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RESEARCH ARTICLE

# Neural correlates of temporal recalibration to delayed auditory feedback of active and passive movements

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## Abstract

When we perform an action, its sensory outcomes usually follow shortly after. This characteristic temporal relationship aids in distinguishing self- from externally generated sensory input. To preserve this ability under dynamically changing environmental conditions, our expectation of the timing between action and outcome must be able to recalibrate, for example, when the outcome is consistently delayed. Until now, it remains unclear whether this process, known as sensorimotor temporal recalibration, can be specifically attributed to recalibration of sensorimotor (action-outcome) predictions, or whether it may be partly due to the recalibration of expectations about the intersensory (e.g., audio-tactile) timing. Therefore, we investigated the behavioral and neural correlates of temporal recalibration and differences in sensorimotor and intersensory contexts. During fMRI, subjects were exposed to delayed or undelayed tones elicited by actively or passively generated button presses. While recalibration of the expected intersensory timing (i.e., between the tactile sensation during the button movement and the tones) can be expected to occur during both active and passive movements, recalibration of sensorimotor predictions should be limited to active movement conditions. Effects of this procedure on auditory temporal perception and the modality-transfer to visual perception were tested in a delay detection task. Across both contexts, we found recalibration to be associated with activations in hippocampus and cerebellum. Context-dependent differences emerged in terms of stronger behavioral recalibration effects in sensorimotor conditions and were captured by differential activation pattern in frontal cortices, cerebellum, and sensory processing regions. These findings highlight the role of the hippocampus in encoding and retrieving newly acquired temporal stimulus associations during temporal recalibration. Furthermore, recalibration-related activations in the cerebellum may reflect the retention of multiple representations of temporal stimulus associations across both contexts. Finally, we showed that sensorimotor predictions modulate recalibration-related processes in frontal, cerebellar, and sensory regions, which potentially account for the perceptual advantage of sensorimotor versus intersensory temporal recalibration.

**KEYWORDS**

cross-modal temporal recalibration, forward model, functional magnetic resonance imaging, prediction, sensorimotor adaptation, sensorimotor temporal recalibration, temporal recalibration effect

## 1 | INTRODUCTION

Effective perception of and interaction with the environment greatly depend on the temporal structure of sensory and sensorimotor events. For instance, the characteristic and highly predictable temporal relationship between actions and their sensory outcomes facilitates the discrimination between self-generated sensory inputs and those originating from external sources (Haggard, 2005; Moore et al., 2009). Since the sensory environment is vastly complex and subject to constant change, an essential ability of the nervous system is to sustain this function even under flexibly changing environmental conditions, such as varying action-outcome delays (Haering & Kiesel, 2015). For instance, dimmed light conditions can delay signals from the retina (Matteson, 1971), motor or sensory systems can be delayed due to fatigue, or a mouse click may lead to delayed responses of a computer due to system overload (Cai et al., 2018).

The compensation for variations in action-outcome delays is thought to be achieved by a sensorimotor temporal recalibration mechanism, which updates the perceived relative timing between actions and their sensory outcomes. Experimentally, temporal recalibration can be induced by introducing a constant delay between a subject's action (e.g., a button press) and corresponding sensory outcomes (Arikan et al., 2021; Cai et al., 2018; Cao et al., 2017; Elijah et al., 2016; Heron et al., 2009; Rohde & Ernst, 2013; Stekelenburg et al., 2011; Stetson et al., 2006; Sugano et al., 2010, 2012, 2016, 2017; Tsujita & Ichikawa, 2012). Following repeated exposure to this manipulation, subjects tend to perceive the delayed action-outcome as synchronous with the action (Keetels & Vroomen, 2012; Sugano et al., 2010, 2012, 2016, 2017; Yamamoto & Kawabata, 2014) and shorter delays are detected less frequently (Arikan et al., 2021; Schmitter & Straube, 2022). Moreover, undelayed outcomes are illusory perceived as occurring before the action (Cai et al., 2018; Heron et al., 2009; Rohde & Ernst, 2013; Stekelenburg et al., 2011; Stetson et al., 2006; Sugano et al., 2010; Tsujita & Ichikawa, 2012). These perceptual changes are known as the “temporal recalibration effect” (TRE). They are interpreted in terms of recalibration of sensorimotor predictions about the action-outcome timing, which results in a perceptual shift toward the presented delay.

These sensorimotor predictions, that is, predictions about the sensory outcomes of actions, are traditionally believed to be produced by internal forward models by using copies of the actions´ motor commands (Backasch et al., 2014; Blakemore et al., 1998; Cao et al., 2017; Elijah et al., 2016; Knoblich & Kircher, 2004; Leube, Knoblich, Erb, Grodd, et al., 2003; Leube, Knoblich, Erb, & Kircher, 2003; Straube et al., 2017). When sensations align with the expected action-outcome timing, they are attributed as originating from the own action. A temporal discrepancy, however, like an unexpected long delay, results in a prediction error and the inference that the sensations were caused externally or by another agent (Haggard et al., 2002; Hughes et al., 2013; Imaizumi & Tanno, 2019; Zapparoli et al., 2020). Therefore, it has been proposed that sensorimotor temporal recalibration can be achieved by internal forward models through the updating of sensorimotor predictions (Cao et al., 2017) to maintain adequate agency attribution despite changes in environmental conditions (Cai et al., 2018; Parsons et al., 2013; Stetson et al., 2006). It has even been suggested that the recalibration of sensorimotor predictions occurs on a supra-modal level and thus affects the general predicted timing for sensory outcomes of an action instead of modality-specific processes. Evidence for this claim has been derived from findings that the TRE can transfer to another modality, that is, after recalibration to a sensorimotor delay in one modality, effects of this procedure on temporal perception were also evident in another modality (Arikan et al., 2021; Heron et al., 2009; Sugano et al., 2010, 2012).

Importantly though, in a purely perceptual context, that is, in the absence of actions and sensorimotor predictions, recalibration of the perceived intersensory timing is also known to occur. For example, repeatedly exposing subjects to delays between auditory and visual stimuli shifts their synchrony perception of these stimuli toward that delay (Fujisaki et al., 2004; Harrar & Harris, 2008; Van der Burg et al., 2013; Vroomen et al., 2004). These effects also appeared not to be modality-specific but to transfer to different modality pairs other than the one used during recalibration (Di Luca et al., 2009). Such a flexible intersensory temporal recalibration mechanism aids the attribution of signals from different sensory modalities to the same or different environmental source despite varying delays in signal transmission and sensory processing systems (Chen & Vroomen, 2013). Considering this, the TRE in a sensorimotor context as described above may at least in part be explained by temporal recalibration of these general intersensory matching mechanisms. For example, in terms of recalibration of the tactile sensation during the button press movement and the resulting visual or auditory outcome (Arikan et al., 2021; Stetson et al., 2006). Therefore, without controlling for the impact of intersensory recalibration, the sensorimotor TRE alone does not provide conclusive evidence for temporal recalibration of sensorimotor predictions.

If the sensorimotor TRE relies on both the recalibration of sensorimotor predictions and intersensory matching mechanisms, it might be expected to be stronger compared to conditions in which only intersensory recalibration can occur. Indeed, the TRE has already been shown to be more pronounced when subjects actively performed the action themselves, as opposed to conditions in which the effector was externally touched (Stetson et al., 2006) or moved passively (Arikan et al., 2021). A TRE observed in passive conditions can be accounted for by intersensory temporal recalibration alone, since there is no motor command and therefore no involvement of sensorimotor predictions. Thus, the less pronounced effect in this condition implies a component in sensorimotor temporal recalibration that is specific to sensorimotor delays and may indeed be related to the recalibration of sensorimotor predictions (Arikan et al., 2021).

The question of the extent to which sensorimotor temporal recalibration can be attributed to intersensory recalibration as opposed to recalibration of sensorimotor predictions also arises with respect to the neural correlates of this process. To date, evidence suggests that neural correlates of sensorimotor temporal recalibration are distributed across a variety of networks, including sensory systems (Cai et al., 2018; Elijah et al., 2016; Stekelenburg et al., 2011), areas involved in sensorimotor processing and prediction generation (Cao et al., 2017; Schmitter & Straube, 2022), and even higher-order brain regions involved in general mismatch or error detection (Stekelenburg et al., 2011; Stetson et al., 2006). However, it remains unresolved whether the involvement of these regions and networks can be attributed specifically to the temporal recalibration of sensorimotor predictions, as opposed to more general mechanisms of intersensory temporal recalibration.

First, sensorimotor temporal recalibration has been associated with processing changes in sensory systems. For instance, after recalibration to audio-motor delays, the auditory N1 ERP component exhibited responses to delayed action-outcomes typically observed for undelayed ones (Elijah et al., 2016). In similar veins, after recalibration to visuo-motor delays, undelayed outcomes led to responses of the visual P1 component typically expected for stimuli deviating from the expected timing (Stekelenburg et al., 2011). These results demonstrate that sensorimotor temporal recalibration affects early sensory processing systems, although their precise role in recalibration remains to be clarified. It also remains unclear if processing changes in these regions reflect recalibration mechanisms specifically related to sensorimotor contexts or whether they may be partly related to the recalibration of more general intersensory matching mechanisms.

