

Perceiving inter-leg speed differences while walking on a split-belt treadmill

Carl Müller, Karl Kopsike

Cognitive Systems Lab, Institute of Physics, Chemnitz University of Technology,
09126 Chemnitz, Germany

Corresponding author:

Carl Müller

email:

carl.mueller@physik.tu-chemnitz.de

telephone:

+49 371 531-37439

address:

Cognitive Systems Lab, Institute of Physics,
Chemnitz University of Technology,
Reichenhainer Str. 70,
09126 Chemnitz, Germany.

Manuscript overall word count: 6480

1 **Abstract**

2 Walking is one of the most common forms of self-motion in humans. Most humans can walk
3 effortlessly over flat uniform terrain, but also a variety of more challenging surfaces, as they
4 adjust their gait to the demands of the terrain. In this, they rely in part on the perception of
5 their own gait and of when it needs to be adjusted. Here, we investigated how well N=48
6 participants detected speed differences between two belts of a split-belt treadmill. As
7 participants walked at a constant speed, we either accelerated or decelerated one of the
8 belts at quasi-random intervals and asked participants to judge their relative speeds in a
9 two-alternative forced-choice task. Using an adaptive psychophysical procedure, we
10 obtained precise perception-threshold estimates for inter-leg speed differences after
11 accelerating or decelerating one belt. We found that most participants could detect even
12 very small speed differences, with mean threshold estimates of just over 7% for both
13 perturbation types. These were relatively stable within, but highly variable across
14 participants. Increased-speed and decreased-speed thresholds were highly correlated,
15 indicating that despite different biomechanics, the detection mechanisms might be similar.
16 This sheds light on how perceiving their own motion helps humans manage interlimb
17 coordination in perturbed walking.

18 Keywords: self-motion, perception and action, just-noticeable differences, walking,
19 sensorimotor adaptation

20 Introduction

21 Walking is one of the most universal forms of locomotion for humans. In order to ensure a
22 safe gait, humans have to continuously adjust their movements to changes in the
23 environment [1] to deal with flat and uniform terrain, as well as slippery surfaces [2] and
24 obstacles [3], taking into account both their environment and their own self-motion. This
25 process of continuous recalibration is common to most motor actions, but especially
26 important in walking, as gait instability caused by disturbances like slips or stumbles can lead
27 to falls, which are highly associated with fractures or serious injuries [4,5].

28 A well-established way to measure motor adjustments is experimentally introducing
29 perturbations and observing the motor output, or physiological responses such as EMG [6].
30 For example, participants may adapt their gait by adjusting kinematics like step length,
31 double-support time or stride-length, the latter in particular being a popular measure of gait
32 adaptation in real-world walking situations, when walking also curves than straight lines [6–
33 9]. Further, gait may be also adapted by changes in kinetics like joint angles, limb positions
34 or the muscular outputs resulting for instance in changes in the ground reaction forces
35 [10,11]. It has been shown that such sensorimotor adjustments can occur both with and
36 without the actor detecting the perturbations, that is, *explicitly* and *implicitly* [12].
37 Sensorimotor learning [13] combines these explicit and implicit adaptation processes [14],
38 with a broad involvement of explicit strategies in adaptation [15]. In walking, relations
39 between detecting perturbations and adaptation were shown by Hoogkamer et al. (2015), as
40 participants with a lower perception threshold walked with less asymmetry in stance time
41 but more asymmetry in limb excursion in response to split-belt speed perturbations. From
42 these results follows the hypothesis that the awareness of perturbations might play a key
43 role in recalibrating sensorimotor actions to prevent falls and injuries. To clarify under what
44 conditions participants consciously perceive the perturbation of their gait and thus could
45 apply explicit strategies for adapting their gait, it is important to determine how well
46 humans can detect typical perturbations of self-motion.

47 Psychophysical investigations of detecting perturbations in walking often measure
48 the perception threshold of inter-leg speed differences by introducing split-belt
49 perturbations [8,16–18]. That is, experimenters will present different belt speeds for each
50 leg, ask participants to judge the relative speeds of the belts, and measure the just-
51 noticeable differences (JNDs) for participants perceiving the motion of the belts and their

52 own perturbed walking apparatus. Typically, participants walk on a split-belt treadmill, while
53 speed is perturbed for a period of time ranging from only a single stance phase [18] or one
54 full stride cycle [17], to multiple steps [9] and even up to 2 minutes walking [16].
55 Perturbation duration mainly depends on methods such as the perception threshold
56 paradigm [16,19], increasing perturbation each second up to a defined maximum speed
57 difference, discrimination tasks [9,18] mostly with short perturbation times and a self-
58 selected walking speed or by using a two-alternative forced-choice (2AFC) task [17], with
59 defined speed perturbations for each participant over a full stride cycle. Mean JNDs of split-
60 belt speed perturbations obtained from these paradigms range from $< 9\%$ [17] up to 13%
61 [16] for young and healthy participants, but vary depending on these different procedures,
62 psychophysical methods and experimental setup. Further, the number of trials combined
63 with small sample sizes and often relatively few trials near the perception threshold, means
64 that estimates of JNDs for split-belt speed perturbations from individual studies can be less
65 precise and reliable than we would wish, and more importantly, certain parameters such as
66 inter-individual variability cannot be sensibly estimated at all.

67 In most recent studies, experimenters looked exclusively at the detection of treadmill
68 belt *acceleration* perturbations [16]. Less is known about detection performance if one belt
69 is suddenly *decelerated*. While mismatches in many classic psychophysics like visual motion
70 perception are symmetrical in that making one stimulus less intense can be considered
71 equivalent to making another more intense [20], this is not the case in self-motion
72 perception, which is typically supported by a variety of signals that may respond differently
73 to externally induced changes, and specifically in walking. Biomechanically, a deceleration
74 leading to stumbling will lead to the braking force compressing joints and limbs while placing
75 the foot, rather than stretching these as happens while accelerating, thus further leading to
76 different receptors being used, respectively [21,22]. These fundamental differences might
77 also result in changes in the JNDs. Thus, it is important to determine the precise perception
78 threshold (JND) for each perturbation type individually to investigate distinct properties
79 leading to a better detection performance, which motivates our main questions: (i) how well
80 can participants detect speed differences between legs, (ii) how large the variability in this
81 between participants is, and (iii) if there are differences in the JNDs and variability between
82 perturbations with *increased* and *decreased* speed. Using a large sample, we investigated
83 the perception thresholds (JNDs) of speed-increase and speed-decrease perturbations while

84 split-belt walking. To do this, we changed the speed of the perturbed belt during swing
85 phase so that participants were exposed to sudden speed differences between belts. As a
86 methodological improvement, perturbations were introduced using an adaptive method, the
87 QUEST procedure [23], which provides an on-the-fly estimate of the threshold after each
88 trial during the experiment based on the previous responses in the 2AFC task, thus
89 characterizing participants' perturbation detection. We also quantify the similarity between
90 perturbation types, which had previously been hard to determine.

