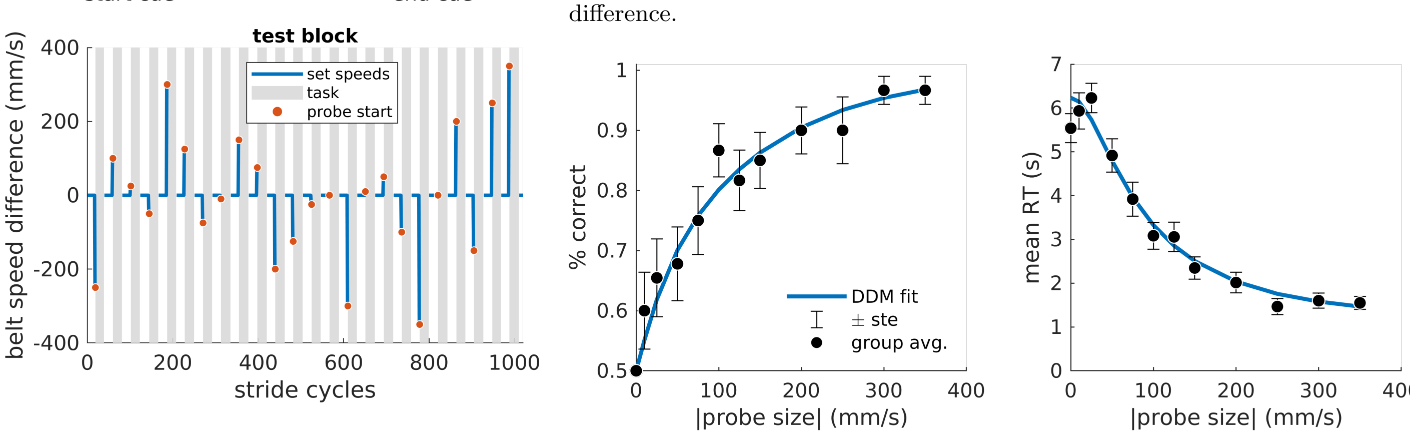


Figure 1: Protocol and results for characterizing the perception of belt speed differences (Experiment 1). **Top:** Example for the two-alternative-choice (2AFC) trial that was used. The trial begun and ended with audio cues. Upon hearing the first cue, subjects were instructed to identify the belt moving slower. A second cue indicated the end of the 2AFC trial and return of belt speeds to their prior value. **Bottom left:** Speed difference profile for a testing block. Subjects performed a 2AFC trial in each of the shaded intervals. **Bottom middle:** Accuracy vs. absolute probe size results. Blue line represents predictions from the drift-diffusion model (DDM) fitted to the data, dots indicate experimental data (± standard error). **Bottom right:** Mean reaction time (RT) vs. absolute probe size results. The DDM can be fit adequately to both mean RT and accuracy provided that both drift and noise (diffusion) rates scale with belt-speed difference.



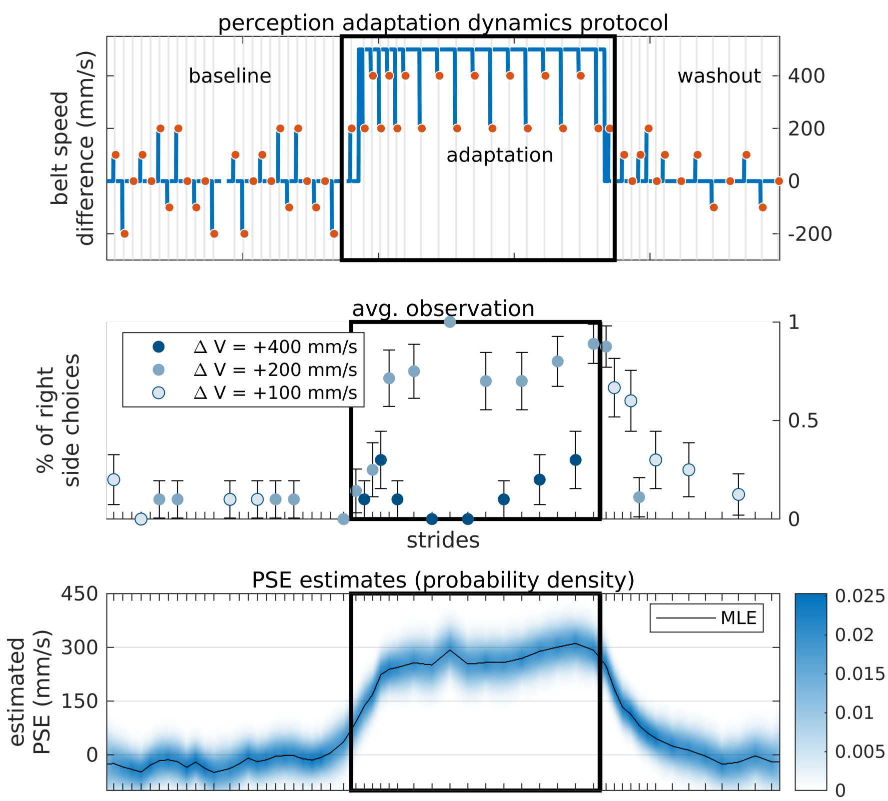


Figure 2: Protocol and results for the assessment of perceptual adaptation during split-belt walking. **Top:** Split-belt walking adaptation and deadaptation protocol with perceptual (2AFC) trials. The protocol was divided into three epochs. In the first (Baseline) and last (Washout), 2AFC trials were interleaved with periods of tied-belts walking. In the third block (Adaptation), the inter-task walking was performed with a belt speed difference of 500 mm/s, with the dominant leg (which was the right leg for all subjects) moving faster than the non-dominant one. Perceptual trials took place at semi-regular intervals (shaded areas) and belt speed differences probed in each trial is indicated with an orange dot. **Middle:** Group avg. responses to perceptual trials, for three different belt speed differences (all corresponding to situations where the right belt moved faster than the left). partial visualization of the transition (eq. 1) and emission (eq. 2) probabilities used for the hidden Markov model. The effect of adaptation is evident in the temporal evolution of responses. For example, +200 mm/s trials elicit over 90% 'left is slow' responses during Baseline, but less than 30 % by the end of Adaptation and during early Washout, returning to 90% later in Washout. **Bottom:** Inference of the Point of Subjective Equality (PSE) from 2AFC responses through the hidden Markov model. Shaded blue areas indicate likelihood of the PSE given subjects' pooled responses. The black line indicates the maximum likelihood estimate at each point in time. The probability distributions assumed for the temporal evolution of PSE (dynamics, eq. 1) and for the observations (eq. 2) are shown at the bottom.

Dynamics:

$$\mathrm{PSE}_{k+1} \sim \mathcal{N}(\mathrm{PSE}_k, Q) \qquad (1)$$

Observations:

$$p(\text{choice=L}) \sim \frac{1}{1+e^{\alpha(\Delta V - \mathrm{PSE}_k)}} \qquad (2)$$