Second, another category of brain regions that have been linked to temporal recalibration are those believed to be involved in recalibration by building and updating internal forward models. Most prominent among these is the cerebellum (Arikan et al., 2019; Blakemore et al., 2001; Leube, Knoblich, Erb, Grodd, et al., 2003; Straube et al., 2017; Tanaka et al., 2020; van Kemenade et al., 2018; Welniarz et al., 2021). Critical dependence of recalibration on cerebellar processes could, for instance, be shown by a transcranial magnetic stimulation study. In this study, recalibration-related activity in auditory processing systems was eliminated after inhibition of the right cerebellum (Cao et al., 2017). A recent tDCS study further showed that anodal stimulation of the bilateral cerebellum influenced temporal recalibration. By comparing the TRE resulting from the exposure to delayed outcomes of actively performed versus passively elicited movements, it appeared that this effect was not exclusive to the sensorimotor context (active movements) but extended to the intersensory context (passive movements) where no action and thus no sensorimotor prediction was involved (Schmitter & Straube, 2022). Thus, further clarification is needed as to what extent recalibration-related processes in the cerebellum are truly specific to the sensorimotor context or whether it also serves comparable functions in the recalibration of intersensory timing.

Third, neural correlates of sensorimotor temporal recalibration have been identified in brain regions known for more general error-related processing. For instance, the processing of undelayed outcomes that were illusory perceived as occurring before the action after recalibration has been associated with activation increases in error processing regions, such as in anterior cingulate cortex and medial frontal cortex (Stetson et al., 2006). In the same line, modulations in the N450 component related to error processing in anterior cingulate cortex could be associated with temporal recalibration to visuo-motor delays (Stekelenburg et al., 2011). This indicates that recalibration elicits changes not only in lower-level sensory, but also in higher-level cognitive processing systems.

Finally, evidence for the neural correlates underlying sensorimotor temporal recalibration may also be derived from a wider range of studies investigating potentially related processes. These include, for example, sensorimotor adaptation, that is, the adaptation of movements to temporal (or spatial) action feedback perturbations. Sensorimotor adaptation is partly thought to rely on learning processes based on sensory prediction errors, that is, discrepancies between the predicted and the observed sensory consequence of the motor commands (Morehead et al., 2017; Standage et al., 2022). As described above, sensorimotor temporal recalibration is also assumed to arise due to the updating of predictions about the sensory outcomes of our actions after repeated exposure to sensory prediction errors. Hence, both processes may be associated with partially similar neural correlates. Indeed, it has consistently been reported that regions such as the cerebellum, medial and prefrontal regions, and anterior cingulate cortex are also involved during sensorimotor adaptation (Anguera et al., 2007; Ruitenberg et al., 2018; Standage et al., 2022; Tzvi et al., 2022). In addition, the hippocampus has been implicated in this process by forming and retrieving new sensorimotor mappings, suggesting that memory systems are involved in sensorimotor adaptation (Scheidt et al., 2011; Standage et al., 2022). Similar processes could be assumed to be involved in sensorimotor temporal recalibration, but so far evidence for this claim is missing.

To conclude, a range of different brain regions and networks can be associated with sensorimotor temporal recalibration. But, it remains unresolved whether their contribution can be specifically attributed to the recalibration of sensorimotor predictions or whether it is partly the result of more general intersensory recalibration mechanisms. Therefore, for the first time, we investigated the neural correlates of temporal recalibration in both sensorimotor and intersensory contexts together, to disentangle common and distinct components underlying recalibration in both contexts. To this end, during fMRI data acquisition, subjects underwent adaptation phases during which they were repeatedly exposed to a fixed delay between actively performed versus passively generated button press actions and an auditory outcome. In a subsequent test phase, they were asked to detect varying delays between button press and outcome to assess to what extent the delay exposure led to temporal recalibration.

We expected the behavioral TRE to be stronger in active versus passive movement conditions due to the hypothesized recalibration of sensorimotor predictions in addition to the expected timing between the senses. Neural correlates for temporal recalibration across both movement types were expected in regions for general error and mismatch detection, such as frontal and anterior cingulate regions, and in regions for early sensory processing. Differences between the neural correlates of temporal recalibration in active and passive conditions were hypothesized to occur in regions known for motor and sensorimotor processes, such as the cerebellum. Finally, we expected that exposure to the delayed auditory stimuli during adaptation would induce a behavioral TRE and recalibration-related brain activation also for visual stimuli during test. We expected this to occur particularly in active conditions, due to the recalibration of sensorimotor predictions on a supra-modal level.

## 2 | MATERIALS AND METHODS

### 2.1 | Participants

Twenty-five healthy volunteers participated in the study (10 female; mean age: 24.76 years, SD = 5.13). All reported being right-handed (Edinburgh Handedness Inventory; Oldfield, 1971: mean laterality quotient = 79.6%, SD = 22.888) and had normal or corrected-to-normal vision. No one reported any current or past psychiatric or neurological disorders. Subjects gave written informed consent and received financial reimbursement for their participation. The study was conducted according to the Declaration of Helsinki and was approved by the local ethics commission (Study 141/17) of the medical faculty of University of Marburg, Germany.

### 2.2 | Equipment and stimuli

Subjects performed button presses with their right index finger using a custom-made MR-compatible pneumatic passive button device (see Figure 1). During the fMRI experiment, the device was placed next to subjects' right leg. In active conditions, they pressed the button actively by themselves, while in passive conditions it was pulled down by compressed air with a force of max. 20 N. As active (sensorimotor context) and passive (intersensory context) movements elicited similar tactile and proprioceptive sensations, this manipulation enabled us to

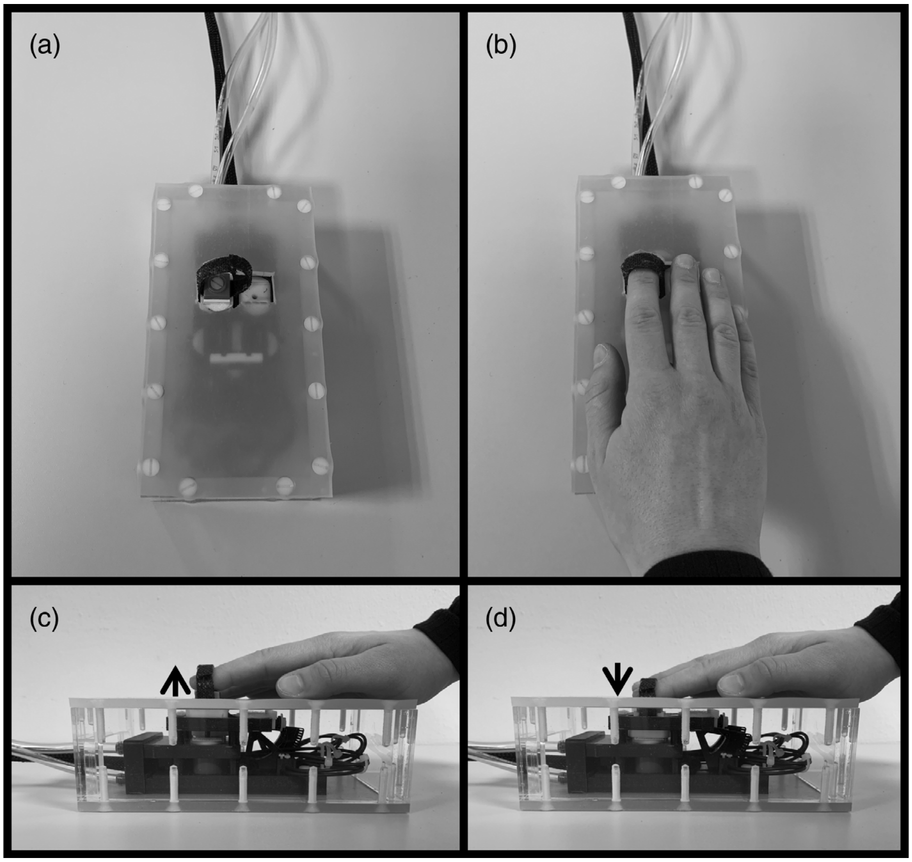

**FIGURE 1** Custom-made MR-compatible pneumatic passive button device. (a,b) Subjects placed their right index finger on the button device. During the experiment, the button could be actively pressed by the subjects, or it was pulled down passively by compressed air. (c) A movement started with the button in the upper position. (d) When the button was moved to the lowest position, the stimulus presentation was triggered, either with or without a delay.

disentangle recalibration effects arising due to changes in sensorimotor predictions from those due to changes in intersensory timing. To ensure that subjects' fingers followed the button movement smoothly during passive conditions, they were tied to the button by using an elastic fabric band. During the movements, optic fibers allowed for the tracking of the button position by custom-written software. Thereby, visual or auditory stimuli could be displayed at the end of a button press movement (i.e., when the button reached the lowest position) with high temporal accuracy with or without an additional delay. The visual stimulus was a Gabor patch (1-degree visual angle, spatial frequency: 2 cycles/degree), which appeared at the center of a monitor (refresh rate: 60 Hz). The monitor was located behind the MRI scanner and subjects could see it through a mirror mounted on the head coil. The auditory stimulus was a sine-wave tone (2000 Hz with 2 ms rise and fall) and was presented through MR-compatible headphones (MR-Confon Optime1, Magdeburg, Germany). Visual and auditory stimuli were presented for a duration of 33.4 ms each.

