Sensorimotor adaptation affects detection of and pupil response to motor perturbations

Karl Kopiske [*], Carl Müller [†]

Abstract

Much recent research on sensorimotor adaptation has focussed on its cognitive side and how adaptation differs when it it cognitively controlled. Here, we investigate more closely what makes different types of perturbations detectable. We used different perturbation schedules to contrast how the magnitude of a motor perturbation and the associated error signal contribute to its detectability. We manipulated perturbation either following an unpredictable de Bruijn sequence, maximising the error signal, or a ramp perturbation, incrementally increasing perturbations and thus minimising error by allowing continuous adaptation. We did this in two different experiments using two perturbed everyday actions, walking with a split-belt speed perturbation (experiment 1) and grasping with a visuo-haptic size mismatch (experiment 2). In each experiment, N=48 participants were asked to judge the relevant dimension, either the relative speed of the treadmill belts, or the relative size of the objects to be grasped, while we measured participants' pupil dilation and investigated if this could serve as a no-report marker of perturbation detection. We found that participants reliably adapted to the incrementally introduced ramp perturbation and concurrently showed reduced perturbation detection relative to de Bruijn sequence perturbations. Tonic pupil-dilation parameters were sensitive to both perturbation magnitude and the type of perturbation, consistent with an effect of uncertainty. Pupil responses also differed depending on the detection response, but not sufficiently to allow trialwise classification. These patterns occurred both in walking and in grasping, with only minor differences, suggesting that the underlying mechanisms may be similar and potentially generalisable across motor actions.

Keywords: Perception & action, walking, grasping, sensorimotor adaptation, pupillometry

Running head: Perturbation detection, adaptation, and pupillometry

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Introduction

Humans are skilled at interacting with their environment. This is in large part because we learn from interacting with it: Over time, our actions are continuously improved through many different processes. They may become more fluent and energetically efficient (Franklin et al., 2008), more precise (Faisal et al., 2008), as well as more accurate, the latter primarily through what we call sensorimotor adaptation (Krakauer & Mazzoni, 2011). This can be thought of as changing a sensorimotor mapping between what is perceived (often seen at a distance) and the corresponding action to minimise the error said action produces (Warren, 2006). Adaptation itself also comprises several processes (Tsay et al., 2024) from sensory to cognitive, and can happen both implicitly, that is, without the actor deliberately changing the action, and explicitly, that is, deliberately and cognitively controlled (Mazzoni & Krakauer, 2006; Smith et al., 2006).

Recent studies have shown major involvement of the cerebellum in controlling sensorimotor adaptation (Shadmehr et al., 2010; Tseng et al., 2007), both in upper-limb (Taylor & Ivry, 2014) and lower-limb actions (Hagen & Fling, 2026), with other areas like the basal ganglia, premotor cortex and primary motor cortex also involved in motor skill learning (Baladron et al., 2023; Diedrichsen & Kornysheva, 2015). More recent research has also investigated the role of specific brain structures with respect to individual components of sensorimotor adaptation, for example with McDougle et al. (2022) finding a specific role of the medial temporal lobe in acquiring memories relevant for adaptation and motor learning.

Sensorimotor adaptation and noticing perturbations

To be able to employ an explicit strategy to deal with a sensorimotor perturbation (Taylor & Ivry, 2011), the actor needs to be aware of this perturbation. In experimental studies where one is interested in properties of explicit adaptation, this is often manipulated (in particular in upper-limb actions) by either instructing participants about the perturbation (Miyamoto et al., 2020; Taylor & Ivry, 2011), by manipulating its noticeability for example by making it very large (Hudson & Landy, 2012), the outcome uniform regardless of the response (McDougle et al., 2015), introducing it gradually rather than suddenly (Kagerer et al., 1997; Modchalingam et al., 2019, 2023; Orban de Xivry et al., 2013), or by distracting participants from it using secondary tasks (Mariscal et al., 2020), though this latter method will also show other influences on adaptation patterns (Bedard & Song, 2013; Torres-Oviedo & Bastian, 2012). Indeed, already Held & Gottlieb (1958) stated that it was important for experimenters to make sure that only one type of adaptation was possible. But how do we as experimenters know if our method of choice achieved its goal? Early studies used post-experiment interview questions to get a rough idea of whether this was achieved successfully (Gentilucci et al., 1995; Säfström & Edin, 2004), but most direct tests came in the form of assessing participants' "ownership" of an action (Gaffin-Cahn et al., 2019) or meta-cognitive judgements about their own performance (Arbuzova et al., 2021; Pereira et al., 2023). Instead, researchers have looked at adaptation performance itself (Herzfeld et al., 2014; Kagerer et al., 1997), or employed indirect no-report markers such as MEPs (Orban de Xivry et al., 2013) or EMG (Albert & Shadmehr, 2016) to get an idea of whether sensing or perceiving perturbations would affect adaptation to them. Until recently, few studies investigated directly what perturbations to upper-limb action are perceived by participants.

In lower-limb actions like walking on the other hand, several studies have investigated the abilities of participants to detect motor perturbations, most prominently split-belt speed perturbations. Researchers typically find just-noticeable differences (JNDs) of on average around 7-9% for young and healthy participants (Iturralde et al., 2020; Liss et al., 2022), but these figures can be higher for other participant groups such as older adults (Lauzière et al., 2014) or patient populations (Hoogkamer et al., 2015), as well as differing substantially between participants within each group (Müller & Kopiske, 2025). Similar to findings in upper-limb actions, Malone & Bastian (2010) showed that distracting participants from the perturbation affected the adaptation patterns. Note, however, that a similar paradigm found no effect of distraction on the perception of split-belt speed differences (Liss et al., 2022), while Hoogkamer et al. (2015) reported, in patients with cerebellar lesions, a correlation between the ability to detect split-belt speed differences and the extent of gait adjustments made to those differences. In upper-limb actions, two studies on perturbation detection in grasping from our own lab (Müller et al., 2025; Pfalz et al., 2025) found that perturbation schedules that allowed participants to adapt to the perturbation correlated with worse (and decreasing) detection performance, consistent with the notion that the error signal plays an important role in detecting perturbations, as has been frequently suggested (Acerbi et al., 2017; Tsay et al., 2021).

Pupillometry in perception, and in action

In recent years, there has been increased interest in using pupil dilation as a window into cognitive and perceptual processes that is unobtrusive and does not require a response from the participants. This has revealed, for example, pupil-dilation signature of arousal (Nassar et al., 2012; Stanners et al., 1979), surprise (Preuschoff et al., 2011), novelty (Naber et al., 2013), changes in perceptual interpretations (Einhäuser et al., 2008), and uncertainty (Lavín et al., 2014). Pertinent to the topic of perturbation detection is that it has also been shown to respond to perceived physical effort (Zénon et al., 2014), multisensory integration (Rigato et al., 2016), predictions about the environment (Lavín et al., 2014; Murphy et al., 2016; Vincent et al., 2019), has been successfully applied in walking tasks as a marker of cognitive load (Saeedpour-Parizi et al., 2020), and – likely due to it reflecting surprise (Roberts & Seidler, 2026) and uncertainty – it has been shown to differ based on perturbation properties typically used to dissociate implicit and explicit adaptation (Yokoi & Weiler, 2022). Thus, pupillometry can be viewed as a window into the cognitive processes involved in motor tasks (Yokoi, 2025).

With respect to perturbation detection, pupil dilation reflecting both sensory and cognitive processes opens interesting possibilities. The two major arguments against testing for perturbation detection directly after each experimental trial are (i) the fact that this alerts participants to the very perturbation one may not want them alerted to and (ii) typical adaptation schedules involving a repeated perturbation in the same direction since this is what participants can then adapt their actions to, which in turn means that participants would have to give the same answer repeatedly and can thus lead to unwanted artefacts (Bosch et al., 2020). Both of these issues would be solved with a no-report marker that would eliminate the need for a direct answer from the participant. To explore this possibility, we (Pfalz et al., 2025) recently tested to what extent pupil dilation reflected stimulus properties in an adaptation paradigm on the one hand, and response properties in a perturbation-detection task on the other hand. While certain stimulus properties showed very clear effects in the pupil-dilation data, the relationship between participants' responses and their pupil dilation was only visible on average and not sufficient to allow trial-by-trial classification, which would be needed for a no-report marker sufficient to replace the direct report.

The present study

Here we investigated three main questions. One, to what extent the reduced error signal following sensorimotor adaptation leads to more difficulty detecting motor perturbations. Two, whether tonic (i.e., more long-term, across trials) and phasic (i.e., more immediate) pupillary responses correlate with and are predictive of participants' abilities to detect motor perturbations. Three, if, regarding the former two aspects, the same patterns can be found in different everyday actions, namely grasping and walking, and thus if the mechanisms involved in these patterns are generalisable across actions as opposed to them being action- and effector-specific.