91 **Methods**

92 ***Participants***

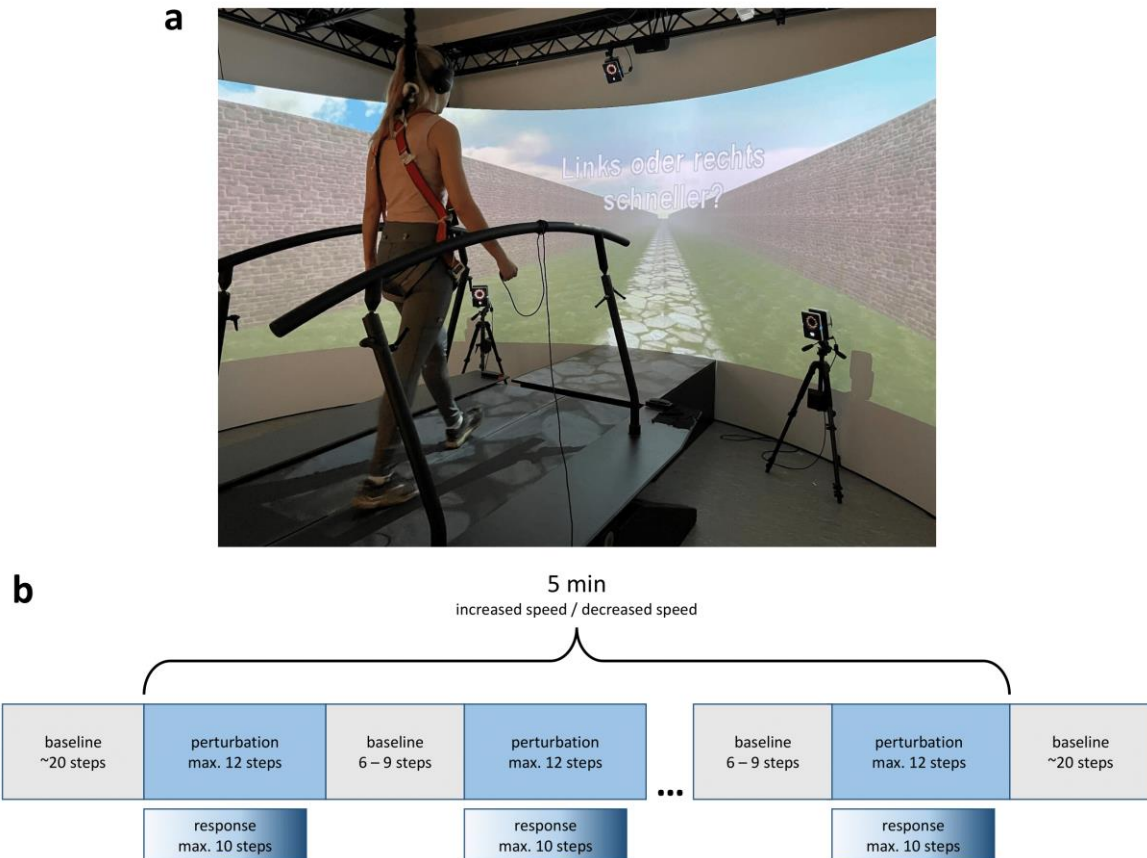
93 A total of N = 52 participants were recruited via a TU-Chemnitz online mailing list.
94 Participants were eligible if they had no neurological or walking impairments and a body
95 mass of less than 130 kg (the latter due to technical constraints of the setup). Four
96 participants had to be excluded from analysis due to technical issues. This left us with an
97 eventual sample of N = 48. No power analysis was conducted since our main goal was not
98 hypothesis testing but parameter estimation and variability was difficult to estimate from
99 previous studies. The analyzed sample included 35 women and 13 men with an average age
100 of 22.0 years (between 19 and 37), average height of 171.5 cm \pm a standard deviation of 8.5
101 cm, average body mass 65 kg \pm 11 kg and average leg length of 92.4 cm \pm 5.0 cm. These
102 measurements were used for motion tracking and collected after participants reported
103 being sufficiently rested and focused to complete the experiment in a questionnaire prior to
104 the experiment. Participants were naïve to the experimental hypotheses. After participation,
105 participants were debriefed and received either course credit or a monetary reimbursement
106 of 10€/h. All experimental procedures were in accordance with the 2013 Declaration of
107 Helsinki as well as approved by the appropriate body (Chemnitz University of Technology
108 ethics committee, reference no. 101628179) and participant data were protected according
109 to institutional regulations.

110 ***Setup and procedure***

111 Participants walked on a split-belt treadmill in a GRAIL system allowing high-precision real-
112 time motion capture in front of a curved 240° projection screen (figure 1a). The visual
113 environment was a naturalistically simulated endless road scene with lateral walls, projected

Perceiving split-belt speed differences

114 2.5 m in front of the participant at 60 Hz enhanced by a floor projection on the treadmill.
115 Each belt could be accelerated separately with minimal delay [24] to induce speed
116 perturbations, which were triggered using ground-reaction forces (GRFs) recorded at 250 Hz
117 by force plates below each belt.



