Can Pupillometry Reveal Perturbation Detection in Sensorimotor Adaptation during Grasping?

Running head: Perturbation detection and pupillometry

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ABSTRACT – Humans adjust their motor actions to correct for errors both
with and without being aware of doing so. Little is known, however, about
what makes errors detectable for the actor. Here, we replicate and extend
prior work showing that motor adjustments may mask the very errors they
correct for. We also investigated pupillometry as an unobtrusive no-report
marker of perturbation detection. N=48 participants grasped objects while a
visuo-haptic size mismatch was applied either sinusoidally or abruptly. When
mismatches started abruptly and thereafter stayed the same, participants
adapted well but also showed decreasing discrimination performance and
decreasing confidence in their responses. This was not the case for
sinusoidally introduced perturbations. We also show that parameters that
characterize phasic and tonic pupil responses were predicted by stimulus
parameters and differed depending on participants' grasping and behavioral
responses. However, predicting response characteristics from pupil-dilation
features using support-vector machine classifiers was not successful. This
shows that while pupillometry may yet prove to be a useful no-report marker
of perturbation and error detection, there are some challenges for trial-by-
trial prediction.

New and Noteworthy

An actor detecting the need to adjust a motor action can make these adjustments more efficient.
We show that error signals play a central role in both humans' detection of and meta-cognition
about motor perturbations. Pupil dilation during perturbed actions reflected perturbation
properties and participants' responses, but trial-wise prediction of responses using pupil-
dilation parameters was close to chance. This is a step towards determining whether
pupillometry can serve as a no-report marker of perturbation detection.

Introduction

Visuomotor mapping and forward mechanisms in motor actions

Imagine that a friend brings you an unusually shaped, extravagant cup from their vacation (Fig.
1). The handle is positioned slightly upper, the diameter is larger, and the shape differs
significantly from your usual cup, shifting its center of mass. As you drink your morning coffee,
you notice that you frequently misreach, fail to grasp the handle correctly, or bump your hand
against the rim. It becomes clear: you need to adapt to this new cup. But why does this process
seem so challenging?

The key to this improvement is sensorimotor adaptation. This process describes how the brain
adjusts movements such as grasping actions to altered conditions (Krakauer & Mazzoni, 2011).
Several components must interact on a physical level: joints in the shoulder, elbow, wrist, and
fingers need to be precisely coordinated to securely grasp the cup. Simultaneously, the physical
properties of the cup – its mass, shape, orientation, and size – affect hand positioning. This
physical adjustment is guided by a neural system that translates perceptual information into
motor commands, a process known as perceptual-motor mapping (Warren, 2006).
Computationally, it is typically modelled with so-called internal forward mechanisms: Based on
the current position and movement of the hand, the brain generates a prediction of where the

hand will land on the object – in this case, on the handle of the new cup. This prediction is
compared with sensory feedback, which provides information on where the hand actually landed
on the object (Miall & Wolpert, 1996). If there is a mismatch, the brain receives an error signal,
and an adjustment is made to avoid the error in the future. This explains why grasping the new
coffee cup becomes easier with each attempt: The mapping is updated with each movement,
improving the grasp over time and increasing the likelihood of a successful, fluid grasp (Wolpert
et al., 1995). Eventually, your movements become as accurate as before.

Figure 1: An unusual coffee cup.

Implicit and explicit processes in adaptation

The adjustment or correction of the grasping movement is considered in large part as an implicit
learning process, that is, outside of cognitive control (Mazzoni & Krakauer, 2006) and controlled
largely by forward models in the cerebellum (Shadmehr et al., 2010). However, explicit,
deliberately controlled processes have also been shown to influence motor adaptation (Taylor &
Ivry, 2011), allowing for rapid, consciously controlled or even strategic adjustments to correct
for errors, with central involvement of memory areas such as the medial temporal lobe
(McDougle et al., 2022). In contrast, implicit learning proceeds more slowly, and without the
actor being consciously aware of them. These processes work in tandem, responding to different
error signals – both the conscious correction after the first attempt and the unconscious
adaptation that occurs over time – and together they optimize motor adaptation to
perturbations (McDougle et al., 2016; Taylor et al., 2014).

In experimental research, these two processes have been separated by specific experimental
manipulations, such as distracting participants from the presence of perturbations (Mariscal et
al., 2020) or by providing them with explicit instructions to compensate for perturbations
(Miyamoto et al., 2020; Taylor & Ivry, 2011). However, in real-world situations, no instructions
are provided, and motor errors are detected based only on their inherent characteristics – if at
all. Research has investigated adaptive behaviors when perturbations were intentionally made
very large (Hudson & Landy, 2012), when participants received identical feedback regardless of
whether their movement was accurate or erroneous, known as a "clamp" perturbation
(McDougle et al., 2015), or when perturbations were introduced abruptly rather than gradually
(Modchalingam et al., 2023; Orban de Xivry et al., 2013). In all these cases, conditions were
chosen such that perturbations should be detected in one condition but not in another (or at

least far more frequently in one condition). Much less research, however, has investigated when
participants can perceive inherent properties of perturbations.