To this end, we conducted two experiments in which participants were exposed to repeated motor perturbations, introduced in such as way that adaptation to the perturbation was either facilitated or prevented (figure 1). This was done using a split-belt speed perturbation to walking in experiment 1 (figure 2), and a visuo-haptic size discrepancy in grasping in experiment 2 (figure 3), an extension of an earlier grasping study in our lab (Pfalz et al., 2025), with an improved experimental design that more clearly contrasted the respective contributions of the perturbation magnitude and the error signal. Pupil diameter was tracked throughout both experiments. We hypothesised that (i) perturbation schedules that are more easily adapted to would make it harder to detect those perturbations, (ii) pupil dilation, and especially tonic responses, as seen in our previous study (Pfalz et al., 2025), would differ between the two perturbation schedules, and (iii) that the patterns would not differ substantially between the two actions.

Methods

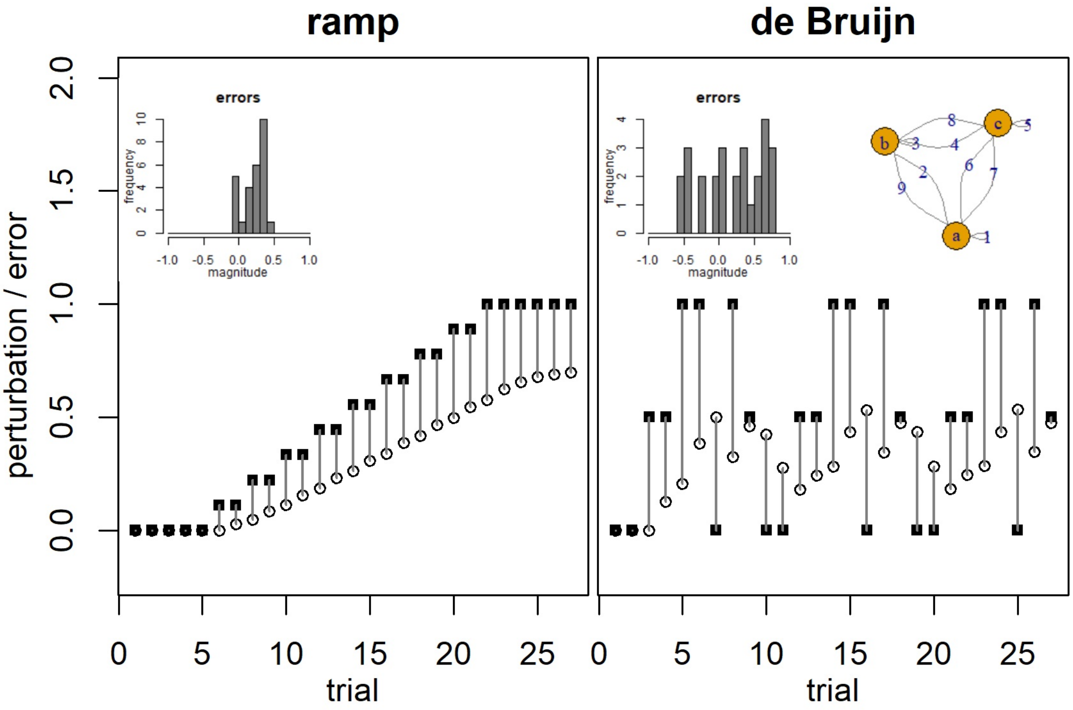

Figure 1: Different perturbation schedules and simulated errors. **Left**: Ramp-type perturbation, **right**: A thrice-repeated de Bruijn sequence for an alphabet size of three where, when looped, each element is equally often followed by every other element and by itself (top-right inset). Top-left insets show simulated errors, obtained by applying equation 1 with standard parameters of A = 0.9 and b = 0.25. The y-axes are normalised to a maximum perturbation strength of 1.

In both experiments, we dissociated the magnitude of the perturbation and that of the error signal. To do this, we contrasted a ramp-type perturbation with the perturbation magnitude increasing in small increments (used, e.g., by Mawase et al. (2013)), which allows participants to adapt to the perturbation very well, with a perturbation schedule designed to provide a maximal error signal with minimal predictability. For this, we employed a de Bruijn sequence (de Bruijn, 1946), which provides a minimally short sequence where, when it is looped, each element (in this case: perturbation magnitude) is followed by each of the other elements and itself with equal probability, which is very desirable for adaptation research (Volcic & Domini, 2018). Figure 1 shows the two perturbation schedules, along with simulated errors (top-left insets) using a state-space model and realistic error-correction parameters taken from K. K. Kopiske et al. (2017). As the ramp-type perturbation allows the participant to continuously adapt their action, there are fewer large motor errors (inset).

Experiment 1: Perturbation detection and pupillometry in walking

The first experiment was conducted using a Gait Realtime Interactive Lab (GRAIL; Motek Medical, Amsterdam, NL) system, see figure 2. This system includes a dual-belt treadmill capable of accelerating and decelerating each belt independently at high precision (Sessoms et al., 2014) with force plates recording at 1,000 Hz under each belt, surrounded by a 240° projection screen and twelve passive motion-tracking cameras (Vicon Motion Systems, Yarnton, UK) capturing the 3D positions of retro-reflective markers at 250 Hz. Participants also wore a Tobii 3 mobile eye-tracking device (Tobii, Stockholm, SE) that recorded eye movements and pupil diameter at 100 Hz, synchronised to the data obtained by the GRAIL system via custom-made triggers (Müller et al., 2023).

Participants

We aimed for a sample size of 48 to achieve a power of 0.9 with an estimated effect size of Cohen's $d = 0.5$ (Cohen, 1988). We invited a total of 50 participants into the lab, of which 2 were excluded from analyses due to technical difficulties during data collection. The data set used for analyses thus consisted of N=48 participants, 29 women and 19 men, with an average age of 25.6 years ± a standard deviation of 7.2 years. The average height was 173.9 ± 11.2 cm, average body mass was 69.3 ± 14.5 kg, and the average leg length was 93.5 ± 6.5 cm. Body measurements were collected after the participant had completed a questionnaire in which they confirmed that they had normal or corrected-to-normal vision, and felt sufficiently rested and focused to complete the experiment. Participants were naïve to the hypotheses of the experiment and debriefed afterwards. Having any impairment of the locomotor system was listed as an exclusion criterion in the recruitment email. Compensation was either course credit or a reimbursement of 10€/h. All experimental procedures were in accordance with the 2013 Declaration of Helsinki and approved by the Chemnitz University of Technology ethics committee (reference no. 101628179).

Procedure

Prior to the experiment, participants first completed a questionnaire. We then took biometric measurements necessary for the motion-tracking model and applied 16 retro-reflective markers following the Vicon Plug-In Gait lower-body model (Vicon Motion Systems, Yarnton, UK) as well as a safety harness. This was always done by the same experimenter to ensure high reliability of the measurements (McGinley et al., 2009). Participants then put on the Tobii 3 eye-tracking glasses, which were also equipped with a tripod, and seven

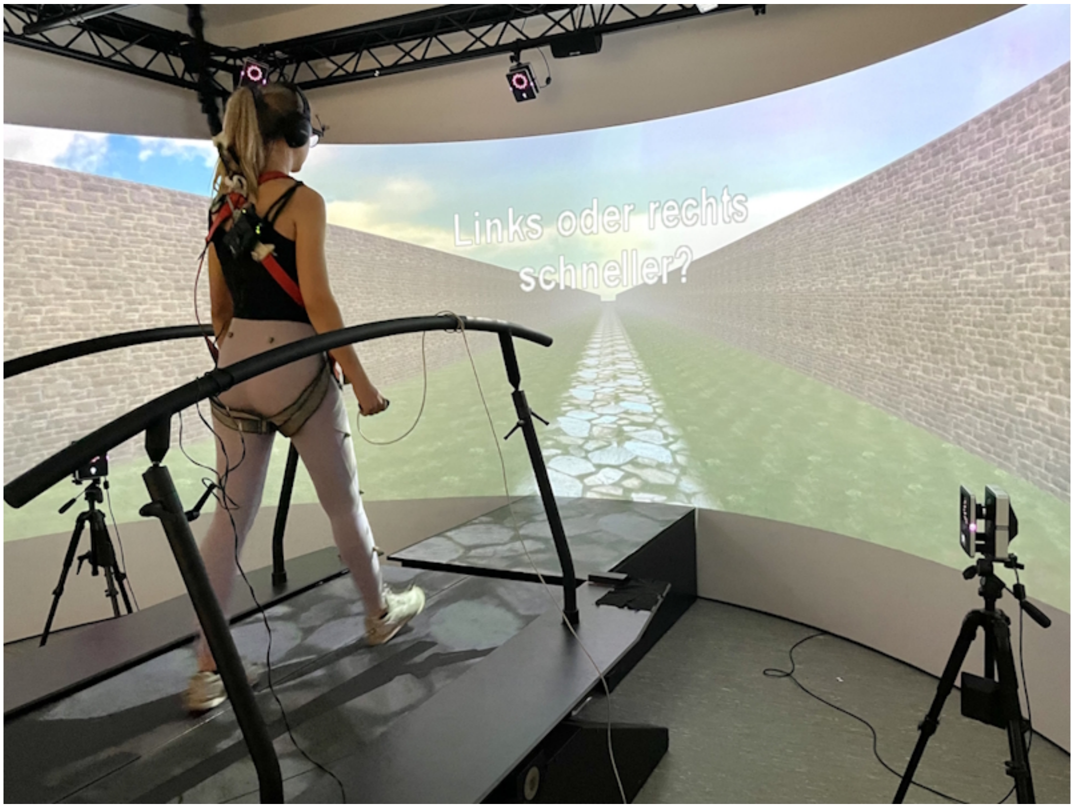

Figure 2: Setup for experiment 1. The participant is walking on a dual-belt treadmill, wearing a safety harness, eye-tracking glasses (Tobii 3 Pro), and retro-reflective motion-tracking markers. Participants also held a two-button controller in their right hand to respond to the jugement task. An endless-road scene is projected on the screen and treadmill in front of the participant. The prompt "Links oder rechts schneller?", German for "Left or right faster?", was presented three steps after each perturbation's onset.