## 2.3 | Experimental design and task description

Subjects underwent multiple pairs of adaptation and test phases. Adaptation phases consisted of two parts separated by the presentation of a fixation cross. During both parts, consecutive button presses had to be performed, either actively or they were elicited passively (factor “movement type”). Each button press was followed by the presentation of the auditory sensory outcome in form of the tone. Importantly, the tone occurred either immediately after the button press was registered (undelayed, 0 ms delay) or after a constant delay of 150 ms (factor “adaptation delay”).

After each adaptation phase, a test phase assessed the impact of the previously presented adaptation delay on perception (the same experimental procedure has already been applied in previous studies, see Arikan et al., 2021 and Schmitter & Straube, 2022). Each test phase comprised six test trials during which the button was pressed once, either actively or passively. The movement type in each of the six test trials always corresponded to the one used in the preceding adaptation phase. In each test trial, the button press elicited the stimulus presentation (visual or auditory, factor “test modality”) with one of six different temporal delays (0, 83, 167, 250, 333, and 417 ms). Each of the six delays was used once in each test phase in counterbalanced order. Subjects were instructed to report whether they detected any delay between the button press movement and the visual or auditory stimulus presentation. Responses were made by using one of two buttons on a button pad that was attached to subjects´ left leg. The assignment of the responses (delay, no delay) to the response buttons was counterbalanced across subjects.

The TRE was defined as difference in delay detection performances after an adaptation phase with delayed versus undelayed tones. The undelayed tone was expected to be in line with the natural prediction of undelayed sensory action-outcomes (active conditions), or with the expectation of temporal alignment between the tactile or proprioceptive and the auditory signals (passive conditions). The detection rates after exposure to the undelayed tones were thus expected to reflect baseline performance in the task without the influence of previous temporal recalibration. Conversely, the delayed tones were expected to induce the need for sensorimotor or intersensory temporal recalibration, respectively. Here, lower delay detection rates compared to baseline performance were expected to reflect a shift of the expected stimulus timing toward the adapted delay and thus temporal recalibration. In summary, the factors “adaptation delay” (0 vs. 150 ms), “movement type” (active vs. passive), and “test modality” (visual vs. auditory) were combined to eight different experimental conditions.

## 2.4 | Procedure

The fMRI experiment was divided into four scanning runs, composed of 16 adaptation-test pairs each. In each run, conditions with the same adaptation delay were blocked. This was done to prevent rapid switches of adaptation delays and thus potential spill-over effects between delayed and undelayed conditions. Whether a run started with the conditions of the 0 or 150 ms adaptation delay was counterbalanced across subjects. Within the block of each adaptation delay, conditions with active and passive movements were also blocked. Which of the movement type was presented first was counterbalanced across runs. In each run, each condition was presented with two consecutive adaptation-test pairs resulting in a total number of eight adaptation-test pairs per condition (see Figure S1 in the supplementary material for an overview of an exemplary experimental run).

An adaptation phase started with an instruction text displayed for 2000 ms on the screen indicating the movement type of the following button presses (see Figure 2). As soon as the instructions disappeared, subjects could start pressing the button or the button started to move passively. Each button press elicited the presentation of the tone, either undelayed or delayed by 150 ms. In passive conditions, nine button presses with a duration of 500 ms and in an interval of 800 ms were performed during the first part of the adaptation phase, followed by the presentation of a fixation cross of jittered length (1000, 1500, 2000, or 2500 ms). After the fixation cross disappeared, a second part of the adaptation phase was executed comprising another nine button presses. In active conditions, subjects had 8000 ms during each of the two parts of the adaptation phase to execute the button presses.

A test phase also started with an instruction text displayed for 2000 ms indicating the movement type and sensory stimulus modality of the following test trials. Before each test trial, the cue “Ready” was presented for 1000 ms. The disappearance of this cue initiated the test trials. In active conditions, subjects had 2000 ms to perform one button press. However, they were instructed to delay their button press by ~700 ms after the cue had disappeared. This was done to ensure that the button press was not reflexive, but a truly self-initiated action (Rohde & Ernst, 2013; Straube et al., 2020; van Kemenade et al., 2016). The onset for the passive button movement was jittered (0, 500, and 1000 ms). Each button press triggered the presentation of the visual or auditory outcome with one of the six test delay levels. Afterwards, the question “Delay?” was presented for a duration of 2000 ms and subjects had to respond via the button pad whether they detected a delay between the button movement and

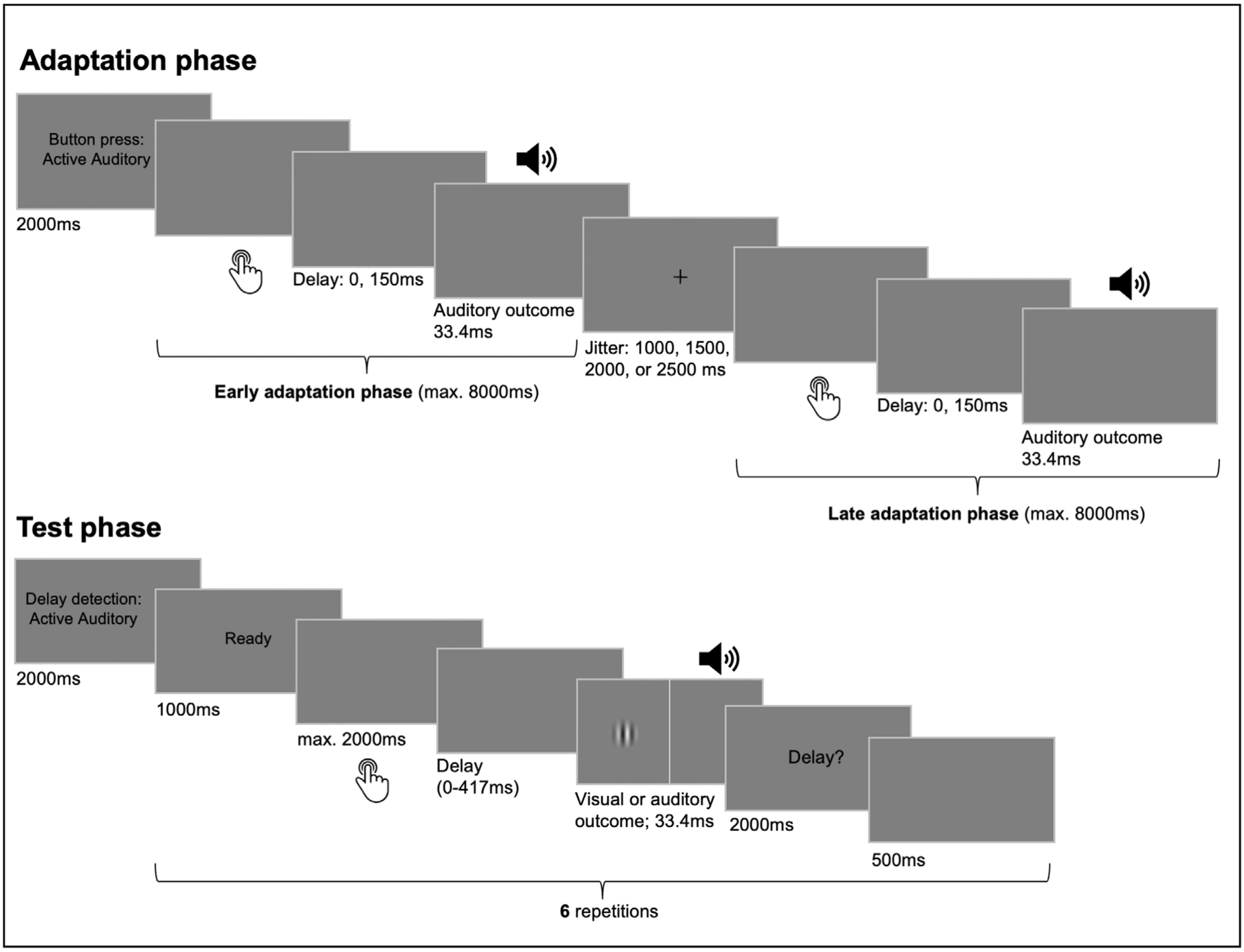

**FIGURE 2** Trial structure and timing of events. Subjects went through multiple pairs of adaptation and test phases. During adaptation phases, the button had to be moved actively by the subjects or it was moved passively. After each button press, a tone appeared, either undelayed with respect to the button press or delayed by 150 ms. Adaptation phases were separated into an early and a late part divided by the presentation of a fixation cross of jittered length. In active conditions subjects had 8000 ms to perform the button presses in each part of the adaptation phase. In passive conditions, nine button presses were automatically triggered in each part. In the subsequent test phases, subjects pressed the button once in each test trial, either actively, or the button was moved passively. Here, the outcome was presented after the button press with one of six delay levels (0–417 ms) and subjects had to report whether they detected a delay in each trial. While the outcome modality was auditory during adaptation it could be visual or auditory during test.

the outcome. After a pause of 500 ms, the cue was presented again to initiate the next test trial. The last trial of each test phase was followed by a jittered intertrial interval before the beginning of the next adaptation-test pair (1000, 1500, 2000, and 2500 ms). To ensure that subjects were familiar with the task and performed the button presses correctly, they additionally participated in a training session outside the MRI scanner on a separate day before the fMRI experiment (for details see section 2 in the Supporting Information).