One example of this is a study by Gaffin-Cahn and colleagues (Gaffin-Cahn et al., 2019). Here,
participants performed a reaching task with distorted endpoint feedback and judged whether
the endpoint shown to them was the result of their own movement. Participants were able to
identify the perturbations, relying primarily on visual endpoint feedback and less on
proprioceptive cues, which indicates that different external factors are weighed differently. Other
studies have investigated metacognitive judgements about motor errors: That is, the extent to
which participants notice and are confident about motor errors during their movements. Pereira
and colleagues (Pereira et al., 2023) had participants perform a target task using a joystick, while
deviations in cursor movement were experimentally introduced. Participants indicated if they
had noticed a deviation and rated their confidence in their decisions while neural activity was
recorded using fMRI. Results showed that participants could adjust confidence in their decisions
according to the accuracy of their responses, even when they were unaware of the deviations.
Similarly, Arbuzova and colleagues (Arbuzova et al., 2021) showed metacognitive awareness of
motor errors during a virtual ball-throwing task. This suggests a level of metacognitive
awareness based on visuomotor information even in the absence of conscious awareness of
errors, although error history might play a crucial role in it (Hewitson et al., 2023).

To examine directly which factors affect perturbation detection, a previous study that our
experiments are based on (Müller et al., 2025) investigated how a size mismatch between a
visible and an invisible target cuboid, as well as the sensory error signal (the difference between
the expected and actual haptic grip feedback), affect motor adaptation and mismatch
discrimination in a grasping task. Two types of perturbations were used: an abrupt perturbation,
where the mismatch between cuboids was introduced in the first trial and then remained
constant, and a sinusoidal perturbation, where the mismatch varied in each trial. Participants
were instructed to indicate in a two-alternative forced-choice (2AFC) task whether the grasped
cuboid was larger or smaller than the visible one, founding that discrimination performance
gradually declined when participants adapted their grip to the mismatch for abrupt
perturbations. However, with a continuously changing mismatch (sinusoidal) without
systematically decreasing error signal, discrimination performance remained constant.

Pupillometry as a physiological measure of perception

To directly capture participants' perception of a perturbation, they must be asked (e.g., "Was the
object you saw smaller or larger than the one you felt?", or "Where will your pointing movement
land?"). However, this can be challenging, as those same questions alert participants to the
perturbations, and with typical adaptation schedules, repeated responses might cause
uncertainty, influencing the participants' answers (Bosch et al., 2020). Therefore, it may be
useful to employ alternative methods espousing direct responses from the participant, such as
physiological correlates.

Pupillometry has served as a way around requiring participants to report their perception
altogether and to circumvent the issues that come with this. For example, Einhäuser and
colleagues (Einhäuser et al., 2008) demonstrated that pupil responses could serve as an
indicator of perceptual selection in multistability, such as the perception of a Necker cube, as
pupil size correlated with perceptual changes. It has also been used as a no-report marker of
perception in binocular rivalry (Naber et al., 2011). Results like these suggest that pupil size may
reflect changes in visual perception and cognitive processes. Similarly, Yokoi and Weiler (Yokoi &
Weiler, 2022) examined changes in pupil size during motor adaptation. Participants performed
reaching movements using a robotic manipulandum, where a lateral force was introduced as a
perturbation through a force-field perturbation. These perturbations were applied either

abruptly with multiple direction changes, or gradually. To assess the effects on pupil dilation of
uncertainty and surprise, the authors focused on trials following the introduction of the
perturbation, and after the perturbation was removed, but without validating the participants'
subjective perception. The results indicated that phasic pupil response, that is, the baseline pupil
diameter, was significantly increased at the onset of each experimental block, also associated
with prolonged reaction and movement times. A pronounced tonic pupillary response, that is,
change in dilation during the movement, was observed both at the start of a new block and
during the introduction of a perturbation. The authors concluded that not only physical exertion
but also the perturbation itself triggers a pupillary response perhaps related to locus coeruleus
activity in response to surprise (Dayan & Yu, 2006; Yokoi & Weiler, 2022). This supports the
notion that larger pupil diameters and faster pupil reactions are associated with increased
uncertainty and more difficult perceptual decisions and that pupil size correlates with subjective
confidence and surprise about environmental changes.

In summary, participants can detect perturbations during grasping tasks, and their pupils
respond to perturbations. This raises the question of whether pupillary responses alone could be
used to predict the participants' current perception – without requiring explicit feedback from
the participants. The aim of this study was to tackle this question by combining (a) a grasping
task with different perturbation schedules with (b) a psychophysics task where participants
judged the relative sizes of visual and haptic (i.e., seen and felt) objects and (c) pupil dilation
during the tasks, which was evaluated depending on stimulus and response characteristics and
used to predict the response.

Methods

Participants

A total of 59 participants took part in this study. Participants were required to be between 18
and 60 years old, right-handed, and have unrestricted arm and hand functionality as well as
normal or corrected-to-normal vision, provided any visual aids needed did not interfere with the
participant's comfort or the measurement process. Of the 59 participants, 11 were excluded
from the experiment due to technical difficulties with achieving a successful eye-tracker
calibration through the PLATO goggles and the cold mirror, resulting in 48 participants included
in the final analysis, the intended sample size to enable counterbalancing of conditions and
provide at least 90% power with an effect of Cohen's d = 0.5 (Cohen, 1988). Of these participants,
33 were women and 15 men, with ages ranging from 18 to 37 years. Participants were
compensated either with course credit or 10€ per hour.