additional motion-tracking markers on the head, glasses and tripod to calculate head orientation (figure 2). They then walked onto the treadmill, the experimenter attached the harness to a hook protruding from the ceiling, and the participant was ready for the experiment.

Each experiment started with the experimenter calibrating the motion-tracking model using an approx. ten second long recording of the participant going from a T-pose to a slow walking motion. Then, the eye tracker was calibrated using a calibration card supplied by the manufacturer. Participants then completed two short practise blocks of two minutes walking that started unperturbed at 1 m/s. After this, perturbed walking began, where each perturbation consisted of one belt changing its speed during swing time of the respective leg, followed by, after three perturbed steps, the participant being prompted to answer which side was running faster. The new speed was maintained for a minimum of 8 s, that is, until the first time the foot on the perturbed belt was lifted after 8 s had passed. If the participant did not respond within 8 s, the response was registered as not given and the participant was prompted to please respond faster. In the two practise blocks, perturbations started at 0.1 m/s speed difference between the two belts and then adaptively moved towards the participant's perceptual threshold following a QUEST algorithm (Watson & Pelli, 1983), with one practise block containing acceleration-perturbations and the other deceleration perturbations.

Each participant then completed a full block in which their individual JNDs for split-belt accelerations relative to 1 m/s walking were measured using a QUEST procedure starting at 0.1 m/s perturbations, maximum perturbations of 0.4 m/s, and a total duration of 5 minutes (resulting in up to 41 trials). This ensured that despite the large inter-individual variability in detecting such perturbations (Müller & Kopiske, 2025), all participants would be presented with stimuli of similar difficulty to detect. The following blocks then used the final estimate of the JNDs for six further blocks: Four ramp blocks and two de Bruijn blocks. In the ramp blocks, the split-belt speed difference gradually increased to either one JND difference or two JNDs difference (2 x 2), with each block containing one ramp on each belt. These blocks started with 20 s of unperturbed walking, followed by four ramps of which two were presented on the right belt and two on the left (in randomised order) that went from 0 to the full perturbation in 7 steps. Between each ramp were 30 s of unperturbed walking. In the two de Bruijn-sequence blocks, the maximal perturbation was again either one or two JNDs. Blocks started with 20 s of unperturbed walking, followed by perturbations being applied to one belt that followed a de Bruin sequence of 5 elements, corresponding to the maximum perturbation multiplied by $\{-1, -0.5, 0, 0.5, 1\}$. The sequence was generated once offline for all participants, randomisation was achieved by quasi-randomly generating, for each block, a mapping of the elements of the sequence to the possible perturbation strengths, with the only constraint being that the element that came first always corresponded to a perturbation of 0. In each de Bruijn-sequence block, the same sequence of perturbations was applied once to one belt, followed by 16 s of unperturbed walking, and then to the other belt. This ensured, as an improvement over our previous studies (Müller et al., 2025; Pfalz et al., 2025), that every block included perturbations in each direction. To prevent speed changes being uncomfortably strong, we set the maximum JND used in ramp and de Bruijn-sequence blocks to 0.1 m/s, meaning that participants whose JND estimate from the QUEST was above 0.1 m/s were presented with the same perturbation strengths as a participant with a 'true' measured JND of 0.1 m/s. This applied to ten out of 48 participants. Overall, the experiment lasted approximately 60 minutes, excluding preparation and debriefing.

Data analyses

Data from all sources were synchronised with the help of custom triggers and custom scripts written in R and run using R version 4.3.3 (R Core Team, 2024). Blink-detection was performed by the Tobii Pro Lab software (Tobii, Stockholm, SE). Eye-tracking and motion-tracking data were then filtered using cubic-spline interpolation and a 110-ms Savitzky-Golay filter (Savitzky & Golay, 1964) for pupil dilation and a 124-mm filter for the motion-tracking data.

From the psychophysical responses, we computed JNDs using the R-package 'quickpsy' (Linares & López-Moliner, 2016) and tested the notion that by comparing mean JNDs by means of t-tests and their Bayesian equivalents (Morey & Rouder, 2018; Rouder et al., 2009). We also quantified the aftereffect of perturbations by calculating the proportion of responses given in each direction after a perturbation ramp had ended.

To quantify sensorimotor adaptation, we calculated, on a per-step basis, the participants' step-length asymmetry (SLA) in per cent, and peak ground-reaction-forces (GRFs), normalised to baseline by dividing them by the mean peak GRFs of the first twenty steps of baseline walking. We used the parameters on the first step of each perturbation as a measure of perturbation response, as well as on the first step after perturbations had ended as the aftereffect. Importantly, these provide measures of both inter- and intra-leg coordination, which can show different adaptation patterns (Reisman et al., 2005). To quantify the effects that both the current perturbation had and the one preceding it (i.e., the adaptation aftereffect), we used the R-package 'lme4' (Bates et al., 2015) to fit linear mixed-effect models (LMEs) in which the factors *previous perturbation magnitude* and *perturbation schedule* were added iteratively as fixed-effects slopes to baseline models of

$SLA \sim perturbation\_magnitude + (1|participant)$ and $GRF \sim perturbation\_magnitude + (1|participant)$, respectively, and discarded if they did not improve the Akaike Information Criterion, AIC (Akaike, 1974).

Trialwise pupil-dilation parameters were computed relative to the initial heel contact (iHC) of each first perturbed step. Specifically, we calculated as a measure of *tonic* response the mean dilation over a 1,000-ms window prior to iHC, and as a measure of *phasic* response the max-min difference in the 2,500-ms window following iHC (referred to as response *amplitude*). To assess how these two measures were affected by perturbation properties, again we fit LMEs in which the trial properties *block number*, *trial number*, blockwise *maximum perturbation*, *perturbation schedule*, *response correctness*, *time to response*, and trialwise *perturbation magnitude* were added iteratively as fixed effects and discarded if they did not improve the AIC.

Experiment 2: Perturbation detection and pupillometry in grasping

Experiment 2 was a grasping task in which a mirror setup was used to dissociate the size of seen ('visual') and grasped ('haptic') cuboid objects. The experiment was conducted in a motion-tracking and eye-tracking lab with an Optotrak 3D-Investigator system (Northern Digital Inc., Waterloo, ON, CA) for motion tracking and a table-mounted EyeLink-1000 (SR Research, Ottawa, CA) for eye tracking. Participants were seated in front of a cold mirror slanted 45° away from them with their head in a chin rest, wearing occlusion goggles (Milgram, 1987) and with infrared-emitting diodes for motion tracking attached to their thumb, index finger, and wrist. The task was to grasp a 'haptic' aluminium cuboid behind the mirror while looking at another 'visual' cuboid in front of the mirror that was projected to the same position (figure 3), and then judge the relative size of the seen and grasped object, similar to our previous study (Pfalz et al., 2025).

Participants

We again aimed for a sample size of 48 to allow for a power of 0.9 with an estimated effect size of Cohen's $d = 0.5$, a realistic estimate as a previous study (Pfalz et al., 2025) had found an effect of Cohen's $d = 0.69$ for the main comparison of AUC differences between blocks where the perturbation was continuously changing vs. when it was quickly adapted to. We invited 53 participants to the lab, of which 5 had to be replaced due to technical issues: Three because of difficulties achieving acceptable eye-tracking quality, one because the motion-tracking system did not record all trials, and one due to an issue with stimulus presentation. This left us again with a full sample of N=48 participants for analyses. This sample contained 38 women and 10 men, with an average age of 22.4 ± 3.9. Prior to the experiment, participants confirmed that they met all inclusion criteria and felt sufficiently rested and focused to complete the experiment. They were naïve to the hypotheses of the experiment and debriefed afterwards. Compensation was either course credit or a reimbursement of 10€/h. All experimental procedures were in accordance with the 2013 Declaration of Helsinki and approved by the Chemnitz University of Technology ethics committee (reference no. 101568507).