## 2.5 | MRI data acquisition

MRI data were collected with a 3 Tesla MR Magnetom TIM Trio scanner (Siemens, Erlangen, Germany) with a 12-channel head-coil at the Department of Psychiatry and Psychotherapy in Marburg. Functional images were obtained parallel to the intercommissural line (anterior commissure–posterior commissure) using a T2*-weighted gradient echo-planar imaging sequence ($64 \times 64$ matrix; repetition time [TR] = 1650 ms; echo time [TE] = 25 ms; flip angle = 70°; slice thickness = 4.0 mm; gap size = 15%; voxel size = $3 \times 3 \times 4.6$ mm; field of view [FoV] = 192 mm). In each run, 560 volumes of 34 slices each were acquired in descending order covering the whole brain. Anatomical images were obtained using a T1-weighted MPRAGE sequence ($256 \times 256$ matrix; TR = 1900 ms; TE = 2.26 ms; flip angle = 9°; slice thickness = 1.0 mm; gap size = 50%; voxel size = $1 \times 1 \times 1.5$ mm; FoV = 256 mm). To prevent motion artefacts, subjects´ heads were surrounded by foam pads during data acquisition.

## 2.6 | Data analyses

Test trials for which the movement was not or incorrectly executed (i.e., the button did not reach the lowest position at which the stimulus presentation was triggered; 2.1% of all trials) were excluded from the analyses of behavioral and fMRI data. Additionally, trials for which a subject's response was missing (6.4% of all trials) were excluded from the analysis of behavioral data.

### 2.6.1 | Analysis of behavioral data

The proportion of detected delays during test phases served as a measure for the subjects' delay detection performance and was calculated separately for each subject and experimental condition. Subsequently, psychometric functions in form of cumulative Gaussian distribution functions were fitted to these data using the Psignifit toolbox version 4 (Schütt et al., 2016) for Python version 3.8.5 (Python Software Foundation, https://www.python.org/). Delay detection thresholds (i.e., the delay that could be detected in 50% of all trials) and slopes (evaluated at the detection thresholds) were derived from the psychometric functions. The detection thresholds were used as measure for the overall delay detection performance (lower values indicate better performance). The slopes represented the increment in detected delays with increasing delay levels, indicating the ability to discriminate between delays.

The detection thresholds and slopes were then forwarded to repeated-measures ANOVAs including the factors “adaptation delay,” “movement type,” and “test modality.” For significant interaction effects including the factor “adaptation delay,” Bonferroni-corrected post-hoc one-tailed *t*-tests were performed to test for significant TREs for the different movement types or test modalities. A TRE was defined as larger detection thresholds indicating a shift of psychometric functions to larger delays or flatter slopes indicating worse performance in discriminating between the delay levels after exposure to the delayed versus undelayed tones. Furthermore, post-hoc two-tailed paired-samples *t*-tests were used to test whether the TRE differed significantly between the active and passive movements or between the auditory and visual test modality. All tests were conducted with JASP (Version 0.14.1; JASP Team, 2020).

### 2.6.2 | Analysis of fMRI data

MRI data were preprocessed and analyzed with the Statistical Parametric Mapping toolbox (SPM12; www.fil.ion.ucl.ac.uk) for MATLAB (Version 2020b, Mathworks, Sherborn, Massachusetts). To correct for head motion, functional images were realigned to the mean image of each run. Anatomical images were co-registered to the functional images, segmented and normalized to the standard Montreal Neurological Institute (MNI) template. Functional images were normalized to the MNI template as well and voxel sizes were resampled to a size of $2 \times 2 \times 2$ mm. Finally, functional images were smoothed with an 8 mm full-width at half maximum kernel.

For the analysis of activity modulations during adaptation and test phases, a General Linear model (GLM) was designed for each subject including the data from both phases. For the adaptation phases, the four experimental conditions composed of the factors “movement type” and “adaptation delay” were each modeled separately for both parts of the adaptation phase (early and late), resulting in eight regressors of interest. Since the focus of our study lies on the fMRI activations related to the stimulus perception and not on activations related to the movement execution per se, for each regressor the button press events during adaptation were included from stimulus onset until stimulus offset. Adaptation phases for which less than three valid button presses were registered in the first (early) or second (late) part were excluded from the analysis as presumably not enough stimulus presentations occurred to allow for recalibration. For the test phases, the eight experimental conditions composed of the factors “movement type,” “test modality,” and “adaptation delay” were modeled as separate regressors of interest. Test trials were included as the entire 2 s during which the button presses could be performed, and stimuli were presented. If a subject's response to the delay fell already into the period of the test trial (i.e., it was not given while the question was presented, but it was given too early), data from the respective test trial were included from trial onset until response onset. Test trials for which no valid button press was registered were excluded from the analysis. The time during the presentation of the instruction texts, the cue “ready,” the jitter (fixation cross) in the middle of the adaptation phase, and the question “delay” were included as separate regressors of no interest, as were the six realignment parameters to account for variance due to head motion. Low frequencies (<0.0078 Hz) were filtered out with a high-pass filter with a cut-off period of 128 s to correct for baseline drifts in the BOLD signal. BOLD responses for all events were modeled with the canonical hemodynamic response function with the onset corresponding to the onset of the respective event. For GLMs at single-subject level, T-maps were obtained by contrasting each of the eight experimental conditions against implicit baseline. This baseline corresponded to the mean activation of all events that were not captured by the regressors in the GLM. For group-level analyses, the resulting contrast estimates for each subject were used in a flexible factorial design.

To correct for multiple comparisons at cluster level, Monte Carlo simulations (Slotnick, 2017; Slotnick et al., 2003) were used to determine the cluster extent beyond which the probability for false-positives does not surpass a threshold of alpha = .05 (considering the estimated smoothness of the data: 7 mm). According to the results after 10.000 simulations, a cluster had to exceed the minimum of 42 activated continuous voxels at $p < .001$ uncorrected to achieve correction for multiple comparisons at $p < .05$ for the data of this study. Activations of the group-level contrasts were anatomically labeled using the Automated Anatomical Labeling toolbox (AAL; Tzourio-Mazoyer et al., 2002) for SPM.

On group level, hypotheses regarding recalibration-related activations in adaptation and test phases were tested by means of

T-contrasts. First, we computed the main effect of the "adaptation delay" separately for adaptation and test phases to assess effects of the exposure to the delayed versus undelayed tones on neural activations. Furthermore, to test for delay-dependent activation differences between movement type (active vs. passive), we assessed the two-way interaction of "adaptation delay" and "movement type" for both phases. Since the impact of the adaptation delay may differ between early and late phases of adaptation, for the investigation of neural activations during adaptation, we further computed the three-way interaction composed of the factors "movement type," "adaptation delay," and "adaptation phase." Finally, to investigate whether delay-dependent activations differed in test phases with the same (auditory) or a different modality (visual) than during previous adaptation, we calculated the interaction of "adaptation delay" and "test modality" as well as the three-way interaction of "adaptation delay," "movement type," and "test modality." Additionally, we used conjunction analyses to test for potential overlapping delay-dependent activations for both sensory modalities. For a sanity check, we further computed the main effect of "movement type" to assess whether stronger motor-related activation was associated with active compared to passive movement conditions.

## 3 | RESULTS

### 3.1 | Behavioral results

Behavioral results are displayed in Figure 3. The repeated-measures ANOVA on the delay detection thresholds revealed a significant main effect for the factor "adaptation delay" [$F(1,24) = 13.691$, $p = .001$, $\eta_p^2 = .353$]. Detection thresholds were larger and detection performance thus decreased after exposure to the delayed [$M = 242.528$, $SD = 77.192$] than to undelayed tones [$M = 222.858$, $SD = 88.307$]. This indicates temporal recalibration to the delay and thus a significant TRE. Moreover, the ANOVA revealed significant two-way interactions of the "adaptation delay" with the factors "movement type" [$F(1,24) = 5.596$, $p = .026$, $\eta_p^2 = .189$] and "test modality" [$F(1,24) = 13.213$, $p = .001$, $\eta_p^2 = .355$]. According to post-hoc paired-