118

119 *Figure 1.* Experimental setup and procedure

120 **a:** Virtual environment with a participant walking on the split-belt treadmill along an endless road
121 scene, secured with a safety harness while holding the response controller. Infrared cameras around
122 the treadmill recorded marker positions. The question used for the 2AFC task was displayed on the
123 screen (German: „Links oder rechts schneller?“, translating to “left or right faster?”), indicating
124 participants to give a response. **b:** Procedure of the experimental blocks, each starting with a
125 baseline phase, then altering between perturbations (block-wise either speed increases or decreases)
126 and short baseline periods for 5 minutes and ending with baseline walking. The number of perturbed
127 steps depended on the response timing with a maximum of 10 steps, baseline steps were
128 randomized between 6 to 9 steps between perturbation trials.

129 For motion capture, we used the Vicon Plug-In Gait lower-body model (Vicon Motion
130 Systems, Yarnton, UK) with 16 retro-reflective markers placed on participants’ body
131 segments. This preparation was always done by the same experimenter to increase
132 reliability [25]. The exact three-dimensional position of the markers was recorded at 250 Hz
133 by 10 infrared cameras at different positions around the treadmill.

134 Prior the experiment, we measured participants' biometric dimensions necessary for
135 the gait model (including height and leg length), applied markers, and calibrated the gait
136 model using a standard procedure (consisting of a T-pose and 5 s of walking). Each
137 experiment started with two training sessions of 1 min perturbed walking, one each for
138 speed being increased on the perturbed belt and one for it being decreased. These were
139 followed by 4 experimental blocks, each with a duration of 5 min perturbed walking and
140 again each consisting of either increased speed on the perturbed belt or speeds being
141 decreased. Walking started by accelerating both belts from 0 m/s to 1 m/s baseline speed in
142 5 steps at 0.2 m/s, followed by approximately 15 s of baseline walking before the
143 experimenter manually started the first perturbation period (figure 1b). A fixed baseline
144 speed was chosen for several reasons: First, keeping the speed constant both within and
145 between participants allows to compare speed differences and perceptual thresholds.
146 Further, using a fixed and somewhat slower speed decreases the risk of too strong
147 perturbations that might lead to falls or injuries and has been shown to not strongly affect
148 the resulting thresholds [16,19]. Motor perturbations were speed differences between the
149 right and the left belt, lasting a maximum of 12 steps on constant speed, with one belt being
150 accelerated or decelerated during first swing phase of each perturbation period and the
151 other continuing to run at baseline speed. We used acceleration and deceleration rates of 3
152 m/s^2 and $-3 m/s^2$, respectively, which was sufficient for the belt to reach the target speed
153 during swing phase so that participants experienced the new speed, but not the acceleration
154 or deceleration. The perturbed side was randomly chosen for each perturbation of up to 12
155 steps, and the magnitude of the perturbation (e.g. the speed difference from baseline) was
156 calculated for each perturbation period by using a QUEST procedure (see section "Stimuli
157 and manipulations"). In a 2AFC task, participants had to respond via button press whether
158 the left or the right belt was running faster. Three steps after perturbation onset, the
159 question (German: „Links oder rechts schneller?“, translating to "left or right faster?") was
160 displayed on the screen. Participants had a maximum of 10 steps within each perturbation
161 period to give their response by pressing either the left or the right button on a handheld
162 controller but were not instructed to respond as quickly as possible. After giving their
163 response or reaching the maximum step count (in which case the response was counted as a
164 wrong answer and a message was briefly displayed on the screen to respond more quickly
165 the next trial: "Bitte etwas schneller antworten!", German for "Respond a bit more quickly,

166 please!”), the perturbed belt returned to back to baseline speed after two more steps, and
167 after another 6 - 9 steps (randomized for each perturbation), the next perturbation started.
168 While walking, participants wore noise-cancelling headphones to prevent them from using
169 auditory cues to which belt was changing speed.

170 ***Stimuli and manipulations***

171 The main manipulation were speed differences between the left and the right belt of the
172 treadmill, to be judged by the participants. These judgements were used to estimate the
173 just-noticeable speed differences and adjust the strength of the next perturbation
174 accordingly, using a QUEST procedure [23], an adaptive psychophysical method for threshold
175 measurement, where the best threshold estimate is updated on each trial and presented on
176 the next trial. This method is often used for estimating various sensory thresholds as it
177 increases trials near individual thresholds, resulting in higher reliability compared to many
178 other threshold measurements [26,27]. For the first threshold estimation and thus strength
179 of the first perturbation, we used a rather conservative estimate based on previous findings
180 in other split-belt setups [16–18] of 10% difference between belts, that is, 0.1 m/s. We set
181 the parameters of the QUEST to account for the properties of our design: the standard
182 deviation was set to the relatively large value of 0.4 m/s, to account for the fact that we used
183 two different perturbation types (speed increased and decreased). We set the other
184 parameters to $\beta = 3.5$ and $\delta = 0.01$, typical values suggested by Watson and Pelli [23]. Thus,
185 each block started with a perturbation of $1 \text{ m/s} \pm 0.1 \text{ m/s}$ and all following perturbation
186 magnitudes were calculated using the QUEST. We did not use a termination criterion but
187 instead used blocks of 5 minutes of perturbed walking, which was comfortable for all
188 participants and avoided fatigue. Thus, number of trials (i.e. perturbations) within the QUEST
189 varied between blocks for each participant. The last JND estimate of each block (which, in a
190 QUEST procedure, represents the current best threshold estimate that is updated after each
191 trial and uses the information of all collected trials) was taken as the threshold estimate for
192 the corresponding participant and block.

193 ***Data processing and analyses***

194 Kinematic data from motion capture was processed by applying a cubic-spline interpolation
195 and a Savitzky-Golay Filter [28] with a window of 124 ms to all relevant markers. The mean
196 proportion of missing data was 0.7 %. For step detection, we measured ground-reaction

197 forces (GRFs), calculated the combined forces of both belts, and used the maxima and
198 turning points of the signal filtered with a width of 524 ms (chosen to cover one, but never
199 two steps) to detect steps robustly offline. These measurements were used to analyze *steps*
200 *to response* and to investigate biomechanical adaptation processes.