Procedure

Prior to the experiment, participants completed a questionnaire confirming that they had full functionality of their right arm and hand, normal or correct-to-normal vision, and felt rested and alert enough to complete the experiment. They then entered the experimental booth, were seated at a table in front of the experimental setup, and fitted with infrared diodes on their thumb, index finger and wrist, as well as LCD goggles. After being instructed about the task, participants completed a five-point eye-tracking calibration using a cardboard sheet projected into the mirror. Then followed twelve practise trials that matched the experimental trials and

Figure 3: Setup for experiment 2. Participants had their head in a head rest and wore LCD goggles to prevent vision between trials. On any given trials, participants saw one of the objects on the rotating disc in the mirror and grasped an object behind the mirror that was in the same location the visual object was projected to. The eye tracker registered gaze position and pupil dilation through the cold mirror. Grasping movements were registered through diodes on the thumb, index finger and wrist, as well as one next to the haptic object that was placed such that it was visible to the 3D-Investigator when the reflective side of the object was next to it, but not visible when the object was moved, thus serving as a marker of object touch.

consisted of: (i) Starting with the right hand in a starting position with thumb and index finger gripping a small bump on the table to the right of the participant and the LCD goggles closed, (ii) the goggles opening and the object in the mirror in front of the participant completing a small back-and-forth movement to indicate the start of the trial, (iii) the participant performing a reach-to-grasp precision grip with thumb and index finger (Jeannerod, 1986; Napier, 1956) towards the object behind the mirror and lifting it briefly, (iv) the participant judging whether the haptic object felt *certainly smaller*, *uncertainly smaller*, *uncertainly larger*, or *certainly larger* than the visual one via a four-button response box (‘Black Box’, The Black Box ToolKit Ltd., Sheffield, UK), and (v) the goggles closing 4 s after the button press. Gaze position was tracked throughout, grasp trajectories were recorded for 5 s after opening of the goggles, which was sufficient to perform a full grasping movement even for participants who grasped very slowly. In the practise block, the experimenter asked participants which response they had intended to give to verify that the mapping of the buttons was correctly understood, and reiterated the mapping if there was any indication that the participant had misunderstood or was unsure. The experimenter also informed the participant when a 12-mm perturbation was experienced (which happened three times during practise) that this was the maximum amount by which visual and haptic object would differ.

Then, the main experiment began, which consisted of three blocks each (with maximal perturbations of 3 mm, 6 mm, or 12 mm, chosen to range from barely noticeable to clearly noticeable following result from Hillis et al. (2002) and Müller et al. (2025)) in which perturbations followed either a ramp, or a de Bruijn sequence. Ramp blocks consisted of two unperturbed trials, followed by 14 trials in which on every other trial the visuo-haptic mismatch was increased by $\frac{1}{6}$ of the maximum perturbation in the respective block. This was then followed by four unperturbed trials, and another 14 perturbed trials where the mismatch had the same magnitude as before, but the opposite sign (the order of signs was randomised), followed by another two unperturbed trials. In total, each ramp block thus consisted of 36 trials. de Bruijn-sequence blocks used a pre-generated de Bruijn sequence with five elements, which was 25 trials long. As in experiment 1, each of the five elements was quasi-randomly mapped to the block's maximum perturbation times one of $\{-1, -0.5, 0, 0.5, 1\}$, with the only constraint that the first element of the sequence was always mapped to "no perturbation". Overall, participants thus completed six experimental blocks and 183 experimental trials. On average, the experiment lasted around 75 minutes, including breaks but excluding preparation and debriefing.

Data analyses

Psychophysical data were modeled using the 'quickpsy' package (Linares & López-Moliner, 2016), obtaining JNDs that were then compared between perturbation types using t-tests and their Bayesian equivalent (Morey & Rouder, 2018; Rouder et al., 2009). We also calculated areas under the curve (AUCs) using all four responses (Green & Swets, 1966), by considering them essentially four criteria of different strictness (Naber et al., 2013). That is, each curve's y-values ('true positives') were computed from physically larger objects, using the proportion of responses "definitely larger" as y1, definitely or probably larger for y2, and so on, with the x-values ('false positives') being computed in the same way but for smaller objects and starting with "definitely smaller". These, too, were compared between the two conditions.

Motion-tracking data were filtered using cubic-spline interpolation and a 22-ms Savitzky-Golay filter (Savitzky & Golay, 1964). The start of each grasping movement was defined as the point in time when both thumb and index finger moved at more than 25 cm/s. The end point was defined as the time point when the diode next to the haptic object was no longer visible to the motion-capture system since its signal was not longer reflected by the reflective side of the object, or when it moved at more than 25 cm/s. Between these two points, the maximum euclidean distance between thumb and index finger was taken as the maximum grip aperture (MGA), our main dependent variable for grasping. To then model adaptation, we used a state-space error-correction model (Wolpert et al., 1995) in which a state, roughly corresponding to a visuomotor mapping between seen object size and the corresponding grip opening, is adapted trial by trial according to equation 1:

$$x_{t+1} = A * x_t - b * E_t \tag{1}$$

This was fit using the 'Nloptr' package in R (Ypma, 2014). We defined E_t as the difference between the observed MGA and the MGA expected given the size of the haptic object and the MGA's response function. In other words, we defined it was the haptic error signal. The main variable of interest was the error-correction parameter b.

Pupil-dilation data were read into R using the EyelinkReader package (Pastukhov, 2025) and filtered using, again, cubic-spline interpolation and a 35 ms Savitzky-Golay filter (Savitzky & Golay, 1964). As measures of tonic pupil response, we calculated the average of the first 1,000 ms of each trial. To measure phasic response, we computed the min-max difference 2,500 ms post object touch (*amplitude*) – see figure 3 of Pfalz et al. (2025) for a visual explanation of these parameters. These were then analysed with LMEs using the 'lme4' package (Bates et al., 2015) to investigate whether pupil-dilation responses depended on trial properties. To do this, predictors *perturbation magnitude*, *perturbation schedule*, *trial number*, *block number*, *response correctness* and *response confidence* were added iteratively and kept as a predictor if the more complex model had a lower AIC (Akaike, 1974) than the simpler one. Finally, support-vector machine (SVM; Boser et al. (1992)) classifiers were used to see if trial properties, pupil-dilation trajectories, as well as pupil-dilation-velocity trajectories could be used to predict response confidence. We chose confidence as a response parameter participants had conscious access to and that would depend systematically on surprise (Yokoi & Weiler, 2022). We used the ‘e1071’ package in R (Meyer et al., 2024) for these analyses. Per participant, we used four experimental blocks as the training set and two remaining blocks – chosen quasi-randomly such that they had to differ both in perturbation magnitude and perturbation schedule – as the test set. We used a sampling frequency of 50 Hz, with equal class weights and a C parameter of 1, building on our results in Pfalz et al. (2025).

Results

Eye-tracking, psychophysical, and motion capture data from both experiments, as well as analysis scripts are available via the Open Science Framework: https://osf.io/s4bvr/overview?view_only=3421f9c8febf4c729cec923a780a2882. These scripts and data allow readers to reproduce all results and figures in this manuscript.

Experiment 1

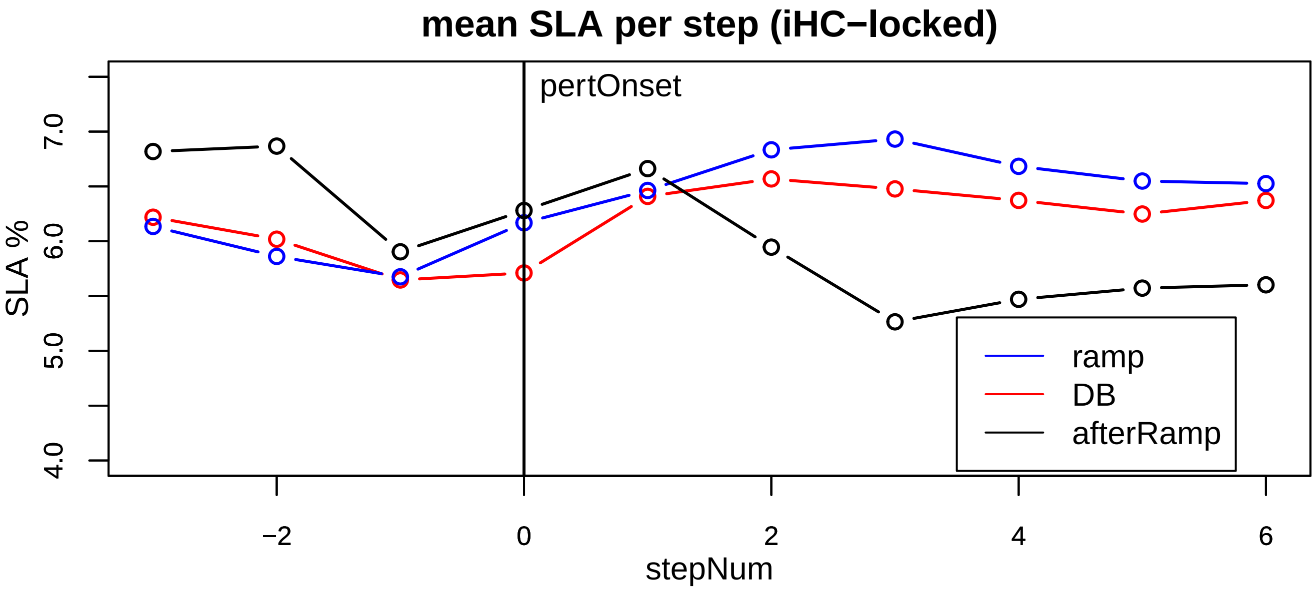

Figure 4: Step-length asymmetry per step, relative to perturbation onset. Data points show overall means across all participants and perturbation strengths, split up by block type. Initial heel contact (iHC) for the first perturbed step is used as t = 0. y-axis shows asymmetry as the percentage by which the longer step in any given stride was longer than the shorter step.