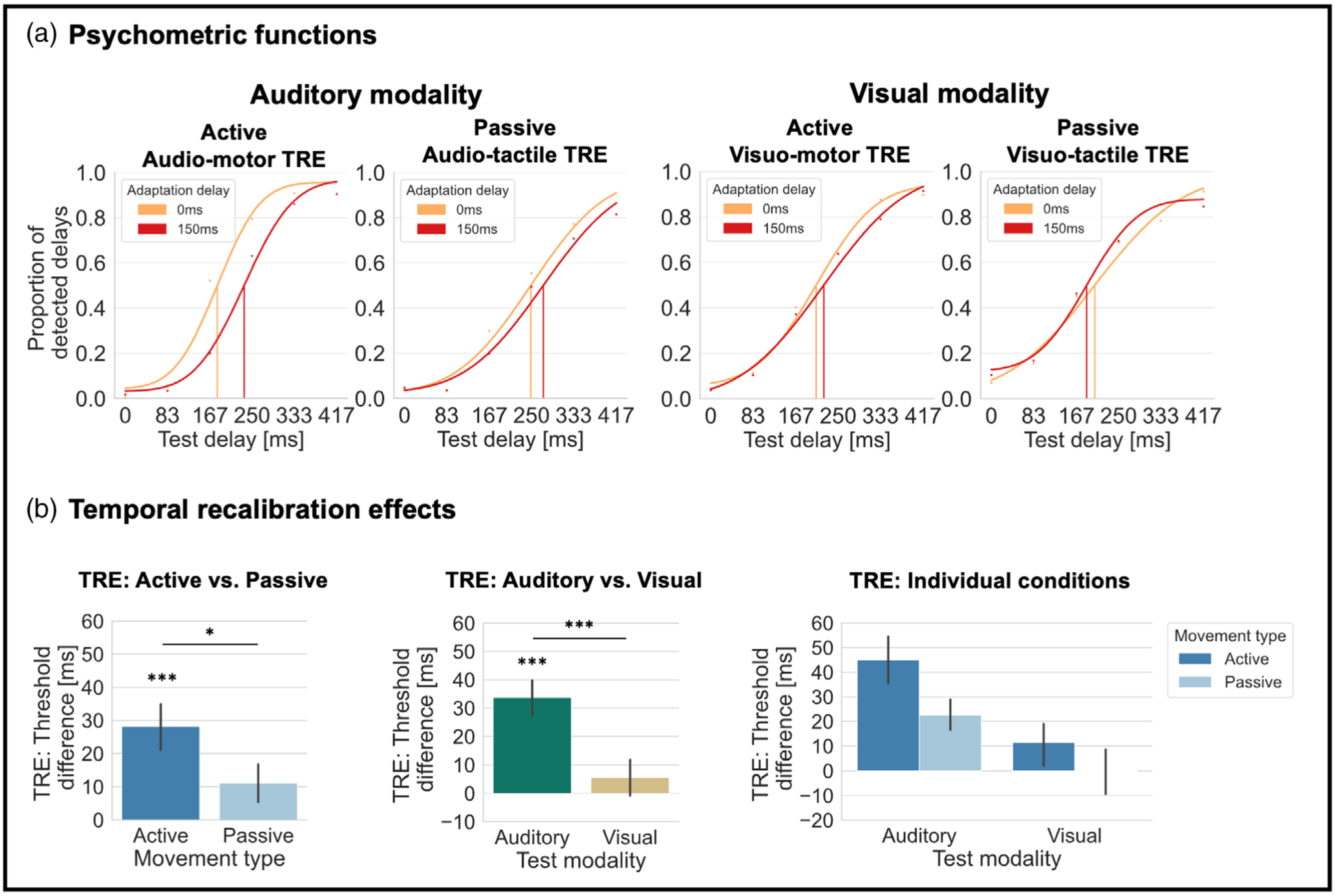

**FIGURE 3** Behavioral results. (a) Psychometric functions were fitted to the delay detection data for each experimental condition. The TRE corresponded to a rightward shift of the psychometric functions after exposure to tones delayed by 150 ms (red) compared to undelayed tones (orange) indicating decreased delay detection thresholds and thus temporal recalibration. Psychometric functions are displayed on group level for illustration purposes. For the statistical analyses, the functions were fitted to the subjects´ individual detection rates. (b) The TRE was significant for active and auditory conditions. Furthermore, the TRE was significantly larger in active than in passive and in auditory than in visual conditions. Error bars indicate standard errors of the means. * $p < .05$, *** $p < .001$.

samples tests, the TRE was significant in active [mean sensorimotor TRE $= 28.205$, SD $= 38.839$; $t(24) = 3.631$, $p < .001$, $d = .726$] as well as in passive conditions [mean intersensory TRE $= 11.135$, SD $= 23.565$; $t(24) = 2.363$, $p = .013$, $d = .473$]. Comparing the TRE in active and passive conditions further revealed that the sensorimotor TRE (active) was significantly larger than the intersensory TRE [passive; $t(24) = 2.366$, $p = .026$, $d = .473$, two-tailed] indicating an advantage of temporal recalibration due to the presence of sensorimotor predictions. Another pair of post-hoc paired-samples tests demonstrated that the TRE was significant for auditory sensory outcomes [mean auditory TRE $= 33.764$, SD $= 29.939$; $t(24) = 5.639$, $p < .001$, $d = 1.128$] while the TRE for visual outcomes failed to reach significance [mean visual TRE $= 5.576$, SD $= 35.613$; $t(24) = .783$, $p = .221$, $d = .157$]. This suggests that the TRE observed in the auditory modality did not transfer to vision. Additionally, directly comparing the auditory and visual TRE revealed a significantly stronger effect in auditory than in visual conditions [$t(24) = 3.635$, $p = .001$, $d = .727$, two-tailed]. The three-way interaction of all factors did not reach significance [$F(1,24) = .336$, $p = .568$, $\eta_p^2 = .014$].

The repeated-measures ANOVA on the slopes of the psychometric functions did not reveal a significant main effect of the "adaptation delay" [$F(1,24) = 4.082$, $p = .055$, $\eta_p^2 = .145$], indicating that exposure to the delayed versus undelayed tones did not impact the ability to discriminate between the delay levels in the delay detection task. None of the interactions with the factors "movement type" and "test modality" became significant (all $p > .197$).

## 3.2 | fMRI results

For a sanity check, we tested whether activations in active and passive movement conditions differed in regions for motor-related processes. Active conditions were associated with stronger activation in large clusters, primarily in left precentral gyrus and in the cerebellum (for details see section 5 in the Supporting Information). This supports the argument that sensorimotor predictions based on motor commands of actions should be specific to the active conditions in our study.

### 3.2.1 | Neural correlates of temporal recalibration during adaptation phases

We tested for differences in brain activation during adaptation phases due to exposure to the delayed versus undelayed tones across movement types. The 150 > 0 ms contrast revealed a cluster in left hippocampus, which showed stronger activations during exposure to the tones that were delayed by 150 ms compared to undelayed tones (see Figure 4a). According a more fine-grained anatomical labeling using the Anatomy Toolbox for SPM (Eickhoff et al., 2005, 2006, 2007), this cluster could be assigned with highest probability to the hippocampal subregion CA1 (35.3.0%) and dentate gyrus (5.9%; Amunts et al., 2005). The reversed contrast (0 > 150 ms) did not reveal significant clusters of activation.

To test whether delay-dependent modulations of neural activations differed between sensorimotor (active) and intersensory contexts (passive), we assessed interaction effects of the factors "adaptation delay" and "movement type." We found no significant activations for the interaction contrast assuming stronger activations during exposure to the delayed versus undelayed tones in active compared to passive movement conditions [(Act150 > Act0) > (Pas150 > Pas0)]. However, the reversed interaction contrast [(Act0 > Act150) > (Pas0 > Pas150)] revealed activations in frontal regions including a cluster in left middle frontal gyrus (MFG) extending

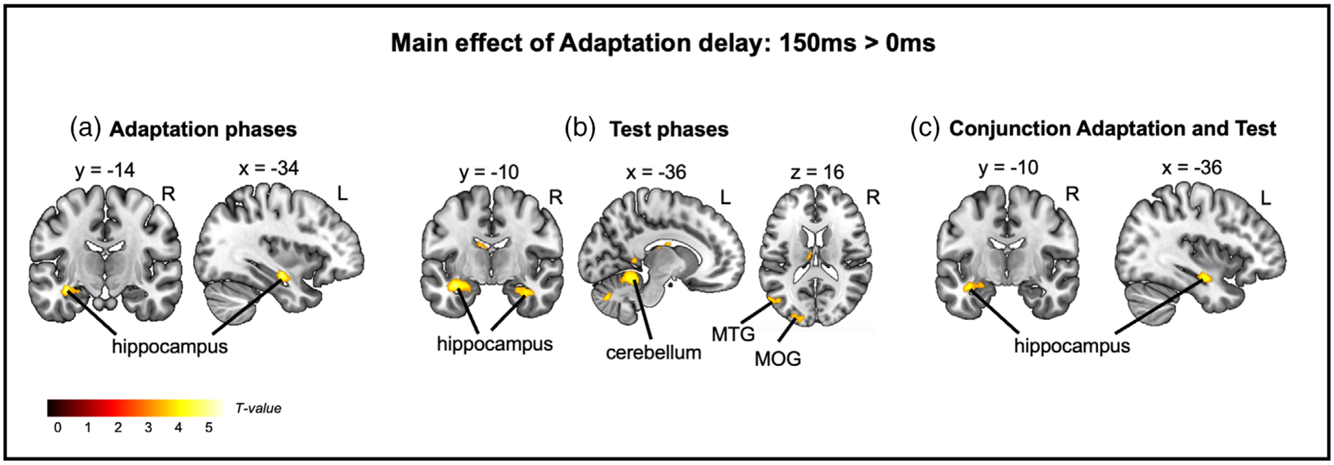

**FIGURE 4** fMRI results: Main effect of Adaptation delay in adaptation and test phases. (a) Stronger activations were found in adaptation phases in hippocampus during exposure to the delayed versus undelayed tones. (b) During test phases, previous exposure to delayed versus undelayed tones was associated with increased activations in multiple regions, including hippocampus and cerebellum, as well as occipital and temporal regions. (c) A conjunction of the main effect of the adaptation delay during adaptation and test phases revealed that a cluster in left hippocampus was similarly modulated by the delay in both phases.