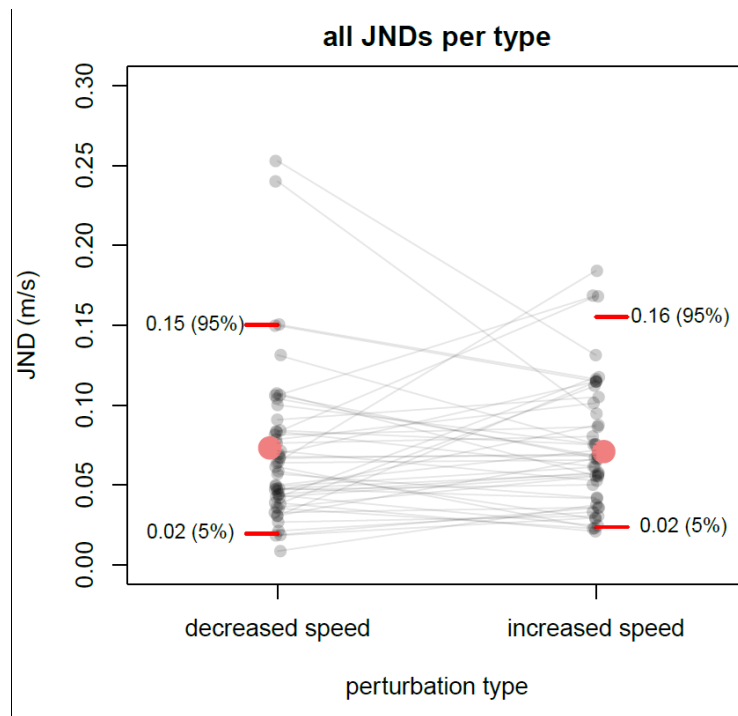
201 Main analyses addressed the threshold estimation of speed perturbations while split-
202 belt walking. For each participant, we received four final threshold estimates, that is, one per
203 block, with two blocks for each of the two perturbation types. We then averaged the JND
204 estimates of the same perturbation type of one participant and compared these JNDs of
205 increased and decreased speeds over all participants using a paired t-test. Further, we
206 calculated 5th and 95th percentiles for JNDs to assess between-participant variability for
207 each perturbation type. Using the block-wise JNDs, we then compared the final JNDs for the
208 two blocks of the same perturbation type by using a paired t-test and further calculated the
209 correlation between block-wise measures within each type to quantify reliability of the JND
210 measurement. These correlations were compared to the correlation between estimates of
211 different types. Considering the relevance of null differences, we additionally calculated
212 Bayes factors corresponding to all t-tests [29], using a medium-width prior ($r = 0.707$ as used
213 by Morey & Rouder, 2018), as well as for all correlation analyses (with a medium-width prior
214 of $r = 0.333$). As additional analyses, we looked at how quickly participants converged to the
215 thresholds, and addressed the question if later responses were aligned with smaller JNDs by
216 correlating the mean *steps to response* and the JNDs separately for the two perturbation
217 types. This could also shed light on possible response strategies, such as that some
218 participants - but not others - deliberately take more time to make the right decision when
219 they are unsure. Data and analysis scripts are available at
220 <https://doi.org/10.17605/OSF.IO/B7K82>.

221 **Results**

222 ***Perception thresholds and variability***

223 We analyzed the detection performance in each perturbation type over all participants and
224 found slightly smaller mean JNDs for decreased-speed perturbations ($JND = 0.071 \pm$ a
225 standard deviation of 0.05 m/s) compared to increased-speed perturbations ($JND = 0.073 \pm$
226 0.04 m/s) but with no statistical difference ($t(47) = 0.34$, $p = .736$), also confirmed by the
227 corresponding Bayesian t-test $BF_{10} = 0.17$. As is standard procedure, non-responses were

228 counted as wrong answers. Their proportion was 2.6 %. As these JNDs are relative to the
 229 baseline speed of 1 m/s, differences in speed can be directly viewed as percentage
 230 differences of 7.1 % (speed increased) and 7.3 % (speed decreased). Individual JNDs per
 231 participant for each perturbation type are shown in figure 2.



232

233 *Figure 2.* JNDs per type for each participant

234 Mean JNDs per participant for increased and decreased speeds. Black semi-transparent dots show
 235 the individual data, the larger red dots the overall mean. Inline descriptions at the red lines indicate
 236 the 5 % and the 95 % quantiles, respectively. Shaded lines connecting threshold of the same
 237 participant.

238 The mean threshold estimates are in the range with typical findings in literature. However,
 239 figure 2 shows that individual thresholds of some participants were much lower than those
 240 means. Making use of our large sample, we looked at the differences between the 5 % and
 241 the 95 % percentiles of JNDs. These were different by a factor of 6.6 for increased speeds,
 242 and a factor of 7.7 for decreased speeds. These factors indicate huge inter-individual
 243 differences in JNDs between the percentiles and within each perturbation type, similarly so
 244 for both types, reaching from 2 % up to 15 % for decreased speeds and up to a JND of 16 %
 245 for increased speeds at the 95 % percentile.

246 ***Stability of the JND measurement***

247 Next, we tested reliability in the mean JNDs of the two blocks for the same perturbation
 248 type. We found descriptively larger JNDs for the first blocks of each type (table 1), but no

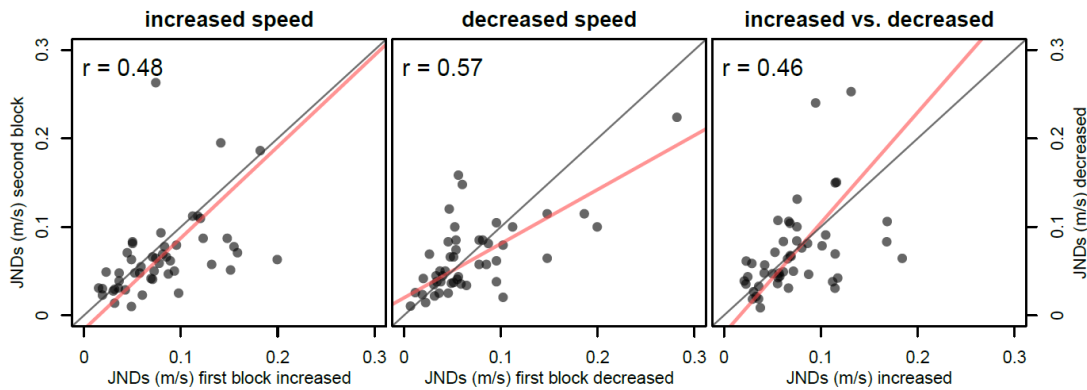
249 statistically significant differences in JNDs compared to the second block, neither for
 250 increased speeds ($t(47) = 1.96, p = .057$) with a corresponding Bayes factor of $BF_{10} = 0.90$,
 251 nor for decreased speeds ($t(47) = 1.18, p = .245$) with $BF_{10} = 0.30$, and again relatively large
 252 variability in the mean threshold estimates. The correlations between the first and second
 253 block were comparable for the two types of perturbation (increase-blocks: $r = .48$, figure3,
 254 panel 1; decrease-blocks: $r = .57$, figure 3, panel 2), indicating high reliability.