Average measured JNDs were 7.3 % ± a standard deviation of 4.1 %. The minimum measured JND was 1.6 %, with a maximum of 27.5 % and total of 10 participants’ measured thresholds were above 10 %, which we had set as the maximum JND to be used in the main part of the experiment, thus setting the range to be [1.6 %; 10 %]. Analysing data quality showed on average 0.2 % of frames missing from our motion-tracking data for markers included in analyses, with only two blocks across all 48 participants exceeding 5 % missing data for one of those markers. Eye-tracking data were missing on average 10.7 % of frames, including blinks, ranging from 0.5 % to 34.5 % per participant.

Motor responses

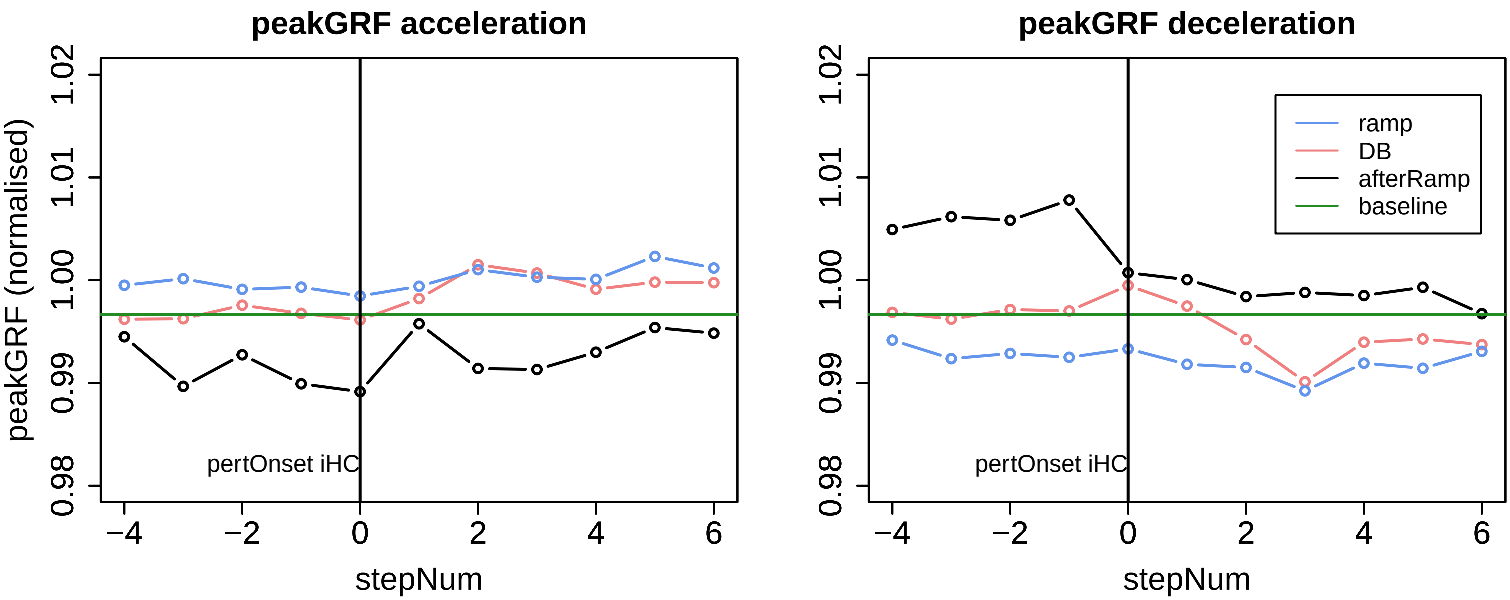

Figure 5: Normalised peak ground-reaction forces per step, relative to perturbation onset. Peaks were calculated from filtered trial-wise force-plate data. Data points show overall means for across all N=48 participants and perturbation strengths, split up by block type as well as accelerations (**left**) and decelerations (**right**). Forces (y-axis) were normalised to the first 20 steps of each participant's baseline walking as 1.

Participants' gait patterns showed an effect of the perturbations in increased SLA following perturbation onset, as well as following perturbation offset in ramp blocks (figure 4). LMEs show that both GRFs and SLAs were related positively to perturbation speed but negatively to preceding-perturbation speed. The full best-fitting models were $SLA \sim 21.52 * perturbation\_magnitude - 21.27 * previous\_perturbation\_magnitude - 1.96 * perturbation\_schedule$, indicating that SLA increased by 21 % for every m/s of perturbation speed and decreased by almost the same amount for every m/s of preceding-perturbation speed and was smaller in de Bruijn blocks, and $GRF \sim 5.83 * perturbation\_magnitude - 1.62 * previous\_perturbation\_magnitude$, showing that normalised peak GRFs were also sensitive to both current and preceding perturbation speed, but less so than SLAs, and did not depend on the block type. Similarly, peak GRFs increased following belt accelerations but decreased following decelerations in both perturbation schedules, with the opposite being true for aftereffects in ramp-type blocks (figure 5).

Psychophysics

As expected, participants showed poorer performance in the discrimination when the perturbation followed a ramp-type schedule vs. when it followed a de Bruijn sequence (figure 6). On average, participants' JND in ramp-type perturbations were 18.9 % ± a standard error of 3.7 %, compared to 12.4 % ± 1.8 % for de Bruijn sequence blocks. This was a statistically significant difference, $t(47) = 2.32$, $p = .024$, $d = 0.34$ – however, a Bayesian t-test revealed the evidence for a difference to be only anecdotal ($BF_{10} = 1.8$). As expected, both

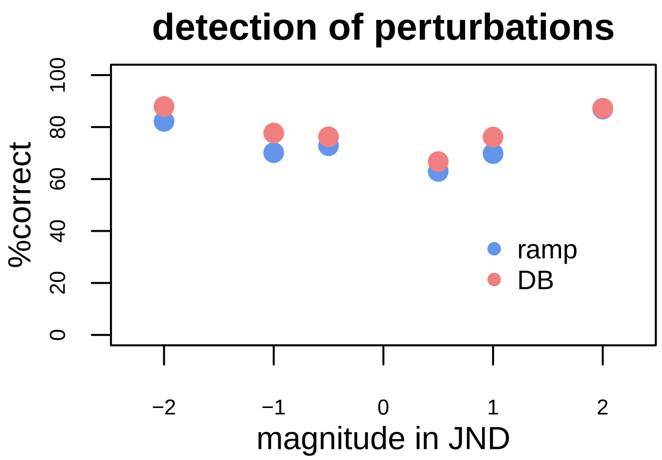

Figure 6: Percent correct in ramp and DB-sequence perturbations. Data points show overall means for all N=48 participants, split up by perturbation type and magnitude. Only perturbation magnitudes presented in both perturbation types are shown.

were larger than JNDs measured using the QUEST procedure, where most stimuli were near threshold. There was also the expected perceptual aftereffect where during unperturbed walking following a ramp perturbation, the belt that had been *slower* during the perturbation was, when perturbation was removed, judged as *faster* in 59.4 % of responses after 1-JND ramps, and in 78.1 % of responses after 2-JND ramps.