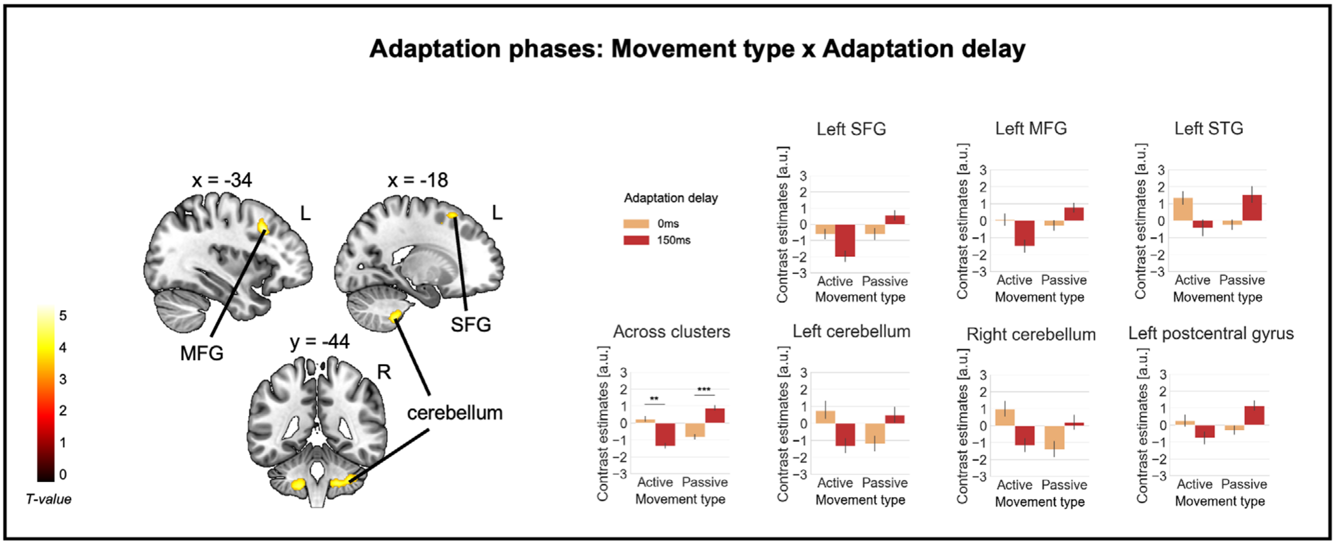

**FIGURE 5** fMRI results: Interaction of Movement type and Adaptation delay during adaptation phases. During adaptation phases, clusters including frontal regions, cerebellum, postcentral gyrus, and STG showed significant activations for the "adaptation delay" × "movement type" interaction with a relative activation decrease in active conditions during delay exposure compared to exposure to undelayed tones, while the opposite pattern appeared in passive conditions. Error bars indicate standard errors of the means. ** $p < .01$, *** $p < .001$.

to inferior frontal gyrus, and a cluster in left superior frontal gyrus (SFG) extending to MFG. Further activations emerged in the left posterior cerebellum, spanning lobules VIII, IX, and X, and in the right posterior cerebellum, involving lobules VI, VIII, IX, and X, as well as crus I and II. Finally, significant clusters were found with peaks in left superior temporal gyrus (STG), left postcentral gyrus, and left middle occipital gyrus (MOG; see Figure 5). According to post-hoc paired-samples *t*-tests performed on activations across all clusters identified by this contrast (i.e., eigenvariates extracted with the VOI function of SPM12), in active conditions, activations in these regions were significantly reduced during exposure to the delayed ($M = -1.343$, $SD = 1.165$) versus undelayed tones ($M = .219$, $SD = 1.514$; $t(24) = 3.682$, $p = .001$, $d = .736$, corrected alpha $= .025$, two-tailed). In passive conditions, the reversed pattern emerged with significantly stronger activations during exposure to the delayed ($M = .884$, $SD = 1.148$) versus undelayed tones ($M = -.822$, $SD = 1.071$; $t(24) = -5.325$, $p < .001$, $d = -1.065$, corrected alpha $= .025$, two-tailed). The three-way interaction contrast including the factor "adaptation phase" did not reveal significant clusters of activation.

While we expected the delayed tones to be associated with increased error-related activations, the relative activation decrease during delay exposure in active conditions was surprising. To further explore potential reasons for this pattern, we assessed whether the decrease in activations observed in this condition was specific to early phases of adaptation but leveled off in late phases after an extended period of adaptation, or whether this pattern persisted consistently throughout delay exposure in active conditions. This exploratory analysis revealed that the significant difference between adaptation delays in terms of reduced activation during exposure to delayed tones was indeed mainly driven by early phases. The activation difference between the delays vanished during late phases of adaptation due to an activation increase for the delayed tones (for details see section 4 in the Supporting Information).

### 3.2.2 | Neural correlates of temporal recalibration during test phases

We tested whether exposure to the delayed versus undelayed tones during adaptation had a differential impact on activations during the delay detection task at test. The 150 > 0 ms contrast revealed stronger activations after previous exposure to the delayed tones in a cluster in left hippocampus and a cluster comprising right hippocampus and right parahippocampal gyrus. As during the adaptation phases, according to the anatomy toolbox, the hippocampal clusters were mainly assigned to the subarea CA1 (left: 36.0%, right: 29.4%) and to the dentate gyrus (left: 17.5%, right: 6.0%). Moreover, a cluster in left anterior cerebellum was found, including lobules IV/V, and crus II, which extended to anterior and posterior parts of the right cerebellum, including lobules IV, V, VI, VII, VIII, and crus I and II. This suggests an impact of temporal recalibration to delayed tones on the recruitment of these areas during delay detection (see Figure 4b). Furthermore, the contrast revealed significant activations with peaks in left posterior orbitofrontal cortex, right putamen, left middle temporal gyrus, left thalamus, and left MOG. The reversed contrast (0 > 150 ms) did not reveal significant clusters of activation.

Since partly overlapping regions showed activations for the main effect of the adaptation delay during adaptation and test phases, we further used a conjunction of this contrast for both phases (Adaptation 150 >0 ms ∩ Test 150 >0 ms) to assess whether clusters of the same areas that were modulated by the delay during adaptation were also differentially recruited during test. This analysis revealed that a cluster in left hippocampus was involved more strongly during exposure to the delayed versus undelayed tones in adaptation phases and was also more strongly activated at test when the tones during previous adaptation had been delayed (see Figure 4c). As during adaptation and test phases separately, the hippocampal cluster of the conjunction was assigned with highest probability to the subregions CA1 (35.3%) and to the dentate gyrus (6.1%).

Exploratorily examining this conjunction analysis separately for both test modalities further revealed that these overlapping hippocampus activations for both phases were specific to the auditory test modality ($x, y, z = -36, -10, -18$, cluster size $= 107$ voxels, $t = 4.00$), but not present for the visual modality (for details see Supporting Information, section 6). For a detailed summary of all clusters involved in the reported contrasts, see Tables S1 and S2 in the Supporting Information. During test phases, the interaction of "adaptation delay" and "movement type" did not reach significance. Furthermore, the interaction contrasts of "adaptation delay" and "test modality" did not reveal meaningful clusters of activation (except for small clusters, which could not be assigned unambiguously to gray matter volume by the AAL toolbox) and the three-way interaction including all three factors was not significant either. Finally, the conjunction of the 150 > 0 ms contrast for the auditory and visual test modality testing for overlapping delay-dependent brain activations did not reveal any significant activations.

## 4 | DISCUSSION

We investigated the neural correlates of sensorimotor temporal recalibration that can be attributed to the recalibration of sensorimotor predictions as compared to the recalibration of intersensory matching mechanisms. Our findings imply important roles for the hippocampus and the cerebellum in recalibration across sensorimotor and intersensory contexts, suggesting processes that are more likely to be attributed to the recalibration of intersensory timing. Context-dependent differences emerged in terms of a stronger behavioral TRE in sensorimotor (active) conditions and differential neural activations in frontal cortices, cerebellum, and sensory processing regions. This suggests the influence of sensorimotor predictions in recalibration-related processes in these regions and potentially accounts for the perceptual advantage of sensorimotor compared to intersensory temporal recalibration.