255 **Table 1:**

256 *Mean JNDs per block and perturbation type with standard deviation.*

JND	increased speed (\pm sd)	decreased speed (\pm sd)
first block	7.99 \pm 4.5 %	7.57 \pm 6.9 %
second block	6.66 \pm 4.7 %	6.61 \pm 4.2 %

257 *Note:* First and second block refers to the first and second block of each perturbation type,
 258 respectively, as each participant completed two blocks with increased-speed perturbations
 259 and two blocks with decreased-speed perturbations. Displayed are arithmetic means across
 260 participants and the corresponding standard deviations.



261
 262 **Figure 3.** Correlations of mean JNDs per type
 263 Correlation of mean JNDs for first and second occurred blocks of increased-speed perturbations
 264 (panel 1) and decreased-speed perturbations (panel 2) as well as for overall increase and decrease
 265 blocks (panel 3). Each dot represents one participant, the red lines indicate the Deming corrected
 266 regression line. Solid black line indicates unity.

267 Being able to calculate reliabilities for each perturbation type also allowed us to compare
 268 these to the correlation between increased-speed perturbations and decreased-speed
 269 perturbations. This was of particular interest, as both types provide some shared, but also
 270 some different sources of information (e.g. biomechanical cues) to detect differences – thus,

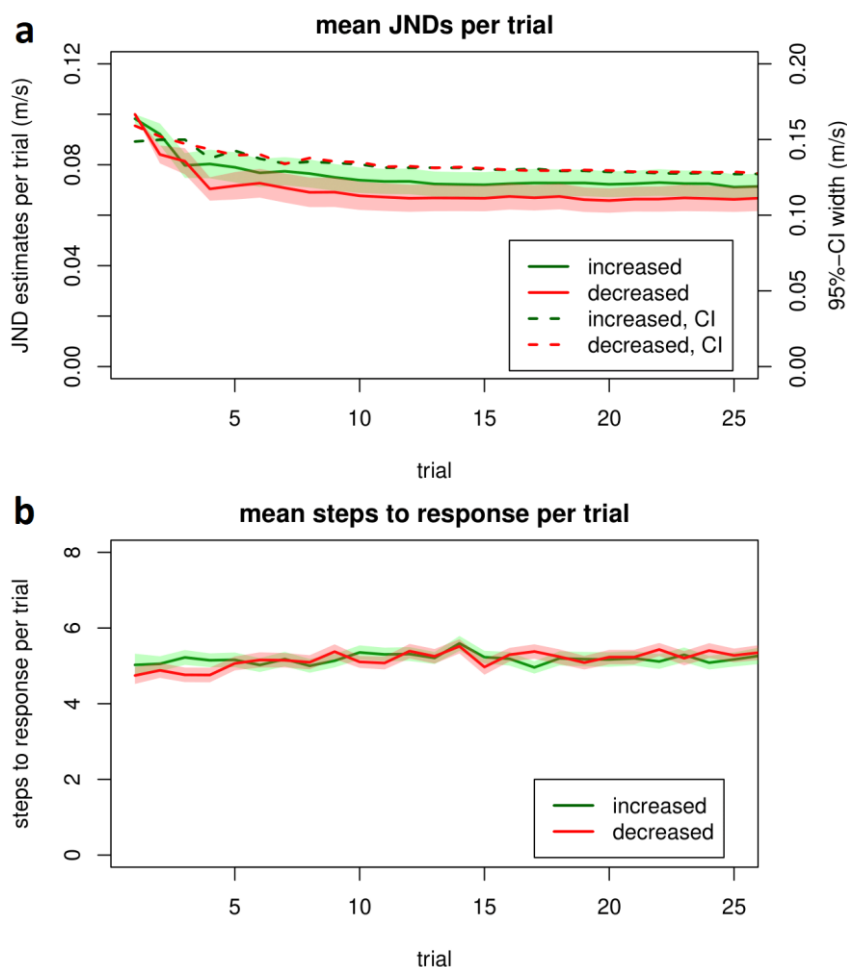
271 it is not clear a priori whether detecting increases and decreases in speed would be based on
 272 the same cues. Across participants, we found a correlation of the mean JNDs for increases
 273 and decreases of $r = .46$ (figure 3, panel 3). This does not differ significantly from the
 274 theoretical upper bound of a correlation of two imperfectly measured variables given their
 275 reliabilities, which is given by

$$276 \quad r_{y_1, y_2 \max} = \sqrt{r_{y_1, y_1} * r_{y_2, y_2}} \quad (1)$$

277 [31]. Here, the observed correlation of $r = .46$ was not significantly different from $r_{\max} =$
 278 $\sqrt{0.48 * 0.57} = 0.52$ with $t(46) = -0.44$, $p = .662$. A Bayesian analysis using the 95%
 279 confidence interval of r_{\max} as the null-interval gave us a $BF_{01} = 20.48$ for the correlation being
 280 within this interval vs. it being outside of it, that is, strong evidence against a difference
 281 between r and r_{\max} . The vast majority of variability in the JNDs was thus between
 282 participants rather than between the different perturbation types.

283 ***Effects of timing and responses***

284 To further investigate possible differences in the detection of speed increases and
 285 decreases, we looked at how quickly the respective thresholds were reached. Figure 4a
 286 shows the mean trajectories of the absolute threshold estimates for increases and
 287 decreases. Both approach the threshold very quickly and then show asymptotic behavior.
 288 SEM (shaded areas; ± 1 SEM) of increases and decreases overlap over the whole trajectories,
 289 indicating again no difference between types. We also plotted the mean width of the 95%
 290 confidence interval of the probability density function for each trial (dashed lines), which
 291 quantify the mean precision of the estimate (in contrast to the shaded error bars, which
 292 quantify between-participant variability and this the precision of the mean estimate). These
 293 widths showed a similar asymptotic behavior as the threshold estimates, also with no
 294 difference between perturbation types.