Pupil responses

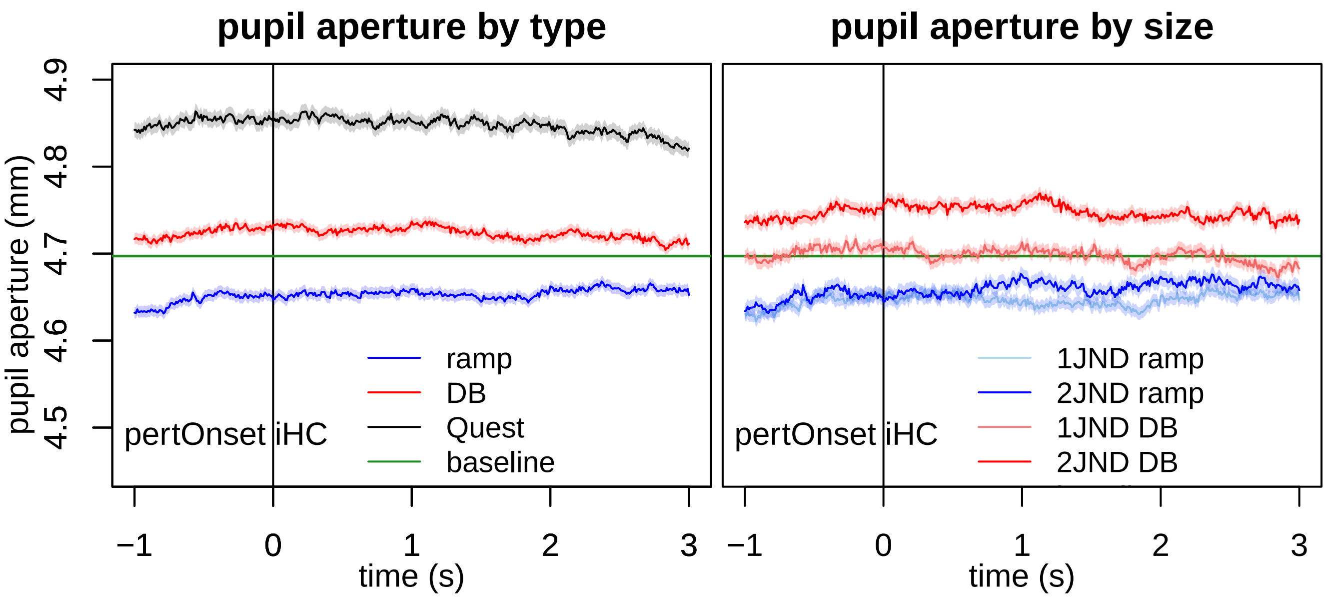

Figure 7: Mean pupil aperture relative to initial heel contact of first perturbed step. Data split up by perturbation schedule (**left**) and magnitude (**right**). We show mean collapsed trajectories over all N=48 participants, time-locked to perturbation onset. Shaded areas display standard errors, calculated as the frame-wise standard error of participant-averaged trajectories.

Pupil-dilation data showed a difference between trials in ramp-blocks vs. de Bruijn-sequence blocks with respect to the *tonic* pupil response. In particular, baseline dilation was higher in de Bruijn-perturbation blocks, but only by .04 mm. on average (figure 7). The full best-fitting model for pupil-dilation baseline was $baseline \sim -0.02 * block\_number + 0.003 * trial + 0.008 * maximum\_perturbation + 0.037 * perturbation\_schedule + 0.414 * perturbation\_magnitude$. Neither response correctness nor time to response improved the model fit as predictors. Our phasic measure *dilation amplitude* decreased as block number increased, with the best fitting model being $amplitude \sim -0.2 * block\_number$, but was not sensitive to any of the other trial or response properties, with all $\Delta AIC > 0$.

Experiment 1 discussion

In summary, results from experiment 1 showed reduced detection performance for ramp-type perturbations, but not very strongly. Both GRFs and SLAs increased when split-belt speed differences were introduced and decreased when they were removed, showing sensorimotor adaptation. Together, these finding support the notion that sensorimotor adaptation makes it harder to detect the perturbation being adapted to. Phasic pupil dilation did not differ depending on any of our predictors, whereas tonic pupil dilation differed depending on trial properties, showing increased dilation in de Bruijn-sequence blocks and when perturbations were stronger, but was independent of response properties. This shows that like in upper-limb actions (Pfalz et al., 2025; Yokoi & Weiler, 2022), pupil-dilation responses during perturbed walking differed depending on perturbation properties.

Experiment 2

Out of a total of 8,734 trials, a total of 453 trials (5.6 %) had to be excluded from motion-tracking analysis due to reaching one of the exclusion criteria laid out in the methods section. In of the remaining trials, grip-aperture data was missing for an average of 2.2 % of frames during grasping. The eye-tracking data contained more missing values, with an average of 44.7 % of frames missing, including blinks. This number was relatively high in part due to the setup with eye-tracking being recorded through occlusion goggles and a cold mirror as well as while the participant was performing an action task that required more movement than is typical for stationary eye tracking, and is in line with the data quality in our previous study (Pfalz et al., 2025). Consequently, we include analyses of data quality when reporting classification results from eye-tracking data.

Motor responses

MGA scaled with visual object size with an average slope of .41 ± .04. Participants adapted their grip to the visuo-haptic mismatch with an mean error-correction parameter of $b = 0.25$. Average adaptation patterns for ramp blocks can be seen in figure 8: Especially for 6-mm and 12-mm perturbations (displayed in green and blue), there is a clear pattern of MGAs following the perturbation, as well as showing aftereffects directly after the perturbation was removed. The random assignment of perturbation sizes to the elements of the de Bruijn sequence make averaging across blocks meaningless, but analysing error-correction parameters as described in equation 1 show that adaptation was actually stronger in de Bruijn blocks (average $b = .30$ compared to $b = .20$ for ramp blocks). This is borne out also in the inference statistics, as we saw a main effect of *perturbation schedule* on bs, $F(1, 47) = 14.46$, $p < .001$, $\eta_p^2 = .24$. Neither the main effect of *perturbation magnitude* ($F(2, 94) = 1.88$, $p = .159$, $\eta_p^2 = .04$) nor the interaction between the two factors(F(2,

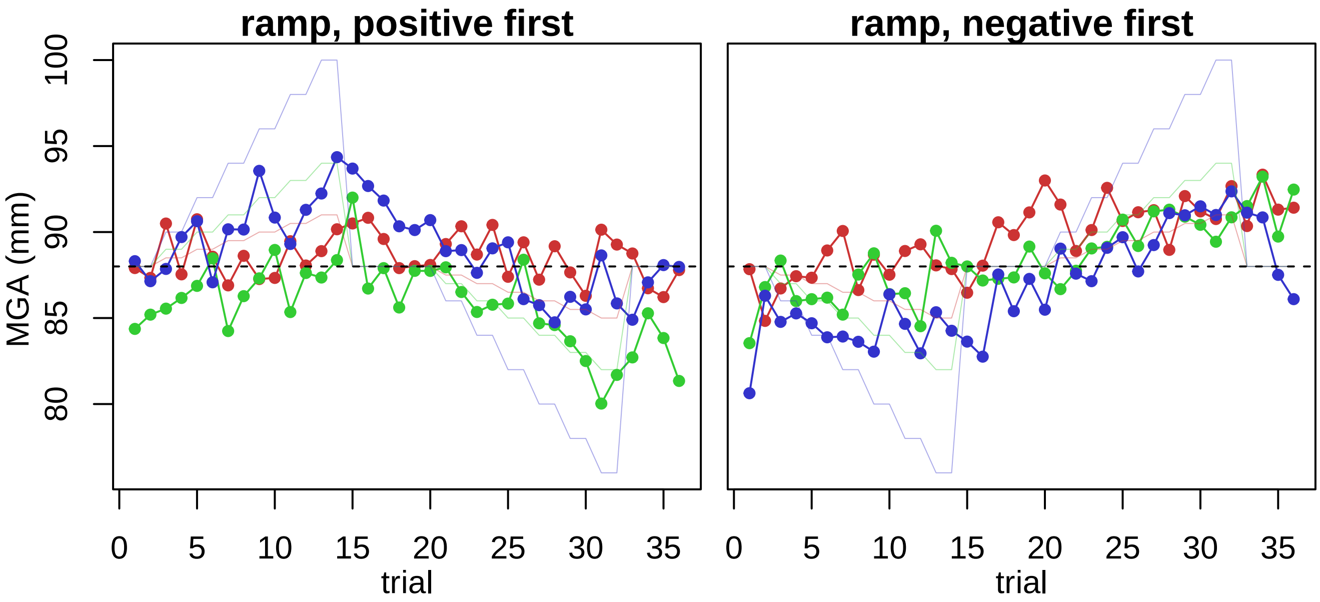

Figure 8: Grip apertures over trials in ramp blocks. Thin lines show perturbations of different strengths by trial, dots of corresponding colours show mean MGAs across all 48 participants for each perturbation. **Left**: Blocks with ramps with positive amplitude (i.e., larger haptic objects) first, followed by negative-amplitude ramps. **Right**: Negative-amplitude blocks. Data points show averages across all participants. Colours differentiate blockwise perturbation amplitudes.

94) = 0.04, $p = .958$, $\eta_p^2 < .01$) were statistically significant.