### 4.1 | Behavioral TRE

At the behavioral level, we found a TRE in both active and passive movement conditions in form of increased delay detection thresholds after exposure to delayed versus undelayed tones. The passive TRE reflects intersensory temporal recalibration in terms of modulations of the perceived relative timing between signals from different sensory modalities (Fujisaki et al., 2004; Harrar & Harris, 2008; Van der Burg et al., 2013; Vroomen et al., 2004). The active TRE reflects sensorimotor temporal recalibration in terms of changes in the expected timing between actions and their sensory outcomes (Arikan et al., 2021; Cai et al., 2018; Cao et al., 2017; Elijah et al., 2016; Heron et al., 2009; Rohde & Ernst, 2013; Stekelenburg et al., 2011; Stetson et al., 2006; Sugano et al., 2010). Importantly, the TRE in active conditions was stronger than the one in passive conditions. Thus, the shift in temporal perception was stronger after recalibration due to sensorimotor delays compared to intersensory delays. These findings are in line with the assumption that recalibration in sensorimotor contexts involves a component beyond the recalibration of the perceived intersensory timing, such as the recalibration of sensorimotor predictions about the timing of a self-generated action-outcome (Arikan et al., 2021).

The comparison between auditory and visual conditions revealed that a TRE manifested only in auditory conditions and did not transfer to the visual modality. Previous studies investigating the modality-transfer of temporal recalibration effects, especially in sensorimotor contexts, reported mixed results. While some found a transfer in both directions, that is, from audition to vision and vice versa (Heron et al., 2009; Sugano et al., 2010), other found this effect to be limited to a transfer from vision to audition (Arikan et al., 2021; Sugano et al., 2012). Generally, the auditory modality has been suggested be more susceptible to temporal recalibration than the visual modality due to a more precise temporal perception and discriminability of auditory stimuli (Grahn, 2012; Grondin, 2010). This also results in a better predictability for the timing of auditory events and predictability is assumed to be important for temporal recalibration effects to occur (Rohde et al., 2014). These inherent differences between the modalities may partly explain why the transfer of recalibration effects to the visual modality was absent in this study. Still, our results do therefore not provide evidence for supra-modal predictive mechanisms in temporal recalibration.

### 4.2 | The role of the hippocampus in temporal recalibration

At the neural level, comparing activations during exposure to delayed versus undelayed stimuli (adaptation phases), revealed increased activations in the left hippocampus. Similarly, during subsequent test phases, activations in bilateral hippocampus were stronger when the stimuli in the previous adaptation phase were delayed. Interestingly, a conjunction analysis revealed that there was an overlap of the clusters in left hippocampus, which responded more strongly to delayed stimuli during adaptation and was also more strongly recruited during subsequent test phases.

The hippocampus has previously been shown to be involved in the acquisition and retrieval of new sensorimotor mappings during sensorimotor adaptation. For instance, during the adaptation of reaching movements to a rotated visual feedback display, the updating of the expected relationship between the motor programs and the visual feedback has been associated with the hippocampus (Anguera et al., 2007; Scheidt et al., 2011; Standage et al., 2022). Also beyond the sensorimotor domain, the hippocampus has been recognized as playing a crucial role in associative learning and the associative binding of events that are separated in space or time (Staresina & Davachi, 2009; Wallenstein et al., 1998). It is known to be involved in detecting mismatches that arise due to the comparison of expected and perceived stimulus associations (Chen et al., 2011; Duncan et al., 2009; Kumaran & Maguire, 2006, 2007; Long et al., 2016), and consequentially in updating the stored associations (Duncan et al., 2012). The detection of these mismatches has specifically been related to the hippocampal subarea CA1 (Chen et al., 2011; Duncan et al., 2012).

In our study, activations in hippocampus could also mainly be assigned to the CA1 area, both during adaptation and during test and across both active and passive conditions. During adaptation phases, the activation increases during exposure to the delayed tones may thus be explained by the detection of violations of the learned temporal stimulus associations. And consequently, by the encoding of the novel association between the auditory stimulus and tactile sensations during the button movement. This indicates the importance of the hippocampus in recalibrating the perceived timing between sensory stimuli with and without the involvement of an action. During test phases, a partly overlapping cluster in CA1 was also more strongly involved when subjects were previously exposed to the delayed tones. The detection of the varying delays during test presumably requires the comparison of the learned and therefore expected delay between the button movement and the tone with the actual delay in each trial. Thus, these results suggest that the encoded temporal association of the stimuli must be retrieved during that task, leading to increasing engagement of the hippocampus, especially when these associations have just been updated to account for the additional delay introduced during adaptation. In summary, our findings imply an important role for the hippocampus during temporal recalibration through the acquisition and recall of new temporal stimulus associations. The fact that it was involved during both active and passive conditions suggests a general role of this region in responding to violations of the expected stimulus timing (intersensory recalibration) beyond the sensorimotor domain.

## 4.3 | The role of the cerebellum in temporal recalibration

Next to the hippocampus, the cerebellum also exhibited stronger activations during the delay detection task after previous exposure to delayed compared to undelayed tones. The cerebellum has frequently been proposed as the location of internal forward models that generate predictions about the sensory outcomes of self-generated actions (Arikan et al., 2019; Blakemore et al., 2001; Leube, Knoblich, Erb, Grodd, et al., 2003; Straube et al., 2017; Tanaka et al., 2020; van Kemenade et al., 2018; Welniarz et al., 2021). In this line, it could also consistently be associated with processes requiring the adjustment of these internal model predictions to environmental changes such as in sensorimotor temporal recalibration (Cao et al., 2017) or sensorimotor adaptation due to action feedback perturbations (Block & Celnik, 2013; Cassady et al., 2017; Galea et al., 2011; Tzvi et al., 2022). However, the role of the cerebellum in implementing and updating internal models does not appear to be not unique to the sensorimotor domain. Similar mechanisms seem to be at play for purely perceptual processes (Kotz et al., 2014; O'Reilly et al., 2008; Schubotz, 2007). In that regard, the cerebellum has been shown to be involved in generating and recalibrating temporal predictions for sensory events also in the absence of actions, and in detecting incongruencies between the predicted and perceived intersensory stimulus timing (Beudel et al., 2009; Coull et al., 2013; Kotz et al., 2014; Moberget et al., 2008; O'Reilly et al., 2008; Roth et al., 2013).

In our study, performing the delay detection task requires the generation of internal model predictions about the expected delay between the stimuli or between action and outcome to judge about the presence of an additional delay in the trial. Considering the significance of the cerebellum in storing and updating these internal models across motor and perceptual domains, the increased engagement of the cerebellum during test phases may be attributed to the storage of multiple internal models or temporal stimulus associations after recalibration. A similar phenomenon has for example been reported for multiple visuo-motor mappings found to be stored in cerebellum after sensorimotor adaptation to different visuo-motor rotations (Kim et al., 2015). Thus, the presence of multiple representations for the temporal stimulus associations in the cerebellum could result in a conflict in the predicted stimulus timing or a broader time window for predictions. Consequently, higher uncertainty or higher processing demands in prediction generation could be associated with our task after exposure to the delayed tones and may account for the increasing engagement of the cerebellum after recalibration. To conclude, our findings suggest that activations in the cerebellum may be related to the retention of multiple internal predictive models during recalibration, which are not specific to sensorimotor predictions about action-outcome relationships. Instead, as the cerebellum contributed to active and passive conditions, our findings highlight the importance of recalibration-related processes in the cerebellum which may rather reflect components of intersensory temporal recalibration across domains of action and perception.

## 4.4 | Differential neural correlates of sensorimotor versus intersensory temporal recalibration

The recalibration-related activations in the hippocampus and the cerebellum discussed above could be observed across both active and passive conditions, suggesting contributions of these regions to more general intersensory temporal recalibration mechanisms. Opposed to that, differences between active and passive conditions emerged during adaptation phases as revealed by the interaction of “movement type” (active vs. passive) and “adaptation delay” (0 vs. 150 ms), including frontal regions (left SFG and MFG), regions for sensory processing (left STG and postcentral gyrus), and the bilateral cerebellum. In active conditions, this manifested in terms of a relative decrease in activations during exposure to the delayed versus undelayed tones, while the opposite pattern emerged in passive conditions (i.e., increased activations during exposure to delayed tones).

