Temporal Dynamics of Sensorimotor Integration for Non-Visual Target Information During Movement Preparation and Online Control

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All data and data analysis scripts are available at the following link: https://osf.io/gnz7u/

Abstract:

Online movement variability in non-visual (auditory and proprioceptive) target reaching is modality-dependent. This study investigated whether such modality-specific effects emerge during movement preparation and whether this phase influences subsequent online control. Participants performed reaching movements toward auditory, proprioceptive, or audio-proprioceptive targets. Electromyography and movement kinematics were recorded to examine the effects of sensory modality on sensory encoding and motor coordination during movement preparation, as well as online control at 5%, 50%, and 100% of movement time. Results revealed a modality-dependent sensory encoding phase, whereas a modality-independent motor coordination phase. Movement variability was greater for auditory targets than for proprioceptive and audio-proprioceptive targets at 50% and 100% of movement. Only motor coordination influenced early online control (5%), but this effect was modality-independent. These findings demonstrate that the influence of sensory modality extends beyond execution to the preparatory phase of movement. The results support a four-stage model of action control: a modality-dependent sensory encoding phase of preparation and late online control, alongside a modality-independent motor coordination phase and early online control. These findings offer new insight into the temporal dynamics of sensorimotor control without vision, indicating that non-visual sensory information is differentially used during distinct phases of movement preparation and execution.

Keywords: Proprioception, Audition, Reaching, Sensory Encoding, Motor Coordination, Online Control.

Introduction

In everyday life, we often perform actions toward targets that we can't see, leveraging information coming from auditory and proprioceptive sensory modalities. For instance, we mostly use audition to catch a flying mosquito in the dark, while proprioception guides us if the mosquito lands on our arm. Even though such actions subserve the same goal (successfully reaching a target), auditory and proprioceptive localization exhibit distinct patterns of directional accuracy and variability (Middlebrooks and Green, 1991; Makous and Middlebrooks, 1990; Wightman and Kistler, 1990; Kato et al, 2003; Kuling et al, 2016; Liu et al, 2018; van Beers et al, 1998; Middlebrooks, 2015; van Beers et al, 1996, 1999a, 2002b, 1999b, 2002a; Camponogara and Volcic, 2021a). This different localization process translates into distinct sensorimotor integration mechanisms between sensory modalities. Although actions share a similar accuracy along the azimuth direction, those directed toward auditory targets exhibit higher endpoint variability than those aimed at proprioceptive targets. Additionally, actions toward audio-proprioceptive and proprioceptive targets show a similar pattern of endpoint variability, suggesting a reliance on proprioception in multisensory conditions (Camponogara, 2025). It is however worth noticing that these findings are grounded in investigations focused on endpoint accuracy and precision (Camponogara, 2025; Cuppone et al, 2018, 2019), thereby limiting insights to sensorimotor integration processes that occur *during* movement execution, when target-related sensory information is used to fine-tune actions (Elliott et al, 2016). This raises the critical question of whether differences in auditory and proprioceptive target reaching are already evident *before* movement onset, during the preparatory phase, and whether such modality-specific preparatory activity may modulate movement performance. In other words, does non-visual sensory information about the target influence how movements are prepared, and if so, does movement preparation affect the subsequent action performance?

Studies on visual target reaching have shown that the sensorimotor integration processes occurring during the movement preparation stage play a critical role in action performance, affecting the early phases of the action (Haith et al, 2016; Sutter et al, 2021; van Beers et al, 2004; Churchland et al, 2006a,b; Orban De Xivry et al, 2017). Multisensory-motor integration studies comparing actions toward *visual* and *non-visual* targets further highlighted the relevant role of target-related sensory information in shaping both movement preparation and execution (Sarlegna and Sainburg, 2009; Camponogara and Volcic, 2021a, 2019; Sober and Sabes, 2003; Sarlegna and Sainburg, 2007). A brief visual exposure to a haptically sensed target during movement preparation improves final action performance compared to purely haptic or proprioceptive target reaching (Camponogara and Volcic, 2021a; Monaco et al, 2010; Cameron and López-Moliner, 2015; Desmurget et al, 1997). Additionally, when both visual and haptic information about the target is available prior to movement onset, the time for movement preparation, measured through the reaction times (RT), was reduced compared to visually guided reaching alone (Camponogara et al, 2024), confirming the pivotal role of target-related sensory information during the movement preparation stage. Recent fMRI and electroencephalographic (EEG) studies further support

such findings, showing a modality-specific activation of motor areas before the movement onset (Bianco et al, 2020b,a; Kreter et al, 2025). Taken together, these studies suggest that movement preparation is contingent upon the sensory modality guiding the action, and, as online control, modulates according to the available target-related sensory information. Additionally, they suggest that the type of target-related sensory modality during motor preparation can influence action performance. However, past studies have primarily contrasted motor preparation for *visual* versus *non-visual* targets, leaving unexplored the specificity of preparatory processes for target-related *non-visual* information, such as audition and proprioception. Although actions toward auditory and proprioceptive targets exhibit different variability (Camponogara, 2025), whether they display a distinct pattern of movement preparation and if this latter affects the action performance remains a subject of debate.

This study aims to explore how the sensorimotor integration in non-visual target reaching unfolds during the movement preparation and online control. The sensorimotor integration process during movement preparation was assessed through electromyography (EMG) recordings and kinematic analysis. These measures were used to dissociate two temporal components of reaction time (RT), the premotor reaction time (PRT) and motor reaction time (MRT), each characterizing a specific sensorimotor process within movement preparation. The PRT is the time from the stimulus onset to the first visible muscle activation. It corresponds to the time taken for the central nervous system to encode the sensory stimulus. The PRT is considered the central component of motor preparation (Ballanger and Boulinguez, 2009), which is the process by which the central nervous system integrates sensory inputs with motor commands. The MRT, instead, is the time from the first muscle activation to the onset of movement kinematics and corresponds to the timing of coordinating the motor response. This involves defining the muscle activation from alpha motor neurons to initiate movement and executing the actual action response (Weiss, 1965; Botwinick and Thompson, 1966; Ballanger and Boulinguez, 2009). The MRT represents the peripheral component of motor preparation (Ballanger and Boulinguez, 2009), which is related to the process coordinating the motor commands (Harris and Wolpert, 1998; Schmidt et al, 1979; Schmidt and Alan Stull, 1970). Both phases are affected by stimulus characteristics and task demands (Nikravan et al, 2021; Servant et al, 2021; Goggin and Christina, 1979; Schmidt and Alan Stull, 1970; Van Donkelaar and Franks, 1991; Botwinick and Thompson, 1966) and are independent: a change in PRT does not correspond to a change in MRT (Schmidt and Alan Stull, 1970; Botwinick and Thompson, 1966).

Thus, studying each component would enable us to define whether modulation in movement preparation under different sensory conditions is related to the sensory encoding process or an effect of sensory information on the coordination of motor commands. In this regard, it is worth noticing that previous studies in visual (Haith et al, 2016; Sutter et al, 2021; Orban De Xivry et al, 2017) or multisensory (Camponogara et al, 2024) target reaching/grasping, mainly investigated motor preparation without segregating these two components, thus limiting the understanding of which specific process (sensory or motor) is affected by the target-related sensory information during movement preparation. In light of current evidence, two distinct hypotheses can be outlined.

On one hand, electroencephalography (EEG) studies have shown a higher preparatory activity following the presentation of somatosensory compared to auditory targets (Bianco et al, 2020b). Interestingly, such brain activity is inversely correlated with RT: the shorter the RT, the higher the preparatory activity (Lucia et al, 2023; Tzagarakis et al, 2010). This suggests that the target-related sensory modality may primarily influence the encoding of upcoming sensory information, without affecting motor coordination. In this case, a modulation in PRT but not MRT is expected, which would suggest that the modality-specific action performance observed in previous studies (Camponogara, 2025) results from specific sensorimotor integration processes occurring during the sensory encoding phase of movement preparation and during online control.

On the other hand, studies have shown that non-visual sensory inputs are processed within an integrated neural system (Farnè and Làdavas, 2002) that includes the frontoparietal areas, such as the auditory cortex (Kayser et al, 2005; Caetano and Jousmäki, 2006; Zierul et al, 2017; Lohse et al, 2022), the ventral intraparietal area (Graziano et al, 1999; Graziano, 1999), and the premotor cortex (Serino, 2019), which are also involved in action preparation (for a review see Camponogara (2023)). This integrated processing suggests a shared movement preparation process across non-visual modalities, and that differences in movement variability for actions toward auditory versus proprioceptive targets reported in previous investigations (Camponogara, 2025) could mainly stem from the way sensory information is utilized during online control. In this case, a comparable PRT and MRT across modalities is expected, suggesting a similar modulation of the sensory encoding and motor coordination phase across conditions.

The online control, instead, was investigated by analyzing the variability of movement kinematics in both depth and azimuth directions at 5%, 50%, and 100% of the movement time. Given the different effect of non-visual target-related information on the endpoint variability (Camponogara, 2025), we expect a different variability across conditions at the end of the movement (100%). If such modality-specific variability arises at the early stages of action performance, just after the release of the motor commands, differences across conditions should be visible already at 5% of the movement. In contrast, if the modality-specific variability arises later in the movement, differences across conditions should emerge at the 50%, but not at 5% of the movement. In this context, a further question concerns the extent to which sensory encoding and motor coordination shape online control in non-visual target reaching, and whether their effect depends on the specific non-visual sensory modality available. Since movement preparation partially shapes online control (Churchland et al, 2006a,b; Haith et al, 2016; Sutter et al, 2021; Orban De Xivry et al, 2017), it may be that the sensorimotor integration processes occurring during the sensory encoding and motor coordination phases may modulate online control, and that this modulation may, in turn, depend on the target-related sensory modality. To shed light on this process, we regressed PRT and MRT with movement kinematics at the 5%, 50%, and 100% of the movement time. Given that PRT and MRT reflect functionally distinct processes (Schmidt and Alan Stull, 1970; Botwinick and Thompson, 1966), whether their respective effect on online movement performance are modality-dependent will ultimately depend on whether each sensory modality impacts each of these phases of

motor preparation.

Material and Method

Participants

We tested a total of thirty-nine participants (right-handed, 14 males, age 33.4 ± 12.3 years). However, eight participants were excluded from the final analysis due to the high background noise in the electromyographic data, which prevented defining the onset of muscle activation. All participants self-reported normal hearing and no known history of neurological disorders. All of the participants were naïve to the purpose of the experiment. The experiment was undertaken with the understanding and informed written consent of each participant, and the experimental procedures were approved by the Institutional Review Board of Zayed University, Abu Dhabi.

Apparatus

The custom-made experimental apparatus consisted of a perforated wooden board of 600 by 600 mm supported by four 100 mm high pedestals placed on the experimental table. Three speakers (Gikfunk, 4O 0hm 3 Watt, 40 mm diameter, 30 mm height) were placed underneath the board, powered through a USB cable, and connected with an external soundcard (Motu 4Pre) via a mini amplifier (PAM8403). The center of the speakers was placed 150 mm far at 0 (i.e., in front), 45, and 90 degrees on the left with respect to a 5 mm high rubber bump that acted as a starting point (Figure 1 A). The bump was placed 100 mm far from the side of the wooden board closest to the subject position. A 5 mm high rubber bump was placed underneath the center of each speaker and was used as a reference for the left index position during the proprioceptive and audio-proprioceptive conditions. The right-hand index finger movement and the speakers' positions were acquired on-line at 200 Hz with sub-millimeter resolution using an OptiTrack system (NaturalPoint, Inc.). The muscle activation of the Anterior Deltoid was recorded using a surface electromyography (EMG) system (four channels Wave Plus EMG system Mini, Cometa Srl). This muscle was chosen because the first muscle activating when performing an arm flexion (Latash et al, 1995). The chin position was set at 25 cm height from the wooden surface, and the chair height was adjusted at the participants' comfortable height. A pink noise of 1000 ms duration (65 db) was used as the auditory target, whereas a 100 ms duration pure tone of 500 Hz (65 dB) was used to signal the end of the trial. The same tone was used to signal the start of the trial in the proprioceptive condition. Pure tones were delivered through two external speakers (Logitech 980-000816 Z150). The motion capture, electromyography and sound delivery were controlled via Malab (Matworks).

Procedure

Participants were blindfolded for the whole duration of the experiment. All the trials started with the participant's head on the chin rest, the index digit of the right hand positioned on the start position, and the left hand on the left side of the chin rest. Two splints were used to immobilize the wrist and index finger of the reaching hand in a fixed position, allowing arm movements to occur only through shoulder and elbow rotation (van Beers et al, 2004). In an Auditory condition (A), the pink noise was delivered, and participants had to reach the point where they felt the noise coming from. In a Proprioceptive (P) and Audio-Proprioceptive (AP) condition, before each trial, participants were instructed to move the index finger of the left hand underneath the specified target speaker over the bump placed at the center of it. As soon as the finger was placed on the bump, in the P condition, the pink noise was delivered from the external speakers, whereas in AP, the pink noise was delivered from the speaker over the left finger. As soon as participants heard the pink noise, they had to reach the point where they thought the tip of their left index finger was, or both the tip of the finger and the pink noise were delivered. In all sensory conditions, after 2 seconds from the onset of the pink noise, the end tone was delivered, and participants had to return their right hand to the start position and their left hand to the side of the chin rest in the P and AP conditions. Before each experiment, participants underwent a practice phase in the A condition, consisting of 10 trials, during which they became accustomed to the task. We performed 20 trials for each target, leading to 60 trials per condition (180 trials per participant). Conditions were randomized between participants.

Data analysis

Kinematic and EMG data were analyzed in R (R Core Team, 2020). For the kinematic data, the x and y coordinates of the index and speakers' positions were smoothed and differentiated with a third-order Savitzky-Golay filter with a window size of 21 points. These filtered data were then used to compute velocities and accelerations of the Index finger in two-dimensional space. Movement onset was defined as the moment of the lowest, non-repeating Index finger acceleration value before the continuously increasing Index finger acceleration values, while the end of the movement was defined by applying the same algorithm but starting from the end of the recorded values (Camponogara and Volcic, 2021a). Trials in which the movement onset or end was not correctly detected were discarded from the analysis (310 trials, 6.2% of the total number of trials). We focused our analysis on the EMG and kinematic signals before and after the movement onset to define the sensorimotor integration process occurring during the movement preparation and online movement control phases.

Movement Preparation was assessed through PRT and MRT. To detect the onset of the muscle burst, the EMG data were first aligned with the kinematic data (Figure 1B, C), then band-pass filtered at 20-450 Hz with a second-order Butterworth filter and rectified. For each signal, the baseline muscle activity was then calculated as the mean muscle activity from the start to 300 ms following the beginning of the trial. This was subtracted

from the EMG signal (Contemori et al, 2022). We then calculated the cumulative integral of the signal using the *cumtrapz* function in R. The onset of muscle activation was calculated by considering the time the cumulative integral (Servant et al, 2021) exceeded a threshold of 0.5 (Figure 1D). The accuracy of onset detection was ensured by a trial-by-trial visual inspection of the EMG signal, which confirmed a more accurate detection of the muscle onset than the classic use of baseline and standard deviation approach in rectified low-pass EMG signals (Bertucco and Cesari, 2010; Delmas et al, 2018). This method was of particular benefit for signals with a relatively high baseline value. Trials in which the muscle background activity was too high and prevented the automatic detection of the muscle onset were discarded (501 trials, 9% of the total number of trials). We then extracted the PRT, defined as the time from the sound presentation to the onset of muscle burst, and the MRT, defined as the time from the onset of muscle burst to the movement onset.

Online Control was assessed by analyzing movement variability at the early and late stages of the movement. Kinematic signals were time-normalized and resampled in 201 points evenly spaced along the three-dimensional trajectory in the range from 0 (movement onset) to 100 (movement end) in 0.005 steps using cubic spline interpolation (Camponogara and Volcic, 2019). We then extracted the index finger position at the 5%, 50%, and at the 100% of the movement (Figure 1E, F). A preliminary analysis was performed on the peak velocity and movement time to exclude any effect of movement speed on motor preparation across sensory conditions (Van Donkelaar and Franks, 1991; Harris and Wolpert, 1998). The analysis revealed a similar peak velocity and movement time across conditions, thereby excluding the possibility that differences in movement velocity or timing could account for the different movement preparations across sensory conditions.

Statistical analysis

The PRT and MRT were modeled through a Bayesian linear mixed-effects regression model (movement preparation section). The index position in azimuth and depth at 5%, 50%, and 100% of the movement was modelled through a Bayesian distributional linear mixed-effects regression model for each movement direction (online control section). Two additional Bayesian linear mixed-effects regression model was used to detect the effect of PRT and MRT on movement control (effect of PRT and MRT on on-line control section) for each movement direction (depth and azimuth). In this case, all the considered variables (PRT, MRT, index position in azimuth and depth) were centered on their mean (Churchland et al, 2006a,b). All models were estimated using the brms package (Bürkner, 2017), which implements Bayesian multilevel models in R using the probabilistic programming language Stan (Carpenter et al, 2017). To avoid model convergence issues, we excluded from the analysis trials where PRT and MRT were lower than zero (i.e., participants anticipated the response or muscle burst occurred at the same time of movement onset). These corresponded to 93 trials in total (1.6% of the data).

Movement Preparation

We fitted a separate model for the PRT and MRT. The model included as predictors the categorical variable

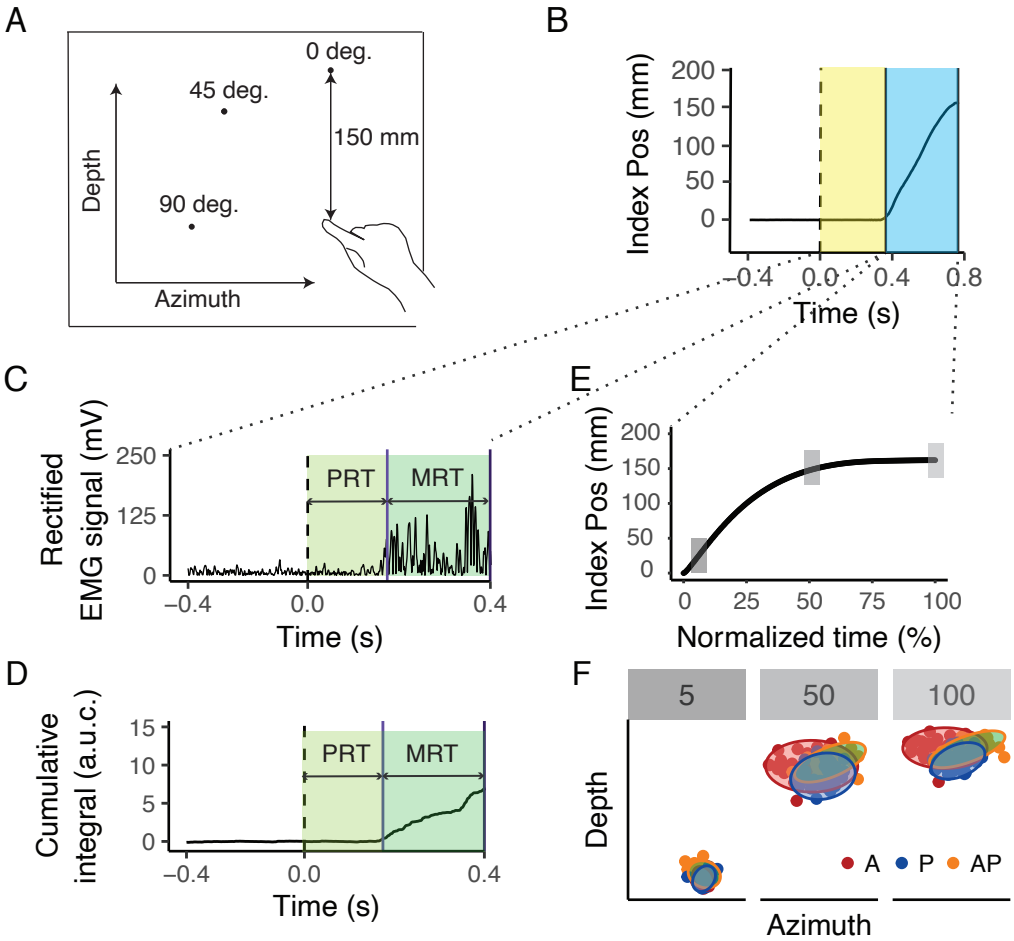

Figure 1: Experimental setup and signal analysis. A) Top view of the experimental setup. Targets were positioned at 150 mm in front (0 degrees) or laterally (45 and 90 degrees) from a start position. B) Index positional signal along the depth dimension. The yellow area represents the movement preparation phase, whereas the blue part represents the movement execution phase. The 0 in the time axis represents the time of auditory stimulus presentation (t0). C) Band-pass filtered and rectified EMG signal, and D) Integrated (cumsum function) EMG signal. The dashed black line represents the t0, whereas the light blue and dark blue lines represent the time of muscle burst and movement onset, respectively. The light and dark green areas represent the premotor reaction time (PRT) and motor reaction time (MRT). E) Time-normalized index position along the depth dimension. The shaded grey areas represent the 5%, 50% and 100% time-normalized points at which movement variability was assessed. F) Index finger positions (dots) in azimuth and depth and their 95% confidence ellipses standard deviation of a representative participant. Each panel represents the finger position at the 5%, 50%, and 100% of the movement.

Condition (A, P, and AP) and the continuous variable Position (0,45, and 90 degrees). Thus, the model estimated the average PRT or MRT and its change as a function of the target position (slope). The model included the independent random (group-level) effects for subjects. We used a shifted log-normal distribution for the estimation of the variables. The model was fitted considering weakly informative prior distributions for each parameter to provide information about their plausible scale. We used normally distributed priors for the Condition and Position fixed-effect predictor ($\beta_{Condition}$: mean = 5 and sd = 4; RT, PRT and MRT $\beta_{Position}$: mean = 0 and sd = 1), whereas for the group-level standard deviation parameters we used zero-centered Student

t-distribution priors, with scale values defined by the "get_prior" function. ($df = 3$, scale = 2.5). Finally, we set a prior over the correlation and residual correlation matrix that assumes that smaller correlations are slightly more likely than larger ones (LKJ prior set to 2). Using a shifted log-normal distribution, the model returned a log-transformed posterior distribution of intercepts and slope. Thus, the intercept was back-transformed to the original scale by exponentiation, whereas the slope was expressed as a percentage change of PRT and MRT for each change in degree of target position (Greenwood, 2022).

Online Control

The two distributional regression models (one for the depth and one for the azimuth directions) allowed us to estimate the posterior distribution of the index position and SD (sigma) in both depth and azimuth directions, taking into account both within and between-subject variability. The models included as a dependent variable the index position in azimuth and depth, and as predictors the categorical variable Condition for each movement phase. Thus, the models estimated the average position in the depth and azimuth directions, and the average SD in the depth and azimuth directions for each movement phase (5%, 50%, and 100%). The models included the independent random (group-level) effects for subjects. The model was fitted considering weakly informative prior distributions for each parameter to provide information about their plausible scale. We used a gaussian distribution priors for the Condition fixed-effect predictors ($\beta_{Condition_5}$ in depth: mean = 200 and sd = 25, otherwise mean = 400 and sd = 25, $\sigma_{Condition_5}$ in azimuth and depth: mean = 2.5 and sd = 1, $\sigma_{Condition_50}$ and $\sigma_{Condition_100}$ in azimuth: mean = 3 and sd = 1; $\sigma_{Condition_50}$ and $\sigma_{Condition_100}$ in depth: mean = 4 and sd = 1). In contrast, for the group-level standard deviation parameters, we used zero-centered Student t-distribution priors, with scale values defined by the "get_prior" function. (azimuth = $df = 3$, scale = 17.9, depth = $df = 3$, scale = 93.7). Finally, we set a prior over the correlation and residual correlation matrix that assumes that smaller correlations are slightly more likely than larger ones (LKJ prior set to 2).

Effect of PRT and MRT on Online Control

Two models, one for the depth and one for the azimuth direction, were fitted to detect the effect of the PRT and MRT on online control. The models included as dependent variables the mean-centered index position in depth and azimuth directions, and as predictors the categorical variable Condition for each movement phase and the continuous variable mean-centered PRT and MRT. Thus, the posterior distribution of the models' slopes reflected the change of the index position in azimuth and depth direction according to a modulation of PRT and MRT of one ms in each Condition. The model included the independent random (group-level) effects for subjects. The model was fitted considering weakly informative prior distributions for each parameter to provide information about their plausible scale. We used Gaussian priors for the Condition, PRT, MRT predictors ($\beta_{Condition}$: mean = 0 and sd = 5, $\beta_{Condition:PRT}$ and $\beta_{Condition:MRT}$: mean = 0 and sd = 1), whereas for the group-level standard deviation parameters, we used zero-centered Student t-distribution priors, with scale values defined by the "get_prior" function. ($df = 3$, scale = 2.5). Finally, we set a prior over the correlation

and residual correlation matrix that assumes that smaller correlations are slightly more likely than larger ones (LKJ prior set to 2).

For all the models, we ran four Markov chains simultaneously, each for 6,000 iterations (1,000 warm-up samples to tune the MCMC sampler) with the delta parameter set to 0.99 for a total of 20,000 post-warm-up samples. Chain convergence was assessed using the $\hat{R}$ statistic (all values equal to 1) and visual inspection of the chain traces. Additionally, the predictive precision of the fitted models was estimated with leave-one-out cross-validation by using the Pareto Smoothed Importance Sampling (PSIS). All the Pareto k values of all the models were lower than 0.7, except for the model of online control in the depth direction, which showed 4 Pareto k values higher than 0.7. This model was refit using the reloo function in brms Bürkner (2017). After the model re-fit, all the Pareto k values were lower than 0.7, and the posterior distributions were summarised.

Statistical Inference

The posterior distributions represent the probabilities of the parameters conditional on the priors, model, and data, and they represent our belief that the "true" parameter lies within some interval with a given probability. We summarize these posterior distributions by computing the medians and the 95% Highest Density Intervals (HDI). The 95% HDI specifies the interval that includes, with a 95% probability, the true value of a specific parameter. To evaluate the differences between the two compared conditions, we have subtracted the posterior distributions between specific conditions. The resulting distributions are denoted as the credible difference distributions and are again summarized by computing the medians and the 95% HDIs. For statistical inferences, we assessed the overlap of the 95% HDI with zero. A 95% HDI of the credible difference distribution that is not included within the zero region is taken as evidence that the two conditions differ from each other for that specific variable. For the sake of clarity, from now on, we will refer to the SD results as variability.

Results

Movement Preparation

Results showed that reaching an auditory target requires a longer PRT (Figure 2A, B, C), than the proprioceptive or audio-proprioceptive target (A-P = 70.8 ms, HDI = 44.4 ms, 99.9 ms; A-AP = 81.6 ms, HDI = 57.6 ms, 116.9 ms; P-AP = 10.8 ms, HDI = -5.7 ms, 26.4 ms). The analysis revealed a slightly higher MRT in A compared to P and AP conditions (A-P = 13 ms, HDI = 0.2 ms, 26.7 ms; A-AP = 12 ms, HDI = 0.15 ms, 25.8 ms; P-AP = -0.3 ms, HDI = -7.5 ms, 6.6 ms) of sensory condition on MRT (Figure 2 D, E, F). However, the lower boundary of HDI differences was very close to zero (∼0.1 ms), which prevents drawing strong conclusions regarding differences between non-visual conditions. The back-transformed posterior slope estimates showed a positive but very small effect of the target position on PRT (A = 0.01%, HDI = 0.0%, 0.04%; P = 0.02%, HDI = 0.0%, 0.06%; AP = 0.03%, HDI = 0.0%, 0.09%) and MRT (A = 0.07%, HDI = 0.0 %, 0.16%; P = 0.06%, HDI

= 0.01%, 0.13%; AP = 0.07%, HDI = 0.01%, 0.16%), which correspond to a change of approximately ∼2 ms in PRT and ∼6 ms in MRT from the front (0 degrees) to the most leftward target position (90 degrees). These results indicate that, within movement preparation, sensory-related target information influences the timing of sensory encoding, rather than the coordination of motor commands.