Materials and stimuli

Participants were presented with cuboids of varying sizes in a mirror setup (Müller et al., 2025),
see Fig. 2. As was done in Müller et al. (2024), three cuboids were positioned on a rotating
platform that could rotate one of them to face the participant on any given trial. The aluminum
cuboids used in this experiment had a base of 15x15 and different lengths, with the smallest
cuboid measuring 28 mm and the largest 60 mm. The three visually presented stimuli had
lengths of 40 mm, 44 mm, or 48 mm. The size of the haptically presented stimuli varied based on
the visually presented size and the visuo-haptic mismatch determined by the perturbation
condition. This mismatch was introduced either abruptly or sinusoidally, with six different
perturbation magnitudes: -12 mm, -6 mm, -3 mm, 3 mm, 6 mm, and 12 mm. Visual and haptic
size was dissociated by projecting the "visual" cuboid towards the participant via a cold mirror
slanted 45° away from them, while a "haptic" cuboid to be grasped was placed behind the mirror
at the location where the participant saw the visual cuboid.

Participants wore PLATO goggles (Milgram, 1987) to remove vision between trials, whose
opaque lenses obstructed vision when closed but minimally altered ambient brightness (to 80-
90%), thereby only slightly affecting pupil dilation. Differing from Müller et al. (2024), responses
were given using a four-button response box ("Black Box"; The Black Box ToolKit Ltd., Sheffield,
UK; Fig, 2, inset). Behind the mirror was an EyeLink-1000 eye tracker (SR Research, Ottawa,
Canada) tracking participants' eye movements and pupil dilation through the cold (infrared-
transparent) mirror, and an Optotrak 3D Investigator (Northern Digital, Waterloo, CA) that
captured hand movements at a frequency of 500 Hz. Infrared diodes were placed on the
participants' thumb, index finger, and wrist. To determine the exact moment of contact with the
object, reflective aluminum was affixed to the long sides of the haptic object, and a diode was
positioned nearby to allow the diode's signal to be reflected. Once the haptic cuboid was lifted,
the signal was no longer reflected.

Figure 2: The experimental setup. Participants sat in front of a cold mirror, slanted away from
them at 45°, with their head in a chin rest and their left hand on a response box. Visual objects
were presented on a rotating platform in front of the mirror, haptic objects were placed behind
the mirror in the same position where participants saw the visual objects. PLATO goggles were
used to prevent vision of the platform rotating, an EyeLink-1000 tracked gaze position and
pupil diameter through the cold mirror. Inset, top left: The responses assigned to the four
buttons of the response box.

Experimental design

For each trial, participants were instructed to grasp the haptic cuboid, lift it briefly, place it back
down, and then judge whether the haptic cuboid was larger or smaller than the visual cuboid.
Four response options were provided: "definitely larger," "probably larger," "probably smaller,"
and "definitely smaller", allowing more nuanced insights compared to a simple "larger or
smaller" decision (Müller et al., 2025) and including subjective confidence as a factor in pupil-
dilation analyses – that is, we considered "definitely larger" and "definitely smaller" as responses
with high subjective confidence, and "probably larger" and "probably smaller" as low-subjective
confidence responses. This is in line with previous work showing uncertainty about the
perturbation on the next action being a predictor of pupillary responses (Yokoi & Weiler, 2022).
We deliberately included confidence in one single judgement on each trial despite concerns that
this can introduce biases (Fleming & Lau, 2014; Mamassian, 2016), since this type of response

ameliorated a key issue in Müller et al. (2024), participants repeatedly having to give the same
response to repeated identical perturbations.

Prior to the main experiment, a training block consisting of 12 trials was conducted to
familiarize participants with the task. This training block contained both unperturbed trials and
trials with the largest positive and negative size mismatch. During training, participants were
informed when they had grasped a perturbed object, helping them develop an understanding of
the potential size differences. In the main experiment, the abrupt-perturbation condition was
presented a total of 6 times (±3 mm, ±6 mm, ±12 mm), and the sinusoidal-perturbation
condition was presented 3 times (3 mm, 6 mm, 12 mm). To control for sequential effects across
blocks, a 6x6 row-balanced Latin Square was used to determine the order of the abrupt blocks,
while the sinusoidal blocks were inserted at randomly selected positions. The order of these
blocks also varied across participants. Consequently, each participant completed 9 blocks, each
lasting approximately 11 minutes (abrupt blocks ~10 minutes, sinusoidal blocks ~12 minutes).
After each block, participants were allowed to take a break for as long as needed.

Each block in the *abrupt-perturbation* condition consisted of 24 trials. The first four trials
presented blocks identical to the visually displayed ones to establish a baseline for the maximum
grip aperture (MGA). In the subsequent 16 trials, the length of the haptic cuboid was either
larger or smaller than that of the visual cuboid by a fixed amount, depending on the perturbation
magnitude assigned to the block. The rotating platform displayed a different cuboid in each trial,
with the size mismatch being constant across each one block of the abrupt-perturbation
condition. For instance, if the visual cuboid in a perturbed trial had a size of 44 mm and the
perturbation magnitude was 6 mm, the haptic cuboid had a size of 50 mm. The final four trials
were washout trials in which the perturbation was removed, and the visual and haptic cuboid
were of equal size again. This allowed for the assessment of the aftereffects of the perturbation
on the MGA and the psychophysical judgments.

Each block in the *sinusoidal-perturbation* condition consisted of 36 trials. The length of the
haptic cuboid was altered according to a sinusoidal function (as proposed by Hudson & Landy,
2012) with each sinus-cycle consisting of 12 trials, thus creating size differences between the
visual and haptic objects without abrupt changes. As a previous study (Müller et al., 2025) found
no significant difference in response patterns between positive and negative perturbation
magnitudes, these were combined in the current study, and each participant completed three
sinusoidal-perturbation blocks with maximal amplitudes of 3 mm, 6 mm, and 12 mm,
respectively. A randomized phase shift was introduced, starting the sinusoidal cycle in either the
positive or negative direction. Across all participants, an equal number of positive and negative
perturbation amplitudes were presented, and each participant completed at least one of each.

Data processing and analysis

Grasping: Maximum grip aperture and adaptation

To filter the motion-tracking data, we applied a cubic-spline interpolation and a third-order
Savitzky-Golay filter (Savitzky & Golay, 1964) using a 55-ms window. For each trial, the onset of
the grasping movement was defined as both the index finger's and thumb's marker moving at
more than 25 cm/s, while the end was defined as the moment when the diode that was reflected
by the target object was no longer visible to the motion-capture system or moved at more than
25 cm/s. Trials were excluded from analysis if the grip-aperture trajectory was missing more
than 20% of frames, or as outliers if the MGA was more than three inter-quartile ranges removed
from a participant's median for the respective visual object size (3.8% of trials combined).

To measure grip adjustment to the different cuboid sizes, the distance between the thumb and
index finger was recorded and their maximal distance during the grasping movement was

computed as the MGA. The MGA is known to increase with object size (Bhatia et al., 2022;
Jeannerod, 1984; Smeets & Brenner, 1999) and reflects sensorimotor adaptation when
participants adjust their grip to visual or haptic perturbations (Cesanek & Domini, 2017;
Gentilucci et al., 1995; Kopiske et al., 2017; Säfström & Edin, 2005). We modelled adaptation of
the MGA in response to the error signal (the size difference between the visual and haptic
cuboids) using a linear state-space model (Cheng & Sabes, 2006; Wolpert et al., 1995) in which a
state, corresponding roughly to a visuomotor mapping of visual input to a motor action, changes
linearly from the previous state based on the error signal from the previous trial, thereby
facilitating a correction or adaptation in the grip movement:

$$x_{t+1} = Ax_t - bE_t \qquad (1)$$

Here x_t represents the current state and is modified trial-by-trial based on the error E_t, which
we defined as the haptic error signal – that is, difference between the observed MGA and the
MGA predicted from the linear response function of MGA $\sim$ haptic size and the haptic object size
on each trial. The retention parameter A indicates the extent to which the previous state
influences the current state. For fitting, the nloptr package (Ypma, 2014) was used. Parameters A
and b were each bounded between [0, 1].

To assess the adaptation process, the correction parameter b was our main parameter of
interest. To assess whether adaptation differed between conditions, we conducted a repeated-
measures ANOVA (rmANOVA) with factors *perturbation schedule* (abrupt or sinusoidal) and
perturbation magnitude (3 mm, 6 mm, 12 mm).

Psychophysics: Size discrimination

We analyzed perturbation-detection, measured indirectly through size discrimination, in three
ways: One, overall performance was assessed by creating receiver-operator-characteristics
(ROC) curves (Green & Swets, 1966) for each participant and each perturbation schedule, with
each of the four response levels to the question "was the felt object larger or smaller than the
seen one?" essentially being treated as different decision criteria (Naber et al., 2013). That is,
each curve consisted of four points with y_1 equaling the proportion of "definitely larger"
responses when the haptic object was indeed larger, y_2 being the combined proportion of
"definitely larger" and "probably larger" responses, etc., and the x-coordinates being the
corresponding values for smaller haptic objects and responses starting with "definitely smaller".
In sinusoidal blocks, only trials with maximum amplitude were used in this analysis, to enable a
fair comparison to abrupt blocks. Two, we collapsed "definitely" and "probably" correct
responses and "definitely" and "probably" incorrect responses, respectively, to get a binary
correct/incorrect scoring that could be used to (i) replicate the finding from previous work
(Müller et al., 2025) and (ii) compute linear slopes for the percentage of correct responses over
trials in each block, which served as a means to estimate if participants got better or worse as
perturbations were presented repeatedly. These slopes were then submitted to rmANOVAs with
factors perturbation schedule (abrupt or sinusoidal) and perturbation magnitude (3mm, 6mm,
12 mm). Three, we conducted these same rmANOVAs for the slopes of response confidence after
dividing responses in confident vs. unconfident.

Pupillometry: Preprocessing, parameters, prediction

Throughout the experiment, eye movements and pupillary responses were recorded at a
frequency of 1000 Hz. Pupil-dilation trajectories from 1000 ms before and 2500 ms after contact
with the haptic cuboid were used. Blinks were automatically identified by EyeLink DataView (SR
Research, Ottawa, Canada), and all data 50 ms around blinks was removed. Plots and basic
analyses were conducted with unfiltered data. To train classifiers, missing data was linearly
interpolated and data filtered with a 35-ms Savitzky-Golay filter (Savitzky & Golay, 1964). An

average of approximately 42% of data points were missing, including blinks. Visual inspection
(Fig. 7) shows that missing data were spread relatively evenly across trajectories and did not
cluster around systematically relative to touch, although perhaps somewhat after the response
was given (Fig. 7, top row), with mean peaks of 48.6%. Trials were excluded from analysis if less
than 500 ms of the trajectory could be evaluated (4.9% of trials). One experimental block in one
participant additionally had to be excluded due to technical issues during recording.

From each trial's pupil-dilation trajectory, we computed a set of three parameters: (i) The
baseline (computed as the mean dilation during a 1,000 ms window after opening of the
goggles) was computed as a measure of tonic pupil response. (ii) We estimated the dilation's
maximum and minimum velocity (i.e., the maximum speed of the pupil opening and contracting)
post-touch and took the difference between the two as a measure of phasic response. (iii) Finally
as another measure of phasic response that was also used by (Yokoi & Weiler, 2022), we
calculated the amplitude (i.e., peak-trough difference) of the aperture post-touch.

To analyze which variables (trial parameters as well as properties of the grasp and the
psychophysical response) influenced the pupillary response, linear mixed-effects models (LMEs)
were applied (Bates et al., 2015). We iteratively fit models with an increasing numbers of
predictors, discarding factors that did not improve the Akaike Information Criterion, *AIC* (Akaike,
1974; Burnham & Anderson, 2004) relative to the current best model. In order, we performed
this procedure with the factors (each fit as a fixed effect with a slope) *perturbation magnitude*,
perturbation type, *trial number*, *block*, *response accuracy*, and *confidence* in correct responses,
and for each of the pupil parameters *baseline* pupil size, post-touch pupil *amplitude*, and post-
touch pupil *velocity difference*. A random effect with a random intercept for each participant was
also included in every model. For each pupil parameter, the model with the lowest AIC value was
ultimately selected as the one that best explained the pupillary response as a physiological
measure of perception influenced by the perturbation.

We used a Support Vector Machine (SVM) to determine whether participants' responses could be
inferred from their pupillary responses and other trial information (Boser et al., 1992). While
ideally, one would predict both the correctness and confidence of the response, here we focused
on the responses' confidence, given that this was a parameter that participants had direct access
to. Further, it has been argued that pupil responses (also in perception-action tasks) are
particularly sensitive to surprise (Yokoi & Weiler, 2022), which also might be reflected in the
difference between confident and unconfident correct responses. Thus, the following analysis
examined the extent to which confidence could be predicted, in correct responses, based on
different groups of predictor variables.

We used five sets of features to compute subject-wise SVM classifiers: (i) trial information (block
number, trial number, perturbation type, perturbation magnitude), (ii) classic "pupil parameters"
as defined above (baseline, velocity difference, amplitude), (iii) pupil-response trajectories
spanning from 500 ms before to 2500 ms after contact with the haptic cube, downsampled to 50
Hz (to make computation feasible), (iv) the first temporal derivative of those trajectories, also
downsampled to 50 Hz, and (v), the grasping error, defined as the difference between the
observed MGA and the MGA expected given the response function and the haptic object size. For
each participant, we used seven randomly selected experimental blocks as the training set to
train a c-classification SVM with radial-basis kernel using the R-package *e1071* (Meyer et al.,
2024), and the remaining two blocks as the test set. Each combination of the four feature classes
was used, with the class-balanced accuracy in the test set being our primary outcome. Since
classification performance would likely depend to some extent on both the sampling rate of the
data and meta parameters of the SVM model (Kuhn & Johnson, 2013), we varied the sampling
rate (ranging from 5 Hz to 50 Hz), as well as the cost-parameter of constraints violations (i.e., the
factor by which residuals are multiplied, ranging from $C = 10^{-5}$ to $C = 10^5$) and the class weights

for responses (using both equal weights and weights inverse to the response distribution). We
report results from our "standard" combination of parameters with 50Hz, a cost parameter of C
= 1, and equal weights for each class of responses in the main text, and the range of model
performance based on varying these parameters in the appendix. Data and analyses are available
at https://osf.io/vh36g/?view_only=9e72dec48ed04b57a1c24fe5df82df6d

Results

Maximum grip aperture and sensorimotor adaptation

Figure 3: Maximum grip apertures (MGAs) in different conditions. Top: Mean MGAs, split up
by perturbation type (abrupt on the left, sinusoidal on the right) and perturbation magnitude (by
color), baseline-corrected relative to non-perturbed trials. Bottom: MGAs, perturbations and
the corresponding models from sample blocks. Models computed following equation 1. We
show data from individual blocks rather than aggregates since the use of the trial-wise MGA,
along with a block-wise correction parameter, makes an average model fitted to average data
hard to interpret. Left: Data from block with an abrupt perturbation. Right: Data from a
sinusoidal-perturbation block. For the top row, absolute values relative to baseline were
computed to enable collapsing of blocks using sinus function with different signs.

Participants scaled their grip to the size of the visual object, mean slope = 0.44 ± a standard error
of 0.05. Mean parameters from our error-correction model (eq. 1) were b = .35 ± .01 and A = .80
± .01. The mean correction parameters by perturbation type were b_{abrupt} = 0.42 ± .01 for the
abrupt condition and $b_{sinusoidal}$ = 0.21 ± .01 for the sinusoidal condition. This difference was

significant in the rmANOVA ($F(1, 47) = 95.40$, $p < .001$), indicating that adaptation to the
perturbation was significantly more effective in the abrupt condition than in the sinusoidal
condition. There was also a main effect for perturbation magnitudes ($F(2, 94) = 4.22$, $p = .02$),
but no interaction ($F(2, 94) = 3.14$, $p = .097$). Grasping data aggregated by perturbation type and
magnitude, as well as from two blocks of a sample participant to illustrate the models, can be
seen in Fig. 3.

Discrimination performance

Participants were slightly more likely to judge the haptic object as larger than the visual one
(56.8%), and also more likely to respond that the object was definitely larger or smaller (64.6%)
than it being only probably so. Both confidence and size judgements were more sensitive to
differences in perturbation magnitude in sinusoidal-perturbation blocks compared to abrupt-
perturbation blocks, see Fig. 4.

Figure 4: Proportion of responses along the two response dimensions, by perturbation type
and magnitude. Left: Proportion of responses saying that the haptic object was larger than the
visual one. Right: Proportion of responses with high confidence. Black squares indicate abrupt-
perturbation blocks, gray circles show values from sinusoidal-perturbation blocks (data from
maximal-perturbation trials only). We show arithmetic means across participants, with
between-participant standard errors as error bars.

We calculated linear slopes for each experimental block for the responses' correctness (with
respect to the direction of the perturbation and binarized, so the combined proportion of dark
and light blue, Fig. 5), so *correctness ~ trial number*. These were submitted to a 2x3 rmANOVA,
revealing a significant effect for the perturbation condition (sinusoidal/abrupt) on response
accuracy: $F(1, 47) = 48.86$, $p < .001$ for the average slope across trials (decreasing by -0.95% per
trial for abrupt conditions, and decreasing by -0.02% per trial for sinusoidal conditions),
consistent with the fact that visually, the proportion of correct trials in Fig. 5 decreased over
trials for abrupt, but not sinusoidal perturbations, as one would expect if sensorimotor

adaptation makes detection harder. However, no significant main effect was found for
perturbation size ($F(2, 94) = 2.72$, $p = .071$), nor an interaction effect ($F(2, 94) = 1.88$, $p = .158$).

For linear slopes of response confidence (combined proportion of dark red and dark blue, Fig. 5),
the 2x3 rmANOVA showed a significant effect of the perturbation condition (sinusoidal/abrupt):
$F(1, 47) = 53.07$, $p < .001$ for the average slope across trials (decreasing by -1.21% per trial for
abrupt conditions, and decreasing by -0.05% per trial for sinusoidal conditions). Additionally,
significant effects were observed of perturbation size ($F(2, 94) = 7.98$, $p = .001$), and an
interaction effect ($F(2, 94) = 6.90$, $p = .002$). The significant interaction suggests that the effect of
perturbation size on the slope of response confidence depends on whether the perturbation is
abrupt or sinusoidal. Similar to the effects seen in the correctness of responses, the proportion of
high-confidence responses (and especially high-confidence correct responses) decreased
substantially during abrupt, but not sinusoidal-perturbation blocks (Fig. 5).

Figure 5: Participants' responses across trials. The y-axis shows the proportions of each
response, cumulatively, such that the height of the dark-blue bar is the proportion of responses
that were correct and high-confidence, the height of the light-blue bar on top of this is the
proportion of low-confidence responses that were correct, and light red and dark red show the
proportions of low-confidence and high-confidence responses that were incorrect. The x-axis
displays trials (left) or sinus half-cycles (right). Left: Data from blocks with abruptly-introduced
perturbations, with mean proportions plotted by trial, starting with the first perturbed trial. Right:
Data from sinusoidal blocks, plotted by sinus-half-cycle, which would contain each perturbation
magnitude in the block precisely once and is thus free of the confounding factor of perturbation
magnitude.

To investigate and compare overall (aggregated) discrimination performance, we constructed
ROC curves for each participant and each perturbation type (Fig. 6) and analyzed the area under
the curve (AUC). On average, participants did quite well in the task, with mean AUCs of .88 for
abrupt blocks and .93 for sinusoidal blocks. This difference was statistically significant, $t(47) =$
4.8, $p < .001$. We also computed just-noticeable differences from binary-coded responses, finding
JND values of 5.43 ± 0.23 mm for the abrupt condition and 3.97 ± 0.17 mm for the sinusoidal
condition.

Figure 6: ROC curves for the two types of blocks. Left: Data from abrupt-perturbation blocks,
right: Data from sinusoidal-perturbation blocks, maximum-amplitude trials only. Each colored
line indicates a single participant, thick black lines indicate ROC curves computed from grand
means across participants.

Pupillary responses

Average pupil dilation depending on trial and response characteristics are shown in Fig. 7. From
these, pupil parameters baseline, velocity difference, and amplitude were computed for each
trial.

Figure 7: Pupil-dilation trajectories split up by perturbation type and by response. Plotted are
grand means across participants. Top row: Trajectories relative to the participant's response.
Bottom row: Trajectories relative to the participant touching the haptic object. Shaded areas
indicate ± one between-participant SEM. Insets show proportion of frames with missing data.

Using LMEs, we investigated if these parameters varied systematically depending on (i)
perturbation magnitude, (ii) perturbation type, (iii) trial, (iv) block, (v) response correctness,
(vi) response confidence, and (vii) the grasping error E. Each of these fixed effects were fit as
slopes in the LMEs. Iteratively adding predictors and comparing them by AIC to the previously
best-fitting model revealed the best model to be the full model for pupil-dilation *baseline* and for
the dilation's *amplitude*, though we note that some predictors did not affect both variables in the
same direction, i.e., one positively and one negatively. For its *velocity difference*, neither trial
number nor response confidence improved the model fit (Table 1). Thus, pupil parameters

responded to stimulus differences and differed by response and grasping parameters, although
with slight differences between tonic and phasic parameters.

Table 1: Eye parameters predicted by trial-information variables.

DV	Pert. magnitude	Pert. type	Trial #	Block #	Resp. correct	Resp. confid.	E
Baseline	FE: -4.2	FE: 34.3	FE: -7.0	FE: -16.1	FE: 24.7	FE: 4.9	FE: -0.7
ΔAIC:		-18.0	-416.4	-143.4	-6.4	-4.4	-35859.7
Amplitude	FE: 4.8	FE: -22.8	FE: 1.2	FE: 6.4	FE: 89.7	FE: -2.8	FE: 0.2
ΔAIC:		-124.9	-0.9	-28.5	-351.2	-15.8	-34304.2
Velocity difference	FE: 0	FE: -0.1	FE: -	FE: 0.1	FE: 0.4	FE: -	FE: -0.01
ΔAIC:		-35.9	9.6	-57.2	-60.6	5.2	-12384.1

453 *Note*: All ΔAIC are given for inclusion of the respective predictor, relative to the previously best-
454 fitting model. Predictors were added iteratively, in order from left to right and discarded (i.e.,
455 not included in more complex models) if the AIC was not improved by including them (cells
456 with red background color). Fixed effects (abbreviated as *FE*) from the final best-fitting model
457 are provided.

Classification of response confidence with SVM

Classification performance using our standard set of meta-parameters (50 Hz, C = 1, equal class
weights) is summarized in Table 2. As we can see, while class-based accuracy in the training set
was quite good for many different sets of features and especially for those involving the
derivative of pupil dilation, only classifiers using trial-information features could predict
responses in the test set. Indeed, adding other features like pupil dilation, its derivative, or
grasping error to a model containing trial information reliably increased the accuracy in the
training set, but *decreased* accuracy in the test set.

The obvious possible explanation here is overfitting: With 50 Hz, we had several times as many
features if we used the dilation trajectories than we had trials in the training set. Thus,
conducted the same analysis with lower sampling rates of 10 Hz and 5 Hz, see Table A.1 and
Table A.2. The main difference here was that while the overall pattern stayed the same – only
trial-information features having any predictive power in the test set – the accuracy in the test
set tended to decrease less than with the higher sampling rate. Thus, it is likely that (i)
overfitting was indeed a problem, and (ii) the information contained in most features was not
sufficient for classification. A multiverse analysis varying not only framerate but also the class
weights and cost factor (Table A.3) showed the same pattern, with only models including trial
information performing consistently above chance in the test set, and none outperforming the
simple trial-information-only model.

Table 2: SVM results with pupil dilation and its derivative sampled at 50 Hz.

Model	Acc. Train	Acc. Test	nSamples Train	nSamples Test
Trial information	90.5%	74.5%	105.1	32.1
Eye parameters	67.5%	47.4%	94.5	32.1
Dilation trajectory	72.4%	48.7%	100.1	27.7
Dilation derivative	96.2%	47.4%	99.1	28.8
Dilation trajectory + derivative	90.5%	49.0%	95.6	27.8
Dilation trajectory + derivative + info	94.8%	50.0%	100.3	25.7
Grasping error	63.2%	50.4%	99.2	31.0
Grasping error + trial info	91.6%	71.9%	99.2	29.3

478   *Note*: We report arithmetic means across participants. "Accuracy" refers to class-balanced
479   accuracy. The number of samples differed as trials with missing values in the features were
480   excluded.

Discussion

We found that as participants adapted to a sensorimotor size perturbation in grasping, their
discrimination performance regarding the same perturbation magnitude decreased, as did the
confidence in their own responses. We replicated and extended previous work (Müller et al.,
2025), who also found reduced discrimination with abrupt perturbations, and generalized the
results to a four-response setting (thereby circumventing methodological problems of
participants repeatedly having to give the same response). We also probed whether pupil
responses could be used to predict the confidence of participants' responses, as a first step
towards using pupillometry as a no-report marker of perturbation detection. While we did find
that pupil parameters responded to not only differences between experimental trials (Yokoi &
Weiler, 2022), but also differed depending on participants' psychophysical and grasping
responses, using pupil information as features in an SVM classifier did not allow us to accurately
predict psychophysical responses.

Having previously found that perturbation schedules that are easy to adapt to correlate with
decreasing perturbation detection (Müller et al., 2025) in a 2AFC task, part of our study was
aimed at improving the prior study methodologically. A major concern about presenting an
abruptly introduced step-function perturbation is that it requires participants to give the same
answer many times in a row, potentially introducing response biases that cannot be dissociated
from the putative effects of sensorimotor adaptation on detection. This was ameliorated by our
use of a four-response task, as participants had multiple correct options on any given
perturbation trial. Not only did we replicate the performance decrease with respect to

correctness, but we also found the same pattern in response confidence, again in line with the
idea that it is sensorimotor adaptation itself that, by decreasing the grasping error, makes it
harder to detect the perturbation participants adapted to and participants more uncertain about
their responses.

Our experiments focused on responses – motor, psychophysical, and physiological – to motor
perturbations, that is, externally induced errors. This is distinct from responses to self-generated
errors, which may be the more common type of error in everyday life. Here, recent work on
metacognition has shown that participants are also able to judge errors that are not induced by
the experimenter (Arbuzova et al., 2021) at an above-chance rate. Interestingly, such
metacognition appears to be preserved in confidence ratings even when detection responses are
incorrect (Pereira et al., 2023). While we found no difference in patterns between the
correctness and confidence of responses (both affected similarly on average by the perturbations
and decreasing over time for abrupt but not sinusoidal perturbation schedules), experiments
targeted at investigating metacognition over time may be an interesting avenue to find out more
about what is used to make metacognitive judgements. More generally, the question is to what
extent the results here generalize to other settings, which includes other motor actions such as
reaching (Gaffin-Cahn et al., 2019) or walking (Iturralde et al., 2020; Müller & Kopiske, 2025), as
well as psychophysical tasks more specifically designed to assess participants' confidence
(Fleming & Lau, 2014; Mamassian, 2016).

Finally, we show that pupil dilation reflects not just the characteristics of experimental trials
(Yokoi & Weiler, 2022), but also characteristics of participants' responses. LME analyses
confirmed that both the tonic response, quantified here by baseline dilation before the start of
each trial, and the phasic response, quantified as dilation change after touching the haptic object,
depended on trial characteristics such as the perturbation as well as trial and block number, and
on response characteristics such as the correctness and confidence of responses in the detection
task and the grasping error. In line with previous results (Yokoi & Weiler, 2022), this is consistent
with involvement of noradrenaline and the locus coeruleus (Dayan & Yu, 2006) as the actor acts
and decides under uncertainty. Such effects are a necessary condition for the overarching long-
term goal: Predicting psychophysical responses from pupil data. In simple terms, for this to be
possible, pupil dilation and psychophysics need to be related at all, which is what the LMEs
demonstrate. To go one step further, we also trained SVM classifiers using different sets of
features – trial information, aggregated pupil-dilation parameters, pupil-dilation trajectories,
and grasping errors – to predict response confidence. This is in line with previous work arguing
that pupil responses can reflect uncertainty and conflicting information (Ebitz & Platt, 2015;
Joshi & Gold, 2020), which is why we attempted to predict response confidence rather than
correctness (which participants also did not have access to when they gave their responses).
This was only partially successful: While many models showed great accuracy (>85%) in the
training set, only trial-information features had any predictive power in the test set, and indeed,
models containing these features only performed substantially better on the test set than those
additionally containing other features. In particular, the derivative of pupil-dilation trajectories
performed exceptionally well in the training set, but at chance level in the training set, even
combined with trial-information features. Using fewer features by downsampling pupil
trajectories to combat overfitting ameliorated the latter problem, but still the pupil data showed
no benefit over just using trial information. Here, we note three things: One, it is possible that
improved data quality could improve classification, although the mean proportion of missing
data was only moderately worse in trials that were incorrectly classified (44.6%) compared to
those that were correctly classified (41.2%) using pupil-dilation features. Two, while we chose to
temporally lock trajectories to the participant touching the object, the time courses plotted in
Fig. 7 suggest that locking them to the participant response might be just as promising –
however, investigating the time course in detail warrants its own study and is beyond the scope

of this manuscript. Three, we deliberately used SVM as a standard, well-tested classifier. Our
study focused on whether there was something in the data, not how well cutting-edge machine-
learning classifiers can perform. In future research, it may be useful to take a step back and
verify if, in a simple adaptation paradigm without psychophysical response, trial characteristics
can be predicted from pupil data.

Conclusion

As humans adapt to motor perturbations, the motor error decreases. This, in turn, makes it
harder for them to detect those same perturbations, and makes them less confident in being able
to do so. Pupil-dilation parameters responded to trial- and response-characteristics, but did not
allow accurate classification of participant responses.

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Appendix

Table A.1: SVM results with pupil dilation and its derivative sampled at 10 Hz.

Model	Acc. Train	Acc. Test	nSamples Train	nSamples Test
Trial information	90.0%	78.8%	105.0	33.8
Eye parameters	67.5%	45.4%	96.4	28.2
Dilation trajectory	72.6%	50.1%	96.8	29.7
Dilation derivative	92.9%	48.4%	98.3	30.1
Dilation trajectory + derivative	88.7%	45.5%	101.3	28.0
Dilation trajectory + derivative + info	96.0%	62.6%	96.3	28.6
Grasping error	65.6%	46.9%	96.6	30.2
Grasping error + trial info	91.0%	73.9%	102.7	28.3

571   *Note*: Variables used as in Table 2.

574   Table A.2: SVM at 5 Hz

Model	Acc. Train	Acc. Test	nSamples Train	nSamples Test
Trial information	91.4%	74.4%	105.4	29.5
Eye parameters	67.9%	41.0%	99.2	28.2
Dilation trajectory	72.1%	45.6%	100.1	27.1
Dilation derivative	89.4%	49.6%	97.0	27.0
Dilation trajectory + derivative	87.6%	48.5%	97.6	28.3
Dilation trajectory + derivative + info	96.1%	69.6%	98.6	27.6
Grasping error	65.6%	54.4%	99.0	29.8
Grasping error + trial info	91.8%	73.3%	102.4	28.1

575   *Note*: Variables used as in Table 2.

578   Table A.3: Multiverse SVM results.

Model	Accuracy Training	Accuracy Test
Trial information	75.3% - 98.5%	55.8% - 100%
Eye parameters	59.8% - 82.1%	24.7% - 52.8%
Dilation trajectory	59.2% - 100%	39.0% - 75.9%
Dilation derivative	75.1% - 99.8%	37.5% - 63.0%
Dilation trajectory + derivative	72.2% - 100%	39.6% - 64.1%
Dilation trajectory + derivative + info	73.3% - 100%	34.9% - 69.6%
Grasping error	56.9% - 72.6%	46.6% - 67.3%
Grasping error + trial info	73.2% - 100%	48.8% - 100%

579   *Note*: Variables used as in Table 2. We report ranges of means across parameter
580   combinations. Frame rate (50 Hz, 10 Hz, 5 Hz), class weights (equal, inverse), and cost factor
581   ($C = 10^{-5}$, $C = 10^{-1}$, $C = 1$, $C = 10$, $C = 10^5$) were varied independently.

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