The activation decreases during exposure to actively elicited delayed tones was surprising at first, since we expected that the delay would deviate from the natural expectation of undelayed action-outcomes, and therefore, would elicit a prediction error signal associated with increasing activations in this condition. Instead, it appeared that the regions involved in the interaction contrast exhibited stronger activation in response to stimuli that occurred in synchrony with the action, resulting in stronger overall activation for the undelayed tones. Consequently, the activation was at least initially suppressed for the delayed tones. A similar activation pattern has been observed in previous studies that aimed at identifying brain regions responding to the feeling of self-control over stimuli or the attribution of self-agency. Action-outcomes presented in synchrony with the action and judged as being self-generated were associated with increased activation in cerebellum, parietal areas (Matsuzawa et al., 2005), and in posterior midline areas, like the precuneus and posterior parietal cortex (Fukushima et al., 2013). In our task this effect appeared in posterior structures of the bilateral cerebellum, and additionally activated frontal regions and areas for somatosensory (postcentral gyrus) and auditory processing (STG). Interestingly though, when exploratorily examining the activation pattern separately for early and late adaptation phases, it appeared that the relative activation decrease during exposure to the actively elicited delayed tones was mainly driven by early phases (see section 4 in the Supporting Information). As the engagement of these regions increased from early to late phases, the difference in activation for delayed and undelayed tones disappeared. A similar phenomenon could be observed earlier, whereby the activation pattern elicited by the processing of delayed stimuli approached the typical pattern observed for the processing of undelayed stimuli after recalibration (Elijah et al., 2016). This may be explained by the delayed tones being perceived as occurring synchronously with the action after a longer period of exposure to the delays. It may even be speculated that initially, the delayed tones were not fully perceived as being generated or controlled by one's own action, but after some exposure time they were and signaled the need for recalibration. Regardless of what the exact explanation for this change is, it appears that after a longer time of exposure to the delay, the delayed tones were similarly processed as the undelayed ones in the regions involved in this contrast. Since the undelayed tones should be naturally in line with sensorimotor predictions, this suggests that after the recalibration of these predictions, the delayed tones were similarly perceived as being in line with them. This is consistent to behavioral findings, where after temporal recalibration, the delayed action-outcome is perceived as occurring in synchrony with the action (Heron et al., 2009; Parsons et al., 2013). However, it is important to note that the explanation of the activation pattern change across adaptation phases is only a post-hoc interpretation, as the three-way interaction of “movement type,” “adaptation delay,” and “adaptation phase” appeared to have lacked sufficient power to reach statistical significance in our study. Thus, the explanation for the exact reason of the activation pattern remains speculative and should be taken with caution.

A question that remains open is how to reconcile these results with a range of studies that reported the reversed activation pattern. Here, increased activations in response to temporal or spatial action-outcome deviations and violations of the sense of agency indicated prediction error processing (Haggard, 2017; Leube, Knoblich, Erb, & Kircher, 2003; Nahab et al., 2011; Zito et al., 2020). One difference between our study and these previous ones, which may be responsible for the difference in activation pattern, is the nature of the task. Unlike many studies investigating agency-related processing (Haggard, 2017; Moore, 2016), we did not ask subjects to rate their subjective feeling of agency over the action-outcome but asked them to just attentively listen to the tones during adaptation. This might have made the detection of regularities in the action-outcome relationship more important for the task than the explicit detection of prediction errors (Wen & Haggard, 2020). Thus, the increasing activations observed throughout adaptation may correspond to the detection of, or increased confidence in detecting, the novel temporal relationship between action and outcome. In line with this assumption, it may be assumed that recalibration in active conditions in our task was not mediated by prediction-error based learning, but rather by the detection of temporal regularities or the detection of synchrony between action and outcome. Notably though, while the expected pattern of increased activation for the processing the delayed versus undelayed tones did not appear in active conditions in our study, it was evident in passive conditions. Here, the delayed tones were associated with higher activations across all regions of the interaction contrast in both adaptation phases. This is consistent with the notion that temporal mismatches between the tactile sensation during the button movement and the tone were detected and resulted in an intersensory error signal (Bushara et al., 2001; Dhamala et al., 2007; Stevenson et al., 2010).

In conclusion, our findings coincide with previous studies in confirming the importance of regions in frontal cortices (Standage et al., 2022; Stetson et al., 2006) and the cerebellum (Cao et al., 2017; Schmitter & Straube, 2022) during temporal recalibration. Additionally, activations in STG for auditory processing and in postcentral gyrus for somatosensory processing are consistent with previous findings of processing changes due to recalibration in sensory regions associated with the modalities engaged in the task (Aytemür et al., 2017; Elijah et al., 2016; Stekelenburg et al., 2011). Importantly, we extend these findings by showing that the exact contribution of these regions to temporal recalibration may differ depending on whether it relies solely on changes in intersensory timing, or whether sensorimotor predictive mechanisms come into play due to the involvement of an action. The presence of sensorimotor predictions may influence the engagement of these regions during temporal recalibration, potentially facilitating the effects of this process on perception. Hence, they could be responsible for the greater behavioral recalibration effect observed in active compared to passive conditions.

### 4.5 | Modality-transfer of temporal recalibration effects

Although behavioral effects of temporal recalibration did not transfer from the auditory to the visual modality in our study, no differential brain activations were observed in test phases between the two test modalities. There were also no overlapping activations for the 150 > 0 ms contrast between auditory and visual conditions. Thus, we did not observe a clear signature for neural correlates for the transfer of recalibration effects to the visual modality. However, when exploring the impact of the adaptation delay on activations during visual and auditory test phases separately (see section 6 in the Supporting Information), it appeared that the hippocampal activations were predominantly driven by the auditory modality. Conversely, cerebellar activations were mainly driven by the visual modality. As described above, the cerebellum has been considered as important for hosting and recalibrating internal model predictions about the outcomes of one's own actions (Arikan et al., 2019; Blakemore et al., 2001; Leube, Knoblich, Erb, Grodd, et al., 2003; Straube et al., 2017; Tanaka et al., 2020; van Kemenade et al., 2018; Welniarz et al., 2021). This has even been suggested to occur on a supra-modal level, that is, for the general predicted timing for action-outcomes of different sensory modalities (Straube et al., 2017; van Kemenade et al., 2016, 2017). The fact that the delayed auditory outcome during adaptation led to increased activation of the cerebellum during the visual delay detection task, could thus imply certain cross-modal interactions in temporal recalibration. Nonetheless, due to the absence of behavioral recalibration effects in vision and of clearly common or distinct recalibration-dependent brain activations for both modalities, our findings do not provide direct evidence for modality-transfer in temporal recalibration and thus for the recalibration supra-modal predictive mechanisms.

### 4.6 | Limitations and directions for future research

Finally, some limitations of the present study and potential directions for future research will be discussed. First, active and passive movement conditions were designed to minimize differences between them, with the only difference being the availability of sensorimotor predictions during active movements. However, it could be argued that unintentional differences occurred, such as differences in the allocation of attentional resources, which have been demonstrated to modulate the magnitude of the sensorimotor TRE (Heron et al., 2010). We explicitly instructed subjects to carefully monitor the stimuli throughout the experiment and close attention to the stimuli during test phases was necessary in all conditions for detecting the delays. Thus, although we cannot rule out the possibility that differences in attention may have emerged, we think it is unlikely that this factor alone can account for the differences between active and passive movement conditions observed in our study.

Second, across the experimental runs, the adaptation delay switched multiple times from 0 to 150 ms and back. It may be argued that this rapid switching of temporal contingencies prevented recalibration effects to consistently manifest in all conditions. However, the occurrence of recalibration effects in both sensorimotor and intersensory contexts, despite these multiple switches, argues against that. It even highlights the flexibility of temporal recalibration mechanisms that can react rapidly to continuously changing environmental conditions. One may also consider that a certain amount of recalibration could have been necessary for the undelayed stimuli during adaptation. It is possible that they did not precisely match the natural expectation for the stimulus timing as we assumed, or that recalibration back to the natural expectation of undelayed stimuli was necessary after being previously recalibrated to the delay. Hence, it could be informative in the future to compare delay detection performance after delay adaptation with a baseline assessment of detection performances without any prior adaptation phases.

Third, the adaptation phases in our experiment were rather short (consisting of a max. of 18 button presses). It may be interesting for future research to study these recalibration mechanisms with a more extended period of adaptation. This may enable the investigation of how differences in neural activation between the contexts manifest when recalibration can be presumed to be well-advanced or even complete. It could also allow us to answer the question of whether context-dependent differences in neural processing can be attributed to differences in how recalibration-related activity dynamically changes over time. It may also be speculated that a longer adaptation period would be necessary for the manifestation of modality-transfer effects of recalibration, which were absent in our study.

Finally, it would be interesting to explore whether the neural correlates of temporal recalibration, and their modulation by sensorimotor predictions, converge across different adaptation modalities. For example, by comparing the correlates of recalibration to delayed auditory and visual stimuli. This could provide insights into whether they share common neural substrates of temporal recalibration or whether they depend on modality-specific circuits.

## 5 | CONCLUSIONS

The aim of the present study was to disentangle the behavioral and neural correlates of sensorimotor temporal recalibration that can be attributed to the recalibration of sensorimotor predictions from those that may be related to recalibration of intersensory timing. We found that recalibration across sensorimotor and intersensory contexts was associated with activation in hippocampus highlighting its role in encoding and retrieving the novel intersensory temporal associations. Additionally, our findings emphasize the role of the cerebellum in recalibration possibly related to the retention of multiple representations of the temporal stimulus associations. Context-dependent differences emerged in terms of a stronger behavioral recalibration effect in sensorimotor versus intersensory conditions and were at the neural level captured by differential activation pattern in frontal cortices, cerebellum, and sensory processing regions. These findings cannot be explained by intersensory recalibration alone but suggest the influence of sensorimotor predictions, which modulate recalibration-related processes in these regions, and potentially account for the perceptual advantage of sensorimotor compared to purely intersensory temporal recalibration.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no competing financial interests.

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Zenodo at 10.5281/zenodo.7886438.

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