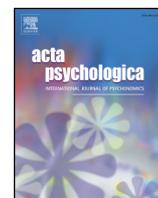




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## Asymmetries in visuomotor recalibration of time perception: Does causal binding distort the window of integration?

Marieke Rohde<sup>a,b,\*</sup>, Leonie Greiner<sup>a</sup>, Marc O. Ernst<sup>a,b</sup>

<sup>a</sup> Department of Cognitive Neuroscience, University of Bielefeld, Universitätsstr. 25, W3-240, 33615 Bielefeld Germany

<sup>b</sup> Cognitive Interaction Technology (CITEC) Centre of Excellence, University of Bielefeld, Universitätsstr. 25, W3-240, 33615 Bielefeld Germany

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### ABSTRACT

The recalibration of perceived visuomotor simultaneity to vision-lead and movement-lead temporal discrepancies is marked by an underlying causal asymmetry, if the movement (button press) is voluntary and self-initiated; a visual stimulus lagging the button press may be interpreted as causally linked sensory feedback (intentional or causal binding), a leading visual stimulus not. Here, we test whether this underlying causal asymmetry leads to directional asymmetries in the temporal recalibration of visuomotor time perception, using an interval estimation paradigm. Participants were trained to the presence of one of three temporal discrepancies between a motor action (button press) and a visual stimulus (flashed disk): 100 ms vision-lead, simultaneity, and 100 ms movement-lead. By adjusting a point on a visual scale, participants then estimated the interval between the visual stimulus and the button press over a range of discrepancies. Comparing the results across conditions, we found that temporal recalibration appears to be implemented nearly exclusively on the movement-lead side of the range of discrepancies by a uni-lateral lengthening or shortening of the window of temporal integration. Interestingly, this marked asymmetry does not lead to a significantly asymmetrical recalibration of the point of subjective simultaneity or to significant differences in discriminability. This seeming contradiction (symmetrical recalibration of subjective simultaneity and asymmetrical recalibration of interval estimation) poses a challenge to common models of temporal order perception that assume an underlying time measurement process with Gaussian noise. Using a two-criterion model of the window of temporal integration, we illustrate that a compressive bias around perceived simultaneity (temporal integration) even prior to perceptual decisions about temporal order would be very hard to detect given the sensitivity of the psychophysical procedures commonly used.

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### 1. Introduction

Humans can recalibrate the perceived timing of multisensory events to compensate for the presence of small temporal discrepancies between the senses for a number of modality pairs, such as vision and audition or vision and touch (e.g., Di Luca, Machulla, & Ernst, 2009; Fujisaki, Shimojo, Kashino, & Nishida, 2004; Keetels & Vroomen, 2008; Roach, Heron, Whitaker, & McGraw, 2011; Yarrow, Jahn, Durant, & Arnold, 2011). The perceived temporal order of a voluntary movement (e.g., a button press) and a sensory stimulus (e.g., a visual flash) is no exception from this (Heron, Hanson, & Whitaker, 2009; Keetels & Vroomen, 2012; Rohde & Ernst, 2013; Stetson, Cui, Montague, & Eagleman, 2006; Sugano, Keetels, & Vroomen, 2010; Sugano,

Keetels, & Vroomen, 2012). This means that a participant accustomed to the presence of systematic delay between such a button press and a visual flash will adjust his or her perception of perceived simultaneity of these events to partially compensate for the lag. It also means that participants who have undergone such adaptation will perceive visual stimuli as preceding a button press, even when they physically occur shortly afterwards. As some researchers observed (Heron et al., 2009; Rohde & Ernst, 2013; Stetson et al., 2006), this shift in perceived temporal order violates the underlying causal structure of this kind of scenario, i.e., that a cause (voluntary button press) has to precede its effect (the visual flash). If voluntary action is involved, there is thus a causal asymmetry around the point of actual simultaneity, an asymmetry that is not present when passively perceiving the temporal order in different modalities, such as a visual flash and an auditory click.

The assumption of a causal link between an action and a sensory event has been shown to distort time perception (compression of perceived timing between motor and visual events; intentional or causal binding, e.g., Buehner & Humphreys, 2009; Haggard, Clark, &

\* Corresponding author at: Department of Cognitive Neuroscience, University of Bielefeld, Universitätsstr. 25, W3-246, 33615 Bielefeld, Germany. Tel.: +49 521 106 5703; fax: +49 521 106 5701.

E-mail addresses: [marieke.rohde@uni-bielefeld.de](mailto:marieke.rohde@uni-bielefeld.de) (M. Rohde), [leonie.greiner@uni-bielefeld.de](mailto:leonie.greiner@uni-bielefeld.de) (L. Greiner), [marc.ernst@uni-bielefeld.de](mailto:marc.ernst@uni-bielefeld.de) (M.O. Ernst).

J.K., 2002; cf. also Eagleman & Holcombe, 2002). Intentional binding likely contributes to the unity assumption (Welch & Warren, 1980), which is a prerequisite for multisensory integration. Integration typically requires stimuli to occur in close temporal proximity, i.e., they should fall within a window of integration (e.g., Bresciani et al., 2005; Shams, Kamitani, & Shimojo, 2000). Intentional or causal binding should only occur for discrepancies where movement leads the temporal order, that is, in cases when participants have a subjective sense of agency (Rohde, Scheller, & Ernst, 2012). Thus, if movement events are produced voluntarily, this could lead to asymmetries in the processing or recalibration of visuomotor time perception due to an asymmetrical window of integration. The competing hypothesis is that recalibration is symmetrical. For instance, Cai, Stetson, and Eagleman (2012) proposed a neural model, where visuomotor temporal recalibration is implemented as the temporal analog of the motion after-effect. If temporal discrepancies are treated just as spatial discrepancies, recalibration will not be expected to be sensitive to the direction of a discrepancy.

In a previous study, we tested whether there are asymmetries in the recalibration of perceived visuomotor simultaneity using a voluntary button-pressing task. To this end, we trained participants in different blocks to the presence of vision-lead and movement-lead temporal discrepancies between the voluntary button press and a flash (Rohde & Ernst, 2013). Using a temporal order judgment (TOJ) paradigm, we compared the amount by which the point of subjective simultaneity (PSS) shifts as a result of recalibration. To our surprise, we found no evidence for an asymmetry; in a relatively short time frame, participants recalibrated for 20–25% of the training discrepancy equally in both directions (movement-lead and vision-lead).