295

296 *Figure 4.* Trajectories of threshold estimates and mean steps to response
 297 **a:** Mean trajectories of the absolute threshold estimates for increased-speed perturbations (green)
 298 and decreased-speed perturbations (red) for each trial per block. The x axes end with the minimum
 299 number of trials presented to any participant in any block (this number could vary as we fixed the
 300 time and not number of perturbations per block). Shaded areas indicate ± 1 between-participant
 301 SEM. Threshold estimates started at 10 % and rapidly and roughly asymptotically approached range
 302 of the final JND for both perturbation types. Dashed lines show the mean width of the 95%-
 303 confidence intervals of the estimates for each trial, computed from the QUEST's probability density
 304 function. **b:** Mean *steps to response* for each trial, depending on the perturbation type. Trajectories
 305 did not differ between increases (green) and decreases (red).

306 Next, we investigated the average number of steps per trial needed to give a response
 307 ("*steps to response*"). Overall, participants responded on average after 5.11 ± 1.8 steps.
 308 Splitting up by perturbation type, no difference was found between increases (5.12 ± 1.8)
 309 and decreases (5.11 ± 1.8), ($t(47) = -0.04, p = .969$) with a corresponding Bayes factor of BF_{10}
 310 = 0.16. In line with these findings, trajectories again did not differ by type and both showed
 311 an asymptotic pattern (figure 4a). We then investigated whether there was an overall
 312 relationship between response speed and threshold – whether participants who responded
 313 quicker were better or worse at detection than those that responded more slowly. To avoid

314 individual differences in how quickly participants got accustomed to the task and maximize
315 the chance of getting trials close to threshold (so the subjective difficulty should be
316 comparable), we looked specifically at trials 16 to 25. These were chosen because no
317 participant completed fewer than 25 trials in any block.

318 The overall correlations of mean *steps to response* and mean JNDs over these trials,
319 calculated per participant and perturbation type was $r = -.28$ ($t(94) = -2.86$, $p = .005$, $BF_{10} =$
320 9.48), and for speed increases $r = -.36$ ($t(46) = -2.58$, $p = .013$, $BF_{10} = 5.13$) and decreases $r = -$
321 $.23$ ($t(46) = -1.58$, $p = .121$, $BF_{10} = 0.95$). Thus, participants who took longer with their
322 responses were descriptively somewhat better at detecting the perturbations, perhaps
323 indicating different response strategies, but the data pattern was not conclusive.

324 Discussion

325 Here, we measured the perception threshold of inter-leg speed differences for increased-
326 speed and decreased-speed perturbations while walking. We provide precise JNDs for speed
327 differences, measured with an adaptive procedure on a large sample. Interestingly, we
328 found no differences in average JNDs between increases and decreases, while our results
329 indicate a considerable variability between *participants* for both perturbation types. Further,
330 we show that the reliability of the JND estimates within each perturbation type was
331 comparable to the correlation between JNDs for each type, suggesting that similar cues are
332 used for each.

333 Knowing when participants are aware of perturbations can be of interest for a variety
334 of reasons: To know when they might apply explicit strategies to adjust the corresponding
335 motor actions, to better understand self-motion perception by understanding when humans
336 notice that it is externally manipulated, or to know whether an experimental manipulation
337 will work. For this, robust estimates of perception thresholds are fundamental. Our average
338 threshold estimates for speed increases and decreases are somewhat lower ($< 8\%$) than in
339 previous findings [16,17]. However, in contrast to studies that perturbing one full stride cycle
340 or a single stance phase [17,18], we induced perturbations over multiple steps, thereby
341 placing less emphasis on responding quickly to instead focus only on accuracy, and finding
342 some participants' individual thresholds seem to be even much lower, as we show for the
343 first time in a large sample. In addition to testing more participants than is typically the case,
344 we also had the advantage of using an adaptive threshold measurement, the QUEST

345 procedure, as it enables individual threshold estimations for a wide range and higher
346 resolution compared to constant stimuli presentation or methods of limits [16]. This has
347 several advantages: Motivation is optimized, ground and ceiling effects are avoided, trials far
348 from thresholds are taken less into account (e.g. difficulties in understanding instructions or
349 response mappings) and particularly, on-the-fly measurements provide a large number of
350 estimates near the actual threshold. In fact, when analyzing our data, we found that we
351 could have likely made even more optimal use of this method, as asymptotic behavior of
352 both the estimates and the estimate precision (figure 4a) was visible after as little as 15
353 trials. Consequently, the measured JNDs were relatively stable, as our reliability estimates
354 (provided by the correlations between consecutive blocks of the same perturbation type)
355 show. It will be interesting to investigate what factors may be behind these strong inter-
356 individual differences in perturbation detection. Starting points for future research could for
357 example be bodily self-awareness, footwear or experience in treadmill walking [32].

358 That said, there are some limitations of our study. One is related to the instruction of
359 the question to be answered. As we were interested in the detection of the perturbation, we
360 used a 2AFC task asking “left or right faster” (instead of “which belt is manipulated”).
361 However, this could lead to an asymmetry in responses, as for example a decelerating
362 perturbation is induced on the left side, but the correct response in this case is “right belt
363 running faster”. It may also lead participants to focus on speed differences rather than
364 immediate biomechanical consequences of an acceleration or deceleration. It can also be
365 confusing to participants if they are close to threshold and hardly able to distinguish the
366 perception of “left belt running faster” and “right belt running faster”. To account for this, a
367 possible approach may be to assess the perturbation detection by using a physiological
368 marker such as pupillometry.

369 We also compared in-depth the detection performances of increased speed and
370 decreased speed, respectively. It is plausible to expect differences here, because
371 biomechanical dynamics, receptors and information differ [33] and could lead to a different
372 perception of the same speed differences. Interestingly, we found no difference in the mean
373 perception threshold for speed perturbations between increases and decreases, despite the
374 physiological differences between perturbation types and for both, our results indicate that
375 participants could detect even small speed differences. Further, individuals’ JNDs for the two
376 perturbation types were highly correlated, to an extent as one would expect from the

377 respective reliabilities with two perfectly correlated constructs, and the majority of
378 variability was between participants, not perturbation types. This means that participants
379 who are good at detecting one perturbation also tend to be good at detecting the other
380 perturbation and suggests that detecting speed differences is based on similar mechanics for
381 speed increases and decreases.