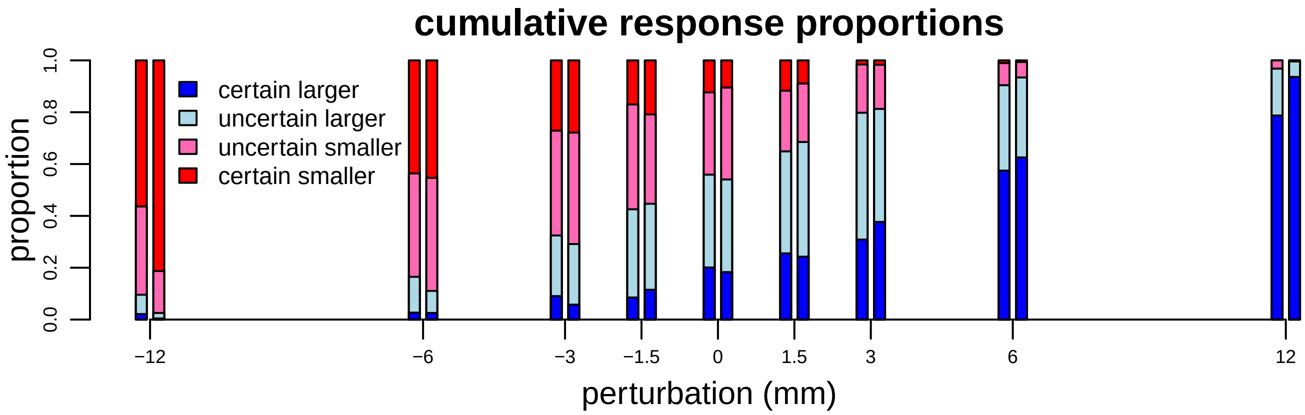

Figure 9: Cumulative response proportions by perturbation size. Perturbation size shown on the x-axis, proportions averaged across all 47 participants included in psychophysical analyses on the y-axis. Bars on the left of each pair show proportions in ramp blocks, bars on the right proportions in de Bruijn-sequence blocks. Colours differentiate response types. Data from all magnitudes present in both perturbation types are shown.

Psychophysics

One participant had to be retroactively excluded from psychophysical analyses since their larger/smaller responses did not scale with the physical differences, leaving us with a sample of N=47 for psychophysical analyses. Mean JNDs were 4.71 mm ± 0.42, similar to the results in our previous studies (Müller et al., 2025; Pfalz et al., 2025). The difference in JNDs between ramp blocks (5.62 mm) and de Bruijn blocks (3.81 mm) was statistically significant ($t(46) = 2.49$, $p = .016$, $d = 0.36$), although Bayesian analysis found the evidence not to be conclusive ($BF_{10} = 2.5$). The same pattern emerged when comparing AUCs (0.86 vs. 0.89; $t(46) =$ -2.37, $p = .022$, and $d = -0.35$, but $BF_{10} = 2.0$). Figure 9 shows that for all perturbation strengths, responses in ramp blocks (left bar in each pair) were more evenly distributed – that is, more similar to responses to null-perturbations – than for the same strength in de Bruijn blocks, but not by much. As in experiment 1, we also found a perceptual aftereffect of ramps, with unperturbed trials directly following ramps being judged as perturbed in the opposite direction of the preceding ramp in 59.9 % of trials following 3-mm ramps, 71.8 % of trials following 6-mm ramps, and 77.9 % of trials following 12-mm ramps.

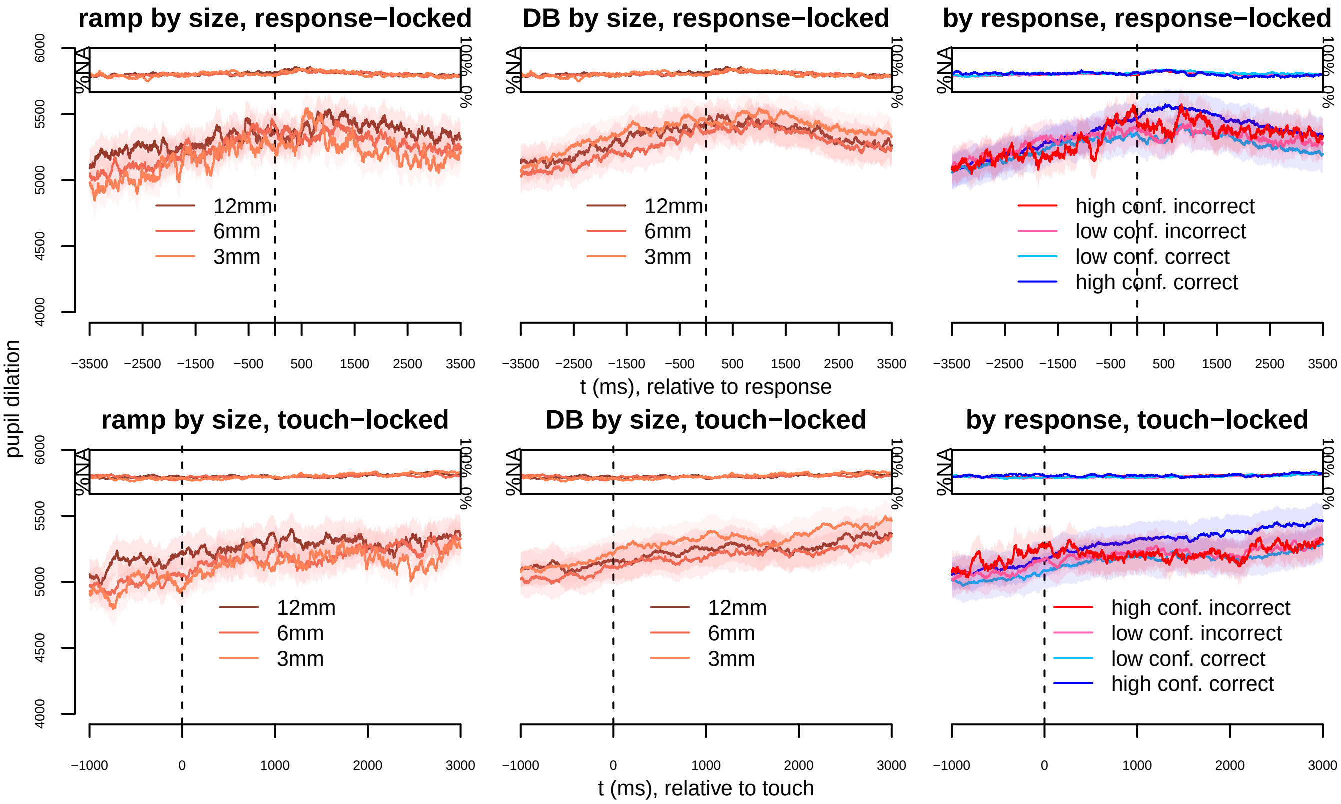

Figure 10: Pupil apertures within trials, experiment 2. Data points show trajectories split up by perturbation type and magnitude (**left** and **middle** column), as well as by response (**right** column). Trajectories are shown relative to the psychophysical response (**top** row) as well as to object touch (**bottom** row). Insets above the trajectories show the proportion of missing pupil-dilation values for each time point. Means across all trajectories of all 48 participants are shown, with shaded areas showing between-participant standard errors.

Pupil responses

With respect to pupil-dilation differences (see figure 10), LMEs revealed that the tonic response differed depending on all our predictors, with the final best-fitting model being $baseline \sim -1.03 * magnitude - 47.97 * perturbation\_schedule - 7.84 * trial\_number - 14.87 * block\_number - 10.36 * response\_correctness - 9.12 * response\_confidence$. For the phasic response, quantified as dilation amplitude, the best-fitting model

Table 1: SVM classification results. We show class-balanced accuracies for different redictor combinations, averaged across all N=48 participants. Average number of usable samples differed slightly depending on data quality and randomisation.

predictors	Balanced.Accuracy	Balanced.Accuracy.test	trainSamples	testSamples
trial info	0.851	0.683	49.857	25.036
eye parameters	0.725	0.479	47.346	22.731
eye samples	0.741	0.491	43.875	23.125
eye derivatives	0.962	0.518	40.727	23.455
eye samples & derivatives	0.921	0.530	43.077	22.077
info & samples & derivaties	0.932	0.485	44.737	21.789
grasping E	0.695	0.468	42.955	20.364
info + grasping E	0.893	0.721	49.429	23.179

$amplitude \sim 10.29 * magnitude + 2.69 * perturbation\_schedule - 0.3 * trial\_number - 4.67 * block\_number + 91.52 * response\_correctness + 0.39 * response\_confidence$ revealed that this was affected by the same predictors, but largely in the opposite direction: While dilation *baseline* was smaller for trials with stronger perturbations, in de Bruijn-schedule blocks, and with more uncertainty about the response, dilation *amplitude* was larger in all of these cases. Both parameters decreased over time. Figure 10 also illustrates, as we had found in Pfalz et al. (2025), that response-locked trajectories (top row) showed clearer patterns than touch-locked trajectories (bottom row).

Trialwise classification of response confidence using trial-information, pupil-dilation, and grasping error as predictors revealed that while pupil dilation and psychophysical responses correlate on average, no trial-by-trial classification in the test set was possible (table 1). Stimulus- and trial-properties were the only predictor that allowed consistently above-chance classification in the test set. As we had found previously (Pfalz et al., 2025), while pupil-dilation trajectories allowed high accuracies in the training set, including them actually *decreased* test-set accuracy compared to using only trial information. On average, trials misclassified in the test set by SVM models including pupil data had 56.7 % frames missing, compared to 55.1 % for trials that were correctly classified, showing that data quality did not explain the poor performance in the test set. Note that these numbers differ from average percentage of data missing due to resampling and different inclusion criteria for the SVM analyses.

Experiment 2 discussion

In summary, results from experiment 2 showed, just like experiment 1, that when participants were able to adapt to a perturbation (i.e., in a ramp-type perturbation schedule), their detection performance was worse than when they could not (i.e., in a de Bruijn-sequence schedule), but this was again not a large effect. Pupil-dilation parameters correlated with trial and response properties in a way that was very consistent with an effect of uncertainty, with reduced tonic and increased phasic parameters in trials with more uncertainty and surprise. For the tonic response, this is also consistent with the results from experiment 1. In fact, even in magnitude the responses were rather comparable: While the EyeLink-1000 provides pupil dilation in arbitrary units that are not directly convertible to mm (which we used in experiment 1), perturbation-schedule effects in both experiment were quite close to 1 % of total dilation. Trial-wise classification of responses was not possible using pupil-dilation data. While trial-by-trial effects were not reliable, like in Pfalz et al. (2025), these results suggest that average effects of perturbations and perturbation detection are quite consistent.

General discussion

In both experiments, participants performed more poorly on the perturbation-detection task when the perturbation was introduced gradually following a ramp-type schedule, rather than an unpredictable de Bruijn sequence. Thus, we replicate earlier findings from our group in grasping (Müller et al., 2025; Pfalz et al., 2025) that showed that participants use both perturbation magnitude and the motor error for perturbation detection, and extend them by finding the same pattern in walking, and using perturbation schedules that more directly isolated the effect of a reduced error signal through adaptation. Participants corrected error similarly in both perturbation schedules, consistent with other works (Coltman et al., 2021), as well as in both motor tasks. Analysing pupil dilation showed consistent tonic responses to the schedule and magnitude of the perturbation across both experiments, consistent with an effect of uncertainty. Phasic responses could be seen in the grasping task, but not in walking. As in our previous experiment (Pfalz et al., 2025), trial-by-trial classification of responses using pupil-dilation data and SVM was not successful.

Pupil dilation responds to perturbations, but is not a reliable no-report marker

As in our previous work (Pfalz et al., 2025), we found that pupil-dilation responses reflected several trial properties. In particular, baseline dilation, a *tonic* response measure, was increased when perturbations were stronger and more sudden. This is consistent with the notion that pupil dilation, and in particular tonic responses reflect primarily the participant's uncertainty (Dayan & Yu, 2006; Nassar et al., 2012). The fact that response characteristics did not affect pupil dilation in the same way on the other hand is in line with recent findings that uncertainty and errors, while correlated, so not affect motor learning in the same way (Hewitson et al., 2023). *Phasic* responses on the other hand were only clearly visible in grasping, and even there did not show a coherent picture. We note, however, that seeing no phasic response in walking may not necessarily show that there was none, but may also point to methodological issues. For example, in our previous study (Pfalz et al., 2025), we showed marked difference between touch-locked and response-locked pupil trajectories, emphasising the importance of analysing relative to a suitable time point. While iHC seemed to us as *a priori* the most sensible starting time point to analyse pupil-dilation trajectories during perturbed walking, it could be that this was not an ideal choice. The time of the psychophysical responses was typically so late and so variable between trials and participants that we did not consider it sensible. Furthermore, unlike in grasping, walking provided continuously more information as the participant took more perturbed steps, making it a more prudent strategy to accumulate evidence before giving a more patient response. That said, from this it does not follow that iHC was the optimal choice. Also in line with our previous work (Pfalz et al., 2025), trialwise classification of responses through pupil data was not possible, and while data quality was not ideal, we found again that percentage of missing data was virtually identical in trials classified correctly and incorrectly. Indeed, including pupil-dilation features *reduced* classification performance in the test set relative to using only trial-information features, which in combination with the very good training-set classification corroborates our conclusion from Pfalz et al. (2025) that this is likely a consequence of overfitting.

These findings have implications both for our understanding of how actors adapt under perceptual uncertainty, and methodological implications for using pupillometry as a no-report marker of perturbation detection. On the former, we not only replicate the pattern that error signal and perturbation magnitude each contribute to perturbation detection, we also show that the clearest physiological responses were tonic responses that are typically associated with uncertainty or, as Yokoi (2025) wrote (p. 5), participants being aware of environmental change. Consistently, these parameters were more predictive of behaviour than surprise-related phasic pupil responses, which underlines that when it comes to dealing with potential motor errors, the key is to make actions robust to them, since to be able to act under difficult conditions, 'prevention is better than cure' (Warren et al., 1986) (p. 259). In walking, markers of such behaviour are multiple, as participants not only adapt directly to perturbations, but also show altered gaze (K. Kopiske et al., 2021) and gait patterns (Dingwell & Cusumano, 2000; Rand et al., 1998) when walking is perturbed. Future research may investigate if such markers can also be seen in grasping, although we note that the cost of not successfully grasping an object is of course not comparable to the cost of falling during perturbed walking. For the use of pupillometry as a no-report marker, our results show that psychophysical responses at this point cannot be replaced by pupil-dilation data. We have conducted three studies each with different motor actions, perturbation schedules, and psychophysical responses types (Müller et al., 2025; Pfalz et al., 2025), with remarkable consistency across results obtained from the different paradigms. In the two of those studies that included pupillometry, we have also twice found the same pattern that pupil-dilation patterns are robust on average, but very variable on a trial-by-trial basis.

Similar data patterns in two very different motor actions

By choosing walking and grasping as our model actions, we used two inherently multimodal actions. To grasp and lift an object, an actor will use visual information about its size, position, as well as material properties (Schmidt et al., 2017), information about their own hand from vision (Volcic & Domini, 2016) as well as proprioception and somatosensation (van Beers et al., 1999; Weiler et al., 2019), and finally haptic information when the object is touched (Lederman et al., 1986). It also forced participants to make essentially cross-modal intensity comparisons, where Molyneux's problem famously asks whether such a comparison is at all possible beyond simply relying on past experiences (Locke, 1690), which we know affect perceptual judgements through short-term and long-term priors (Constant et al., 2025). Similarly, walking, especially under conditions of greater difficulty, will also involve vestibular (Nashner et al., 1982), but also visual (Laurent & Thomson, 1988), proprioceptive or haptic cues (Dietz et al., 1987). These of course differ from those used in grasping, in terms of the limbs, muscles and joints, as well as innervation involved (Boyd, 1980; Nashner, 1976) as well as the time scales (Crevecoeur et al., 2020; K. Kopiske et al., 2021). The key point is that choosing two experimental designs with all of these factors involved was a deliberate choice to make the actions more generalisable and applicable to everyday life, where all actions have multimodal components, as was already noted by Woodworth (1899) (p. 72). Finding robust effects of adaptation affecting perturbation detection and correlating with tonic pupil responses *despite* the multitude of modalities and factors involved underlines the generalisability of our findings.

Limitations and outlook

Our study improved on our previous works by making the results more generalisable, both by replicating them in a different motor action, but also by using perturbation schedules that were chosen specifically to isolate perturbation magnitude and the error signal. We also removed the previous issue of presenting in some blocks only perturbations with the same sign, which can lead to response biases masking the perceptual effects (Bosch et al., 2020). Here, all blocks contained an equal number of perturbations in each direction. The key result of reduced detection performance when participants could adapt to the perturbation was generalisable and robust to these methodological improvements – however, we note that it was also notably reduced. This in turn may indicate that while participants do rely on their motor errors for such judgements, the role of the perturbation magnitude itself is stronger than we had previously concluded. We also concede that data-quality issues with our eye tracking in the grasping setup should be taken into account when interpreting these data, and in particular the failure of classification which, if it worked, would be one of the key advantages of establishing pupil dilation as a marker of perturbation detection. While we believe that ultimately, ecologically valid experimental designs like ours are the best test of its utility as such a marker, it may be interesting in future work to employ designs closer to classic psychophysical studies to see how far pupillometry can go as a predictor of perception and cognition in action.

Conclusion

We show that adapting to a perturbation impairs the actor's ability to detect the perturbation, in walking and grasping similarly. We also demonstrate concurrent tonic pupil-dilation responses that are consistent with an effect of uncertainty. While pupil dilation could not be established as a reliable no-report marker of perturbation detection, this sheds more light on the role of cognition and strategies in sensorimotor adaptation.

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