Using a TOJ task, however, we could only determine changes in time perception around the one point of perceived simultaneity, not along the entire range of perceived temporal intervals between a button press and the visual flash. Shifts in PSS in temporal recalibration studies do not always generalize across the entire range of stimulus onset asynchronies (SOAs). For instance, Yarrow et al. (2011) recently showed, using an audiovisual SJ temporal recalibration paradigm, that temporal recalibration is better modeled as a uni-lateral expansion of the window of perceived simultaneity, on the side of the trained discrepancy only. This non-linearity in recalibration is not captured in TOJ paradigms (Yarrow et al., 2011). Similarly, Roach et al. (2011) have used an interval estimation (IE) paradigm to study audiovisual temporal recalibration. They observe non-linear distortions in the perceived timing of visuoauditory intervals after temporal recalibration, i.e., recalibration was stronger for short intervals (close to perceived simultaneity) and less pronounced for long intervals. Again, these distortions are of a nature that TOJ paradigms cannot detect (cf. Roach et al., 2011).

In order to illustrate what information the different psychophysical tasks provide with respect to the temporal interval perception between

sensory signals, Fig. 1 depicts a common model for simultaneity judgment (SJ), TOJs, and IEs (the model is adapted and extended from Yarrow et al., 2011). The grey identity line shows the relationship between physical and perceived asynchrony, which, for simplicity, we assume to be veridical and thus a linear function with slope = 1. Furthermore, we assume that the asynchrony estimates are not perfect but corrupted by Gaussian noise (blurred diagonal). In this model, IE judgments would intuitively be expected to reproduce the blurred diagonal itself. A TOJ involves the perceptual decision about whether a stimulus occurred before or after the other (sensed SOA = 0 implies perceived simultaneity), which results from integrating the probability that the sensed asynchrony for a given SOA is above or below 0. This yields a cumulative Gaussian function (Fig. 1A and B, inset).

The probability distribution of SJ responses is often not quite correctly modeled as a Gaussian probability distribution (cf. Vroomen & Keetels, 2010; also discussion in Yarrow et al., 2011), which roughly corresponds to a cross section through this blurred diagonal (Fig. 1A). Cravo, Claessens, and Baldo (2011) and Yarrow et al. (2011) recently proposed that SJs should be better modeled as a two-criterion decision process. A window of simultaneity is defined between two criteria  $\mu_V$  and  $\mu_M$ . The probability of perceiving simultaneity then is the integrated probability of a registered SOA falling between these two criteria, i.e., the difference between the two cumulative Gaussian functions flanking this window (bell-shaped curve in Fig. 1B inset). That is, even with Gaussian distributed noise on the interval estimates, the resulting SJ curve will not be Gaussian, which becomes more apparent the further apart the two criteria are set.

How is temporal recalibration realized in such a model? The PSS shifts observed in TOJ paradigms imply that the mid-section of the diagonal (around the sensed SOA = 0) is shifted sideways into the direction of the adapted SOA. This would lead to a shift in the cumulative Gaussian function for temporal order perception. The simplest possible way of generalizing such temporal recalibration of the mid section across the range of SOAs would be a shift in a set point, which would mean that the entire blurry diagonal is shifted along with the PSS (cf. Fig. 2A). However, the mentioned results on non-linear recalibration (Roach et al., 2011; Yarrow et al., 2011) show that this is not the case in audiovisual temporal recalibration. Roach et al.'s (2011) results showed that the shift evident in the mid-section (recalibration of PSS) decreases as the size of SOAs grows, leading to a distortion in the IE profile (Fig. 2B). Yarrow et al.'s (2011) results showed that recalibration involves a uni-lateral widening of the window of simultaneity (criterion shift, Fig. 1B). Such phenomena concern the perception of intervals along the range of SOAs and are not captured in TOJ paradigms.

It is possible that similar to the audiovisual case, also in visuomotor temporal recalibration, distortions in the generalization of recalibrated time perception exist but go undetected by a TOJ task. To look for such

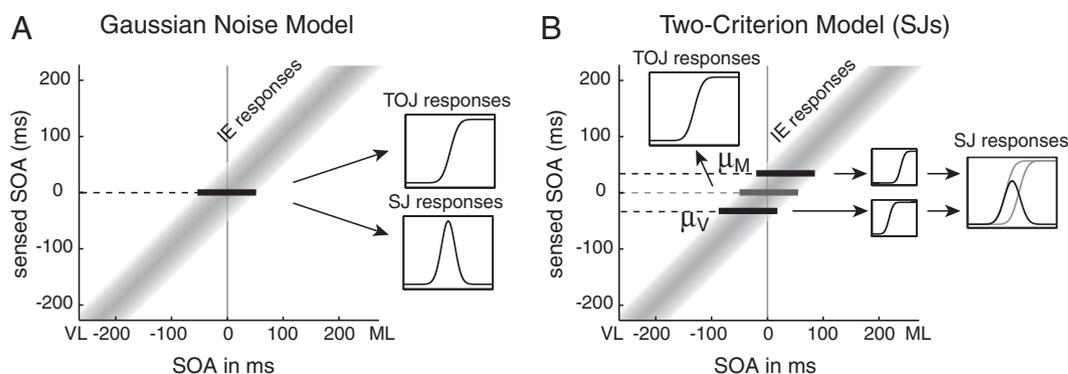
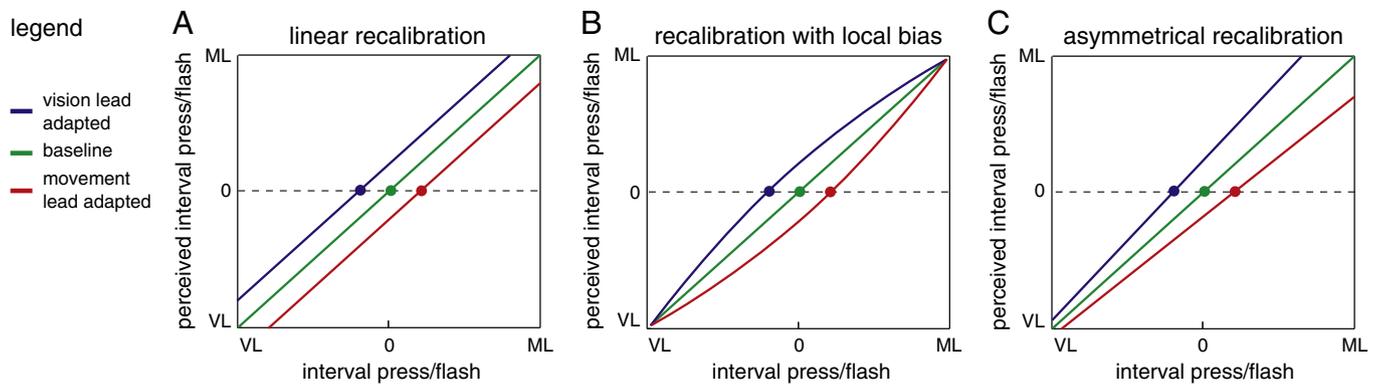


Fig. 1. Illustrations of statistical assumptions underlying models of time perception. (A) The Gaussian noise model. (B) The two-criterion model for SJs, which is an extension of the Gaussian noise model (Cravo et al., 2011; Yarrow et al., 2011). Illustrations are adapted from Yarrow et al. (2011).