382 As expected, participants rapidly reached an asymptote while approaching their
383 individual threshold. Here, too, we found similar trajectories for both perturbation types
384 when looking at the mean trial-wise threshold estimates (figure 4a). Finally, we investigated
385 whether response strategies may be behind the large observed variability between
386 participants. A potential explanation might be that participants with smaller JNDs may use
387 more steps for collecting more information about the perturbation before giving a (then
388 more thorough) response. We calculated the correlation of the mean *steps to response* and
389 the JND of each participant, finding – though only descriptively for speed decreases – the
390 suspected negative trend overall and for increases as well as decreases, indicating that more
391 steps were associated with lower JNDs.

392 In our experiment, we focused on the precise measurement of individual JNDs.
393 Certain related measures or experimental variations may also be of interest, but beyond the
394 scope of this particular study. First, perturbations lasted a maximum of only 10 steps, so we
395 can exclude adaptation effects, as most split-belt adaptation paradigms last about 2 minutes
396 [16]. Within 10 steps, one might look at fast adjustments in step length asymmetry or
397 carefully at motor aftereffects, but it may not be feasible to distinguish fast and slow
398 adaptation components and analyze gait patterns [8,34,35]. However, even short-term
399 adjustments are difficult to quantify since we used an adaptive procedure to determine the
400 strength of the perturbations, meaning that each participant was exposed to a different set
401 of perturbations. Second, in contrast to previous gait studies [9,18], we did not use a self-
402 selected walking speed but a fixed baseline speed of 1 m/s for our QUEST procedure. While
403 this speed has been proven to be a comfortable speed to induce motor perturbations while
404 participants performed another task in previous studies using the same setup [36], one
405 might conceivably obtain different results with self-selected speeds [37], or by applying
406 normalization procedures based on leg length or stability [38], which could be interesting to
407 investigate. Third, generalizability is an important issue as walking behavior depends on a
408 large range of parameters and their interactions [8,37,39], only some of which can be

409 manipulated here. For example, using young and healthy adults likely affected our results
410 [16,19], as did the choice of the baseline speed [16,18]. Environmental setups often varied
411 between experiments, for example with visual environments sometimes reduced [9] or even
412 largely missing [18], so we aimed for a more ecologically valid set of parameters using this
413 dynamic environment that might improve detection performance by providing also visual
414 information to make walking more realistic. Comparing different environments and
415 manipulating visual information might also reveal differences in thresholds [16].

416 Taken together, we report precise estimates of speed-difference thresholds in split-
417 belt walking for increased-speed and decreased-speed perturbations in young and healthy
418 participants. We show that individual threshold for speed increases and decreases are
419 comparable within participants and variability is mainly found between participants. These
420 results emphasize the importance of considering individual differences while investigating
421 perturbation detection and potentially explicit sensorimotor adaptation, and thus provide
422 implication for a variety of research in self-motion perception, sensorimotor adaptation, and
423 fall prevention.

424 **Acknowledgements**

425 We thank Alina Schenk for her help during data collection and Alexandra Bendixen for
426 helpful comments on the manuscript. This work was supported by a grant from the German
427 Research Foundation (DFG) to KK (DFG KO 6478-1/1; project number 466287772).

428 **Additional Information**

429 ***Competing interests***

430 On behalf of all authors, the corresponding author states that there are no competing
431 interests.

432 ***Consent to participate***

433 After being fully informed about the study, participants consented in writing to participate
434 prior to the experiment.

435 ***Consent for publication***

436 Participants consented in writing for their data to be made publicly available prior to the
437 experiment.

438 ***Data Availability***

439 Merged data for all experiments are available at <https://doi.org/10.17605/OSF.IO/B7K82>.

References

1. Gibson, J. J. Visually controlled locomotion and visual orientation in animals. *Br. J. Psychol.* **49**, 182–194 (1958).
2. Marigold, D. S. & Patla, A. E. Strategies for Dynamic Stability During Locomotion on a Slippery Surface: Effects of Prior Experience and Knowledge. *J. Neurophysiol.* **88**, 339–353 (2002).
3. Weerdesteyn, V., Nienhuis, B., Hampsink, B. & Duysens, J. Gait adjustments in response to an obstacle are faster than voluntary reactions. *Hum. Mov. Sci.* **23**, 351–363 (2004).
4. Luukinen, H. *et al.* Fracture Risk Associated with a Fall According to Type of Fall Among the Elderly. *Osteoporos. Int.* **11**, 631–634 (2000).
5. Oliver, D. Risk factors and risk assessment tools for falls in hospital in-patients: a systematic review. *Age Ageing* **33**, 122–130 (2004).
6. Iturralde, P. A. & Torres-Oviedo, G. Corrective Muscle Activity Reveals Subject-Specific Sensorimotor Recalibration. *eneuro* **6**, ENEURO.0358-18.2019 (2019).
7. Hoogkamer, W., Bruijn, S. M. & Duysens, J. Stride length asymmetry in split-belt locomotion. *Gait Posture* **39**, 652–654 (2014).
8. Reisman, D. S., Block, H. J. & Bastian, A. J. Interlimb Coordination During Locomotion: What Can be Adapted and Stored? *J. Neurophysiol.* **94**, 2403–2415 (2005).
9. Wutzke, C. J., Faldowski, R. A. & Lewek, M. D. Individuals Poststroke Do Not Perceive Their Spatiotemporal Gait Asymmetries as Abnormal. *Phys. Ther.* **95**, 1244–1253 (2015).

10. Mawase, F., Haizler, T., Bar-Haim, S. & Karniel, A. Kinetic adaptation during locomotion on a split-belt treadmill. *J. Neurophysiol.* **109**, 2216–2227 (2013).
11. Ogawa, T., Kawashima, N., Ogata, T. & Nakazawa, K. Predictive control of ankle stiffness at heel contact is a key element of locomotor adaptation during split-belt treadmill walking in humans. *J. Neurophysiol.* **111**, 722–732 (2014).
12. Taylor, J. A., Krakauer, J. W. & Ivry, R. B. Explicit and Implicit Contributions to Learning in a Sensorimotor Adaptation Task. *J. Neurosci.* **34**, 3023–3032 (2014).
13. Krakauer, J. W. & Mazzoni, P. Human sensorimotor learning: adaptation, skill, and beyond. *Sens. Mot. Syst.* **21**, 636–644 (2011).
14. Mazzoni, P. & Krakauer, J. W. An Implicit Plan Overrides an Explicit Strategy during Visuomotor Adaptation. *J. Neurosci.* **26**, 3642–3645 (2006).
15. McDougale, S. D., Ivry, R. B. & Taylor, J. A. Taking Aim at the Cognitive Side of Learning in Sensorimotor Adaptation Tasks. *Trends Cogn. Sci.* **20**, 535–544 (2016).
16. Hoogkamer, W. *et al.* Gait asymmetry during early split-belt walking is related to perception of belt speed difference. *J. Neurophysiol.* **114**, 1705–1712 (2015).
17. Iturralde, P. A., Gonzalez-Rubio, M. & Torres-Oviedo, G. *High-human acuity of speed asymmetry during walking.* (Bioengineering, 2020). doi:10.1101/2020.10.28.359281
18. Liss, D. J., Carey, H. D., Yakovenko, S. & Allen, J. L. Young adults perceive small disturbances to their walking balance even when distracted. *Gait Posture* **91**, 198–204 (2022).
19. Lauzière, S., Miéville, C., Duclos, C., Aissaoui, R. & Nadeau, S. Perception Threshold of Locomotor Symmetry While Walking on a Split-Belt Treadmill in Healthy Elderly Individuals. *Percept. Mot. Skills* **118**, 475–490 (2014).

20. Anobile, G., Tomaiuolo, F., Campana, S. & Cicchini, G. M. Three-systems for visual numerosity: A single case study. *Neuropsychologia* **136**, 107259 (2020).
21. Dietz, V., Horstmann, G. & Berger, W. Involvement of different receptors in the regulation of human posture. *Neurosci. Lett.* **94**, 82–87 (1988).
22. Redfern, M. S. *et al.* Biomechanics of slips. *Ergonomics* **44**, 1138–1166 (2001).
23. Watson, A. B. & Pelli, D. G. Quest: A Bayesian adaptive psychometric method. *Percept. Psychophys.* **33**, 113–120 (1983).
24. Sessoms, P. H. *et al.* Method for evoking a trip-like response using a treadmill-based perturbation during locomotion. *J. Biomech.* **47**, 277–280 (2014).
25. McGinley, J. L., Baker, R., Wolfe, R. & Morris, M. E. The reliability of three-dimensional kinematic gait measurements: A systematic review. *Gait Posture* **29**, 360–369 (2009).
26. Höchenberger, R. & Ohla, K. Estimation of Olfactory Sensitivity Using a Bayesian Adaptive Method. *Nutrients* **11**, 1278 (2019).
27. Nguyen, A., Rothacher, Y., Lenggenhager, B., Brugger, P. & Kunz, A. Individual differences and impact of gender on curvature redirection thresholds. in *Proc. 15th ACM Symp. Appl. Percept.* 1–4 (ACM, 2018). doi:10.1145/3225153.3225155
28. Savitzky, Abraham. & Golay, M. J. E. Smoothing and Differentiation of Data by Simplified Least Squares Procedures. *Anal. Chem.* **36**, 1627–1639 (1964).
29. Rouder, J. N., Speckman, P. L., Sun, D., Morey, R. D. & Iverson, G. Bayesian t tests for accepting and rejecting the null hypothesis. *Psychon. Bull. Rev.* **16**, 225–237 (2009).
30. Morey, R. D. & Rouder, J. N. Package ‘BayesFactor.’ Retrieved from. (2018). at <<https://cran.r-project.org/web/packages/BayesFactor/index.html>>
31. Nunnally, J. C. *Psychometric theory.* (McGraw-Hill, 1967).

32. Meyer, C. *et al.* Familiarization with treadmill walking: How much is enough? *Sci. Rep.* **9**, 5232 (2019).
33. Tideiksaar, R. in *Slips Stumbles Falls Pedestr. Footwear Surf.* 17–27 (ASTM International 100 Barr Harbor Drive, PO Box C700, West Conshohocken, PA 19428-2959, 1990). doi:10.1520/STP15498S
34. Malone, L. A. & Bastian, A. J. Thinking About Walking: Effects of Conscious Correction Versus Distraction on Locomotor Adaptation. *J. Neurophysiol.* **103**, 1954–1962 (2010).
35. McDougle, S. D., Bond, K. M. & Taylor, J. A. Explicit and Implicit Processes Constitute the Fast and Slow Processes of Sensorimotor Learning. *J. Neurosci.* **35**, 9568–9579 (2015).
36. Müller, C., Baumann, T., Einhäuser, W. & Kopiske, K. Slipping while counting: gaze–gait interactions during perturbed walking under dual-task conditions. *Exp. Brain Res.* (2023). doi:10.1007/s00221-023-06560-6
37. Fukuchi, C. A., Fukuchi, R. K. & Duarte, M. Effects of walking speed on gait biomechanics in healthy participants: a systematic review and meta-analysis. *Syst. Rev.* **8**, 153 (2019).
38. McCrum, C., Willems, P., Karamanidis, K. & Meijer, K. Stability-normalised walking speed: A new approach for human gait perturbation research. *J. Biomech.* **87**, 48–53 (2019).
39. Scataglini, S., Verwulgen, S., Roosens, E., Haelterman, R. & Van Tiggelen, D. Measuring Spatiotemporal Parameters on Treadmill Walking Using Wearable Inertial System. *Sensors* **21**, 4441 (2021).

Authors' contributions

Carl Müller: Methodology, Software, Validation, Formal analysis, Investigation, Data Curation, Writing – Original Draft, Visualization. **Karl Kopiske:** Conceptualization, Methodology, Software, Validation, Formal analysis, Data Curation, Writing – Original Draft, Visualization, Project administration, Supervision, Funding acquisition.