**Fig. 2.** Examples of possible mappings of physical intervals (x-axis) to perceived intervals (y-axis) after adaptation to vision-lead (blue), baseline (green) and movement-lead (red) discrepancies.

distortions along the entire range of SOAs, and, specifically, for asymmetries in processing or recalibration, we here use an IE task: Participants have to estimate the length of intervals between a visual stimulus and a button press event (cf. Humphreys & Buehner, 2009; Moore et al., 2009).

Fig. 2 depicts three possible classes of results for the generalization of recalibrated visuomotor interval perception with symmetrical shifts in PSS (we focus here on symmetrical shifts in PSS to conform to our previous research; Rohde & Ernst, 2013). First, the generalization of recalibration could be a *linear shift* with respect to baseline (A). Second, there could be *local non-linear biases* in recalibrated time perception, e.g., local shifts around the PSS, while perceived asynchronies far away stay unaltered (B), similar to what Roach et al. (2011) reported for audiovisual recalibration. Even though this kind of recalibration is non-linear, it is still symmetrical around the negative diagonal, which would indicate that the mechanisms for recalibration are not sensitive to direction (i.e., which modality leads the temporal order in the trained discrepancy). A third option (C) is that there are *asymmetries around the point of actual simultaneity*, either in processing (asymmetrical distribution of responses already in baseline condition) or in the generalization of recalibration. Changes due to recalibration could, for instance, be more pronounced for movement-lead events (right side of the range in Fig. 2C), where intentional binding can be expected to occur. Note that even in this asymmetrical example the shifts in PSS (intercept with dashed horizontal lines) are still symmetrical.

In the IE visuomotor temporal recalibration experiment, participants were trained to the presence of one of three visuomotor lags in three different blocks: 100 ms vision-lead (VL), 0 ms discrepancy (baseline, B), 100 ms movement-lead (ML). To be able to present visual stimuli even before a voluntary action (VL temporal discrepancies), we used the same setup as in earlier work (Rohde & Ernst, 2013), where the timing of a button press is predicted in real-time from early onset of finger movement, which is continually tracked. The differences in interval perception after recalibration were compared between conditions.

## 2. Method and materials

### 2.1. Setup

We used the same setup as in earlier work (Rohde & Ernst, 2013). In a dark room, participants placed their head on a chin rest. During the experiment, subjects looked down in the direction of their hands, which were occluded from vision by a mirror (see Fig. 3). Participants' right index fingers were attached to a PHANTOM force-feedback device with an elastic band. The right lower arm rested on a board. The device was programmed to simulate a virtual button (mass  $m = 0.1$  kg) with a throw of 8 mm, containing a 4-mm spring (spring constant  $k = 500$  kg/s<sup>2</sup>) and a dead band of 4 mm (see Fig. 3A). After full

compression, the button was pressed back up with a small restoring force (0.3 N; see Fig. 3B and C). Participants did not receive visual feedback about the position or compression of the button.

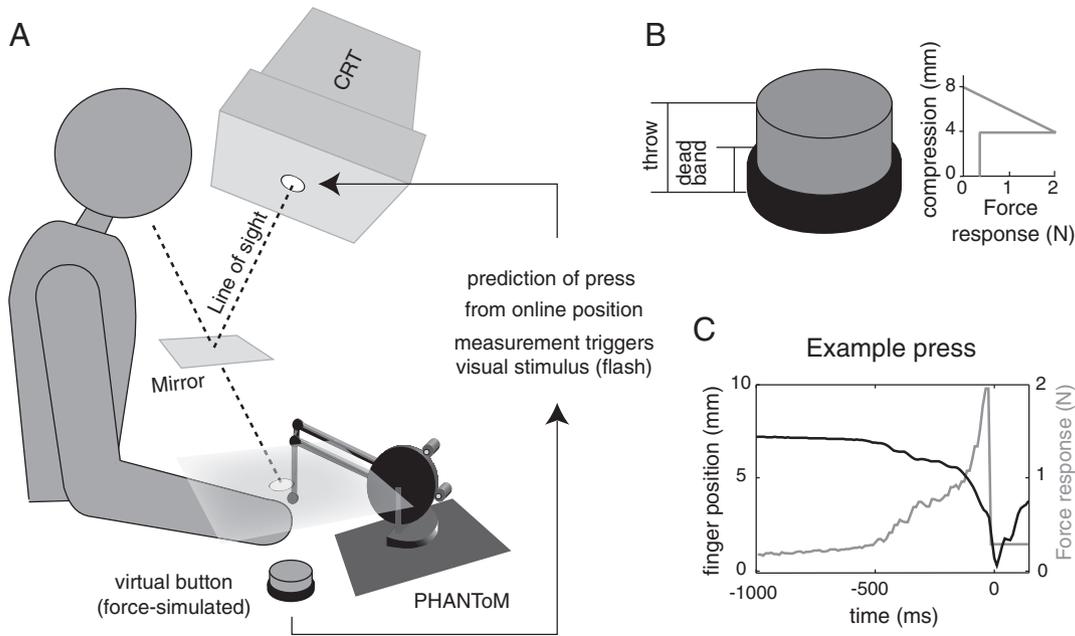
For the prediction of the timing of full compression of the button from early movement onset, the vertical displacement of the participant's finger during the button press was tracked in real time. An adaptive threshold predictor method (Rohde & Ernst, 2013) was used to predict online the time of full button compression early on from the movement onset. This prediction could be used to display visual stimuli even before a button press occurred. For very large target vision-lead SOAs (vision leads by more than 250 ms), this method becomes unreliable, and the timing of the button press is predicted instead from the average press rate. For the entire range of vision-lead SOAs, the prediction contains some prediction error. To ensure a uniform distribution of SOAs, an algorithm dynamically rearranged target SOAs in case of such prediction errors (cf. Rohde & Ernst, 2013). For adaptation trials, the inter-quartile range (IQR) of prediction error across subjects and conditions was  $50 \pm 28$  ms (median and IQR). This prediction noise, which is inevitable in the VL condition, was mirrored (trial by trial) to the ML condition, in order to ensure that recalibration conditions remain comparable. In the B condition, the visual signal was always timed right after the button press.

A cathode ray tube (CRT) monitor was mounted upside-down above the mirror. The mirror was used to project the visual probe stimuli into participants' field of view (white disks of 1.5° visual angle on a 50% gray background). The visual probe was projected at a fixed location in the area where participants pressed the button but was not spatially aligned with the fingertip. Stimuli were flashed for one frame (90 Hz refresh rate of monitor). The inherent end-point-to-end-point system latency between a button press and a corresponding flash on the screen is  $34.5 \pm 7$  ms. SOAs given here in the paper do not yet subtract this inherent latency. That is, a baseline visuomotor lag of 0 corresponds to a scenario where a button triggers a visual stimulus that then flashes on the screen 34.5 ms later.

### 2.2. Procedure and task

Six participants (2 of the authors, 2 other lab members, 2 paid volunteers; 4 female, age range 20–32 years; all right-handed as by self-report) were tested in seven sessions on seven different days (overall ca. 10 h of experimentation per subject). The experiments were approved by the Ethics Committee of the University Clinics Tübingen, Germany. The procedure is in large parts adapted from an analogous study of audiovisual recalibration (Roach et al., 2011). Visual stimuli were generated using the psychophysics toolbox (Kleiner, Brainard, & Pelli, 2007).

In the first session (cf. Fig. 4A), participants were acquainted with the task. Firstly, in order to learn how the scale maps to intervals,



**Fig. 3.** Illustration of the experimental setup. (A) The experimental setup. (B) The force response of the haptically displayed simulated button. (C) Digit height (black) and force response (grey) in an example press.

they were presented with two visual stimuli (Fig. 4B). Red and green dots (vertically displaced) were flashed after one another with SOAs uniformly distributed in  $[-300, 300 \text{ ms}]$  for 60 trials. After each trial, participants had to adjust the position of a black dot on a scale to indicate the perceived SOA, using the left and right cursor keys on a keyboard with the index and middle finger of the left hand. Participants submitted their response using the space key and were given feedback afterwards (blue dot at “correct” location on the scale). The initial position of the dot on the scale was random. The range of the scale corresponds to the interval  $[-300, 300 \text{ ms}]$ , the same range from which the SOAs were drawn. The width on the screen was  $33^\circ$  visual angle. The dot velocity was  $270 \text{ ms}$  (on the scale) per second (steps of  $3 \text{ ms}$  read in at  $90 \text{ Hz}$ ). The scale had no labels but had vertical bars at intervals corresponding to  $50 \text{ ms}$  (see Fig. 4B). This implies that the centre of the scale is clearly visually marked, as in Roach et al.’s (2011) study.

After this practice with visual stimuli only, participants pressed the virtual button for 30 times to initiate the prediction algorithm for VL discrepancies. Throughout the experiment, participants were instructed to wait for at least  $700 \text{ ms}$  and as long as they wanted after a trial started before pressing the button to avoid that the signal that starts a trial has an influence on time perception. If participants pressed the button too early, trials were repeated (7% of all trials for all subjects in the experiment). Participants then performed 20 visuomotor IE trials (Fig. 4D) with feedback, during which they were only presented with SOAs from the extreme ends of the scale ( $|\text{lag}| > 200 \text{ ms}$ ). They were instructed to estimate the interval between the full compression of the button and the flashed dot, using the same adjustment method described above for the visual–visual practice. Afterwards, they performed 60 IE trials without feedback, where SOAs were uniformly drawn from the full range of SOAs  $[-300, 300 \text{ ms}]$ .

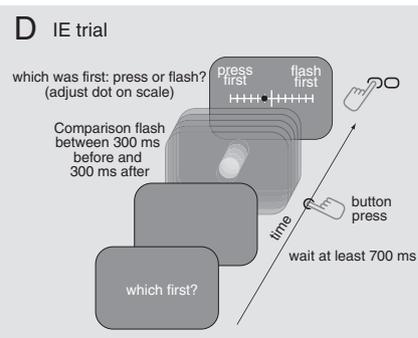
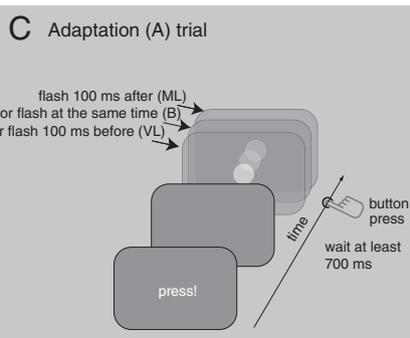
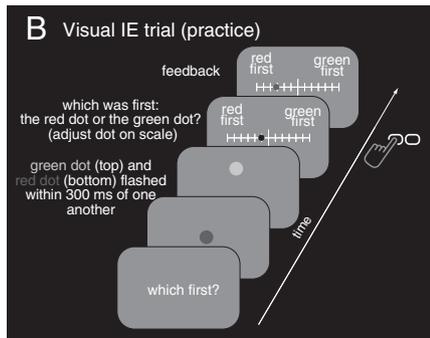
**A Procedure**

Screening session (1st)

50 x IE visual (feedb.)	30 press (practice)	20 IE (feedb.)	60 IE (no feedb.)
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Experimental session (2nd-7th)

30 press (practice)	20 IE (feedb.)	100 A	125 x 3 A (top-up), 1 IE	break	100 A	125 x 3 A (top-up), 1 IE
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**Fig. 4.** Illustration of procedure and task. (A) Timeline of the procedure in different blocks. (B) Learning of the scale (vision only with feedback). (C) Adaptation trials. (D) IE trials.

This corresponds to the experimental task in later blocks. If participants missed a trial, they could indicate this, and the trial was repeated at a later stage during the experiment (1% of all trials for all subject in the experiment).

In the six following sessions, participants were trained with one of the three training lags (VL:  $-100$  ms, B:  $0$  ms, ML:  $100$  ms) for two subsequent experimental sessions, where each session consisted of two blocks (Fig. 4A). The order of these conditions was counter-balanced across participants. An experimental session started with 30 button presses to initiate the predictor. Then, participants performed 20 IE trials with large SOAs ( $|\text{lag}| > 200$  ms) with feedback to remind them of the temporal interpretation of the scale. Afterwards, participants performed two identical blocks where they were first exposed to 100 adaptation trials (Fig. 4C) during which they only saw a flash timed relative to their button press. Then they performed the IE task for 125 trials where SOAs were drawn uniformly from the interval  $[-300, 300$  ms], with 3 top-up adaptation trials in between IE trials. This means that there were 500 responses to the IE task for each subject and condition at the end of the experiment. No feedback was provided.

### 2.3. Analysis

As in the study by Roach et al. (2011), results were pooled across participants, given that results from individual participants are too sparse for individual analysis.

The results were pre-processed to filter outliers due to errors in the measurement technique. Trials where the timing between the press and the flash was larger 500 ms were discarded. Also, trials where the adjusted value was within 12 ms of either end of the scale were discarded because it is not clear if participants perceived them to be at that location or even further outside the scale. In the later experimental blocks, a regression line was fit using the Matlab function *robustfit* (Statistics toolbox—iteratively reweighted least square). This very coarse approximation served to detect clear outliers in the adjustment. Outliers were discarded if the re-weighting assigned them a weight smaller than 0.2. Taking these three filters together, 7% of trials were thus discarded, leaving on average 2740 data points pooled across subjects per condition.

To test for differences between the conditions along the range of SOAs, IE responses were binned in 25 ms bins, and 95% confidence intervals (CIs) were computed using non-parametric bootstrapping (Matlab function *bootci*, 1000 iterations). The IE judgments were also interpreted as ternary (flash first, simultaneous, press first) temporal order decisions (cf. Allan, 1975; Ulrich, 1987; Yarrow et al., 2011) to be able to compare the results with those obtained in other studies. IE responses with an absolute value larger than 12 ms were rated as TOJs, i.e., either vision-first or movement-first. IE responses with an absolute value smaller or equal to 12 ms were rated as simultaneous responses. Within this interval, the dot to be adjusted (cf. Fig. 4D) overlapped with the vertical bar indicating simultaneity. Some subjects reported that they used this criterion to indicate perceived simultaneity (a more exact placement of the dot at the centre of the scale was difficult given the speed of the dot in response to the key press).

A psychometric function in form of a cumulative Gaussian was fit to the TOJ responses generated from the IE settings to derive the PSS and the just noticeable difference (JND). PSS and JND were the only free parameters. This was done using the Matlab toolbox *psignifit* (Wichmann & Hill, 2001a, 2001b). The simultaneous responses were not considered in this analysis (cf. Discussion Section 4.3). Another psychometric function (two-criterion model; cf. Cravo et al., 2011; Yarrow et al., 2011) was fitted to the simultaneous responses (least mean square fit). With this approach, the bell-shaped probability distribution obtained with SJ tasks is modeled as the difference between two cumulative Gaussian functions. The centres ( $\mu_V$  and  $\mu_M$ ) of the flanking Gaussians mark the corners of a window of perceived simultaneity. The model was fitted with three free parameters (the midpoints  $\mu_V$  and  $\mu_M$  and the variance

$\sigma$  of the two cumulative Gaussians). CIs were computed using non-parametric bootstrapping.

## 3. Results

### 3.1. Interval estimation

All subjects were able to perform the task. The IE responses at the end of the practice session correlated significantly with the SOAs presented (all Pearson's  $r \geq 0.79$  and all  $p \ll 0.001$ ). As common for magnitude estimation tasks, there was a centering bias in the responses (Poulton, 1979). The slope of regression lines fitted varied between 0.56 and 0.81. There is also an overall bias to perceive more stimuli as movement lead (i.e., all PSS are positive). Important for our study, however, are the differences between the three different training conditions.

As in Roach et al.'s (2011) study, there is a compressive bias at the centre of the scale, where participants perceive close to simultaneity over an extended range of SOAs (Fig. 5A). Concerning the comparison between the three conditions, the only significant differences are on the ML side of the range of SOAs (right in Fig. 5A). There the distribution of IE responses shifts in the predicted order (VL top, B middle, ML bottom) and in a fashion that is roughly consistent with an explanation of a general shift in perceived intervals (cf. Fig. 2A). For ML SOAs  $> 150$  ms, the differences between conditions were ca. 40% of the difference in trained discrepancy between conditions. However, there are no significant differences between the three conditions on the VL side of the range of SOAs. A striking asymmetry in recalibration is revealed. This discontinuity appears to be due to an expansion and contraction of the range of SOAs that are perceived as simultaneous. The compressive bias extends more or less into the ML range of SOAs as a result of recalibration. The larger the training discrepancy, the more stimuli are perceived as simultaneous.

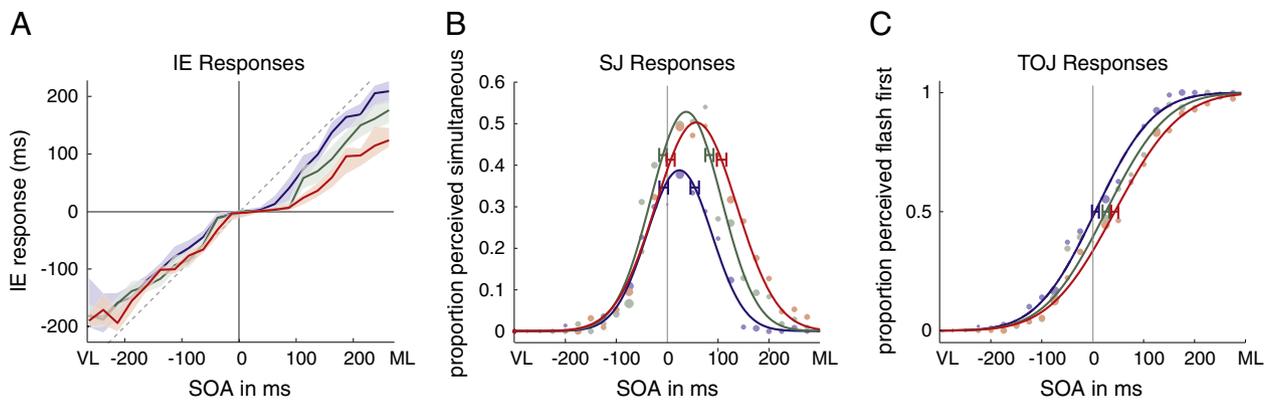
### 3.2. Simultaneity judgments

The results from the SJ reinterpretation of the IE responses (Fig. 5B) confirm this observation. The window of perceived simultaneity grows and shrinks only on the ML side of the range of SOAs following the trained discrepancy. This is confirmed by fitting the two-criterion model to the responses (cf. Introduction and Methods sections). The  $\mu_V$  criterion hardly changes between conditions (VL:  $\mu_V = -7$  ms; B:  $\mu_V = -8$  ms; ML:  $\mu_V = 7$  ms; no significant differences), whereas the  $\mu_M$  criterion shifts substantially in the predicted direction (VL:  $\mu_M = 55$  ms; B:  $\mu_M = 83$  ms; ML:  $\mu_M = 107$  ms; all conditions have different  $\mu_M$  at  $p < 0.05$ ). There are no significant differences in estimates of the slopes (all  $\sigma$  estimates in [61, 73 ms]).

### 3.3. Temporal order judgments

The PSS estimates that result from the TOJ reinterpretation of the IE responses vary in the predicted fashion between conditions. Recalibration to VL discrepancies moves the PSS to the VL side of the range. ML adaptation moves PSS away from it (see Fig. 5C). There are no sizeable differences in magnitude of these shifts (estimates and CIs in ms: VL PSS = 5, CI =  $[-1, 12]$ ; B PSS = 26, CI =  $[20, 33]$ ; ML PSS = 44, CI =  $[37, 50]$ ). PSS was shifted approximately 20% of the trained discrepancy in both directions. This is consistent with our earlier results (Rohde & Ernst, 2013), where participants shifted 20–25% of the trained discrepancy but less than in other studies, where PSS-shifts of the order of 30–44% are reported for visuomotor delay adaptation (Heron et al., 2009; Stetson et al., 2006; Sugano et al., 2010).

There were also no significant differences in the JNDs between the conditions (all JNDs in [90, 101 ms]), which is a surprising result; at least intuitively, one would expect a decrease in perceptual precision given a larger window of perceived simultaneity. This is not the case (cf. Section 4.3). The asymmetrical generalization of recalibration



**Fig. 5.** Perceptual responses after adapting to VL (blue), B (green), or ML (red) discrepancies. (A) IE responses. Median and CIs (25 ms bins) for all conditions. (B) SJ responses. Psychometric curves and perceptual responses (binned for visualization). Bootstrap CIs of  $\mu_V$  and  $\mu_M$  in plots. (C) TOJ responses. Psychometric curves and responses (binned for visualization). Bootstrap CIs on the estimated PSS.

measured by IE is thus not accompanied by an equally asymmetrical recalibration at the PSS. Just as in Roach et al.'s (2011) study, important information about the generalization of temporal recalibration is contained in the metric size of sensed intervals, i.e., where exactly SOAs are reported by subjects to be located on the y-axis in Fig. 5A. This information is discarded when re-interpreting these responses as TOJs to identify the decision boundary (PSS, Fig. 5C).

#### 4. Discussion

The observed pattern of recalibration does not correspond to either of the three options considered in Fig. 2. It involves a unilateral contraction or expansion of the area in which SOAs are perceived as simultaneous. While the responses on the VL side of the range of SOAs barely change, changes on the ML side of the range are substantial. This result raises several questions. What is the relationship between visuomotor temporal recalibration, which involves an active component and thus may be affected by the cause-effect relationship underlying agency, and other cases of multisensory temporal recalibration involving passive stimulation only? What is the role of intentional action and the sense of agency in recalibration? Why does a widening of the window of simultaneity not lead to a decrease in perceptual precision, and how can this result be reconciled with the Gaussian noise model of time perception (Fig. 1A)? These questions are discussed in the following.

##### 4.1. Visuomotor vs. visuo-auditory temporal recalibration

What are the conditions for asymmetrical temporal recalibration? The mechanisms of multisensory temporal recalibration tend to nearly work symmetrically, if both sensory events are passively sensed (e.g., Di Luca et al., 2009; Fujisaki et al., 2004; Keetels & Vroomen, 2008; Roach et al., 2011; Yarrow et al., 2011). Our previous work using a TOJ paradigm showed that also visuomotor PSS were recalibrated symmetrically (Rohde & Ernst, 2013). This led us to conclude that the mechanisms of visuomotor recalibration may also work symmetrically, just like in the case of passively sensed stimuli.

Such a similarity between audiovisual and visuomotor time perception is not at all obvious, as there is no evidence that the same neural processes are involved in temporal recalibration of audiovisual and visuomotor simultaneity. Yet, symmetrical recalibration would be simplest possible scenario. A recent computational model by Cai et al. (2012), for instance, predicts symmetrical recalibration in the visuomotor case, proposing that visuomotor temporal recalibration may rely on similar neural circuits as a purely visual motion aftereffect, which would mean that “identical

neural mechanisms may be used to make perceptual determinations about both space and time” (Cai et al., 2012).

The current results subsume and reproduce our earlier result (TOJ reinterpretation of the results shows symmetrical PSS-shifts and no changes in JND). However, the analysis of the IE and SJ responses reveal that there are strong asymmetries in the generalization of visuomotor delay adaptation that the TOJ responses do not capture. This asymmetry distinguishes visuomotor temporal recalibration from recalibration of passively sensed stimuli pairs. Audiovisual recalibration of IE may not be linear (Roach et al., 2011), but this non-linearity is symmetrical around physical simultaneity. Audiovisual recalibration of SJ may involve uni-directional expansions of the window of perceived simultaneity (Yarrow et al., 2011), but this is independent of whether the visual or the auditory stimuli leads the temporal order in the trained discrepancy. The observed asymmetries appear to be specific to the visuomotor, or possibly the sensorimotor scenario.

Previous research to a large degree is agreement with the current results. Keetels and Vroomen (2012) reported a widening of the window of simultaneity in a visuomotor recalibration experiment using SJs, but also a shift of this window. While this result supports our conclusion that ML recalibration is biased towards a shift of the  $\mu_M$  criterion, it also suggests a small shift of the  $\mu_V$  criterion. In a similar paradigm, Heron et al. (2009) only reported the midpoint of the distribution (PSS), but graphical depiction of results from an example participant suggest a result similar to that reported by Keetels and Vroomen (2012). However, both Heron et al. (2009) and Keetels and Vroomen (2012) measured SJ responses at only five SOAs from the ML-side and use a Gaussian function to approximate the responses. While this is sufficient for estimation of PSS, it does not give a good impression of the shape of the response profile.

The asymmetrical recalibration we observe here appears to be a hallmark of visuomotor temporal processing and distinguishes it from other forms of temporal recalibration that involve the sensation of external sensory events.

##### 4.2. Asymmetrical visuomotor temporal recalibration and the sense of agency

What causes the asymmetry in visuomotor temporal recalibration? If a person believes that she is the causal origin of a sensory event (sense of agency), it likely plays into the *unity assumption* (Welch & Warren, 1980), i.e., the belief that two sensory cues belong together. Assuming unity is the prerequisite for multisensory integration. The temporal compression observed under intentional (or causal) binding (Buehner & Humphreys, 2009; Haggard et al., 2002) could then be explained as an instance of the more general phenomenon of

multisensory integration, which involves the merging of cues from different modalities into a single percept (Ernst & Bühlhoff, 2004). This occurs only within a small temporal window around simultaneity, often called the temporal window of integration (e.g., Bresciani et al., 2005; Shams et al., 2000). The plateau-like compressive bias around simultaneity could well be a consequence of this window of temporal integration. Naturally, the sense of agency occurs asymmetrically with respect to a voluntary action event (Rohde et al., 2012). If the sense of agency affects visuomotor temporal integration, this could explain the asymmetries in visuomotor temporal recalibration. Changes in the window of integration (how much later after the intentional action sensory feedback is expected) are more likely to occur on the side of the effect (visual feedback), not on the side of the cause (intentional movement).

It is impossible to draw firm conclusions on this matter from the current results, as we did not measure or directly manipulate the sense of agency. We can also not be sure if temporal recalibration is preceded, followed, or accompanied by a re-learning of the causal structure underlying the experimental situation. Yet, the underlying causal asymmetry seems to offer the only convincing explanation for the strongly asymmetrical recalibration that distinguishes our results from recalibration studies of other, passively sensed stimuli pairs.

#### 4.3. Temporal precision and the width of the window of integration

How can the window of perceived simultaneity widen without a decrease in precision of TOJs? Assuming the Gaussian noise model of integration (Fig. 1A), one would expect that a widening of the window of simultaneity (larger area in which we cannot distinguish order) would be accompanied by a marked decrease in discriminability (JND) in TOJs. The width of the SJ response profile, in this model, represents the amount of estimation noise (i.e., graphically speaking, the amount by which the diagonal is blurred). The Gaussian noise model can thus not explain our result (widening of the window of simultaneity without increase in JND).

Cravo et al.'s (2011) and Yarrow et al.'s (2011) two-criterion model is a better candidate for explaining the results. A uni-directional criterion shift (Fig. 1B) could explain the SJ results presented here well (Fig. 5B). If one then assumes that the midpoint of the window of simultaneity is used as a criterion for TOJs (Fig. 1B), this could also explain the symmetrical PSS shift we observed in our earlier results (Rohde & Ernst, 2013). However, the TOJ interpretation of the results presented here is more difficult to fit into this model. In a ternary response task (movement-lead, simultaneity, vision lead), such as our reinterpretation of the IE responses as TOJs and SJs, the “simultaneous” responses are usually included into TOJ analysis (once for each side; cf. Ulrich, 1987; Yarrow et al., 2011). The analysis we performed here (i.e., leaving out the simultaneous responses) would instead be expected to lead to statistical irregularity, i.e., a plateau or gap at perceived simultaneity in the TOJ response profile (Fig. 6A inlay and 6B left). The TOJ results (Fig. 5C) should but do not reveal such a plateau.

This points out a third, novel theoretical possibility for the processes underlying perceptual judgments about relative timing. Temporal integration (or intentional binding) could occur prior to processing SOAs for perceptual judgments. We illustrate this possibility with a model depicted in Fig. 6A. If asynchronous stimuli become integrated (i.e., they are perceived synchronously), this will show up in Fig. 6A as a flat plateau. Therefore, such an integration (or intentional binding) process could easily explain the compressive bias at simultaneity in the IE responses, as it occurred in our (Fig. 5A) and Roach et al.'s (2011) results. According to this model, TOJs do not follow a cumulative Gaussian distribution. Instead, they follow the distorted distribution depicted in Fig. 6B (left): As the window of integration widens, the plateau around the PSS gets larger. Importantly, if realistic parameters for the width of this window

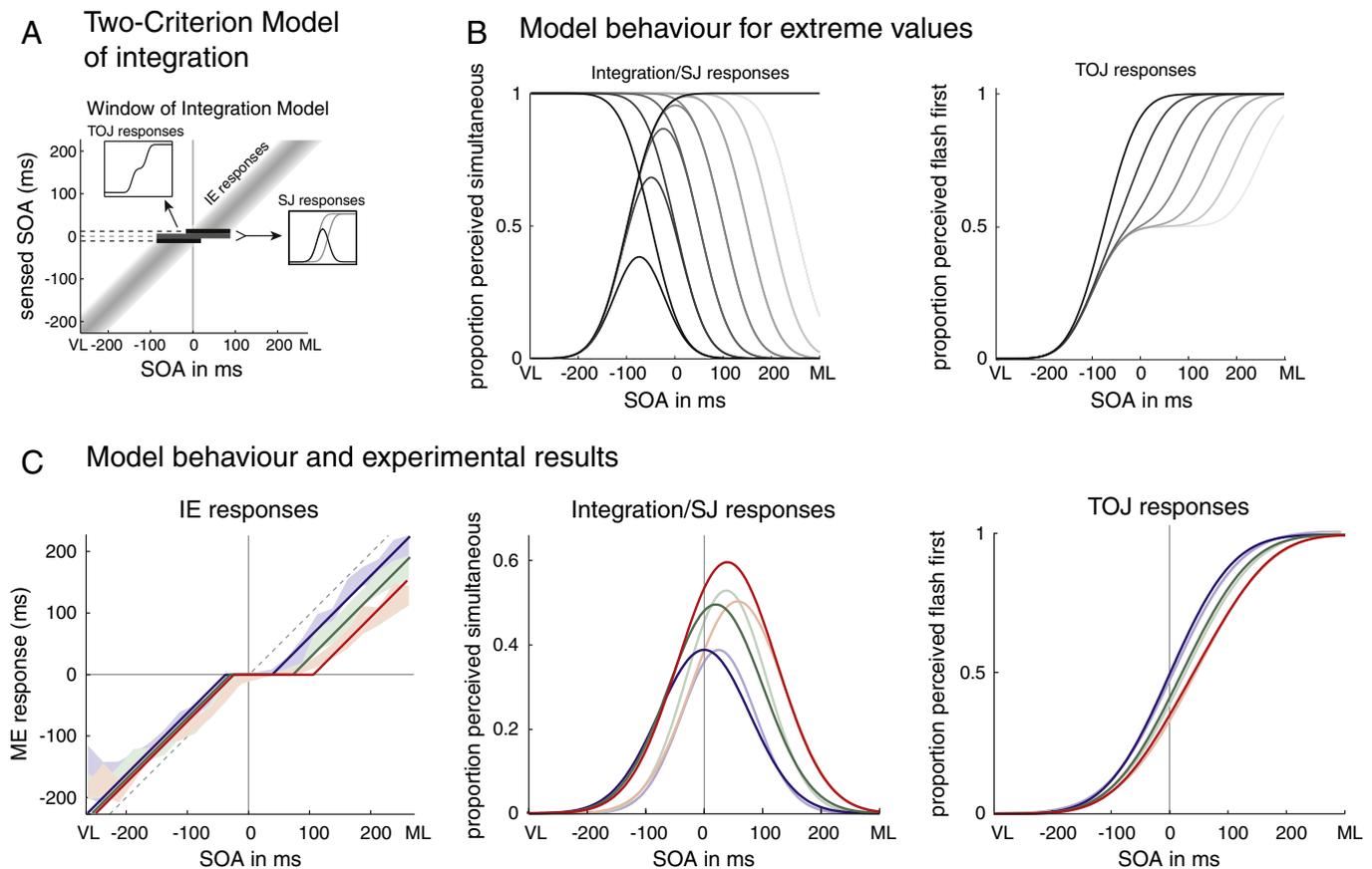
and the perceptual noise are used for the modeling (Fig. 6C, parameters are taken from the current experimental results), we see that the resulting psychometric functions are not steep enough to notice this distorting plateau. Varying the size of the window of simultaneity on one side (Fig. 6C middle) leads to cumulative probability density functions for TOJs that are virtually indistinguishable from cumulative Gaussian functions with a mere shift in PSS (Fig. 6C right). There are very small differences in slope, but these would be impossible to detect given the number of decisions usually sampled and thus the amount of measurement noise usually present determining a typical psychometric function.<sup>1</sup>

This example (Fig. 6C) is not meant as an actual generative or descriptive model of the results. Such a model would be impossible, given that, for instance, the SJ and TOJ interpretation of the result do not exactly correspond in their estimate of PSS. Also, a biologically plausible model of the window of integration would probably involve a softer compressive bias than discontinuously cutting out a chunk of registered SOAs. It is also not proposed as a better model to describe precision and bias in TOJ tasks. The purpose of this model is to call into question the underlying assumption that time perception generally and TOJs specifically rely on a simple registration process with Gaussian noise (Fig. 1A). It has been shown that multisensory integration involves the loss of access to the uni-sensory estimates (Hillis, Ernst, Banks, & Landy, 2002). It seems possible and plausible that this could occur at a very early stage of processing. Researchers gradually start to tackle the problem of the neural mechanisms of multisensory time perception and its recalibration (e.g., Cai et al., 2012; Roach et al., 2011). It is there that it becomes important to consider the possibility of perceptual integration and a consequent distortion of temporal registration at an early stage of processing on the level of generative mechanism and to recognize that our most common formal tools to describe human time perception will fail to register such processes.

#### 4.4. Limitations of the results

What can we conclude? There are several advantages and disadvantages to using an IE paradigm. Firstly, magnitude estimation tasks are generally prone to cognitive bias (Poulton, 1979). In particular, the existence of a clearly demarcated point of simultaneity on the scale could exaggerate the density of responses at perceived simultaneity, which could be used as an argument against our interpretation that this plateau is evidence for temporal integration. Secondly, it is not clear in how far the interpretation of the IE responses as ternary TOJs (vision first, simultaneous, movement first) is comparable to results from SJ or TOJ paradigms. Thirdly, the results presented may include distortions, as results were pooled across participants that may well have differed in biases or perceptual precision, and the statistical power is comparably low on both the individual and the population level. Another factor to consider is that large vision-lead SOAs may sometimes trigger a button press action, which may bias the perception of such events at the extreme end of the VL range of stimuli. However, the interesting differences between conditions are close to simultaneity and on the ML side of the range of SOAs, where this cannot happen. In summary, the IE paradigm used has a number of arguments for and against it. However, none of the limitations discussed can explain the existence of the strong asymmetries in recalibration. This asymmetry poses a challenge for models of temporal recalibration that are not sensitive to whether vision or movement leads the temporal order (e.g., Cai et al., 2012). Also, none of these issues concern the theoretical possibility of early integration that we illustrate using the integration model (Fig. 6).

<sup>1</sup> In linking the IE results to the TOJ re-interpretation, it is important to recall that in Figs. 5A and 6C, the shaded area depicts the CI of the median, not the spread of the data, which is considerably larger, also around compressive bias.



**Fig. 6.** The two-criterion model of integration. (A) Illustration of the two-criterion window of integration model. (B) The expected SJ responses (left) and TOJ responses (right) for different criteria placements demonstrate the behavior of the model for extreme values.  $\mu_V$ : always  $-100$  ms,  $\mu_M$  (from black to light grey):  $-50, -0, 50, 100, 150, 200,$  and  $250$  ms. All  $\sigma = 50$  ms. (B) Model behavior (dark lines) for an example parameter set of the model and empirical results (pale).  $\mu_V = -37, -29, -24$  ms;  $\mu_M = 37, 69, 104$ ;  $\sigma = 75$  ms. The locations of  $\mu_V$  and  $\mu_M$  are computed from the IE results by fitting an identity line with a plateau (least mean squares, left panel).

## 5. Conclusion

The results presented show an asymmetry in the temporal recalibration of visuomotor interval perception. This asymmetry implies that active visuomotor temporal recalibration is qualitatively different from, e.g., passive visuoauditory recalibration and suggests a link between visuomotor temporal recalibration and the asymmetrical window of sensed agency (cf. Rohde et al., 2012). The comparison with our earlier results (Rohde & Ernst, 2013) raises questions about how different types of perceptual judgments in time perception (SJ, TOJ, and IE) relate and suggests the possibility that temporal integration may occur even before the perceptual decision processes about order, interval, or simultaneity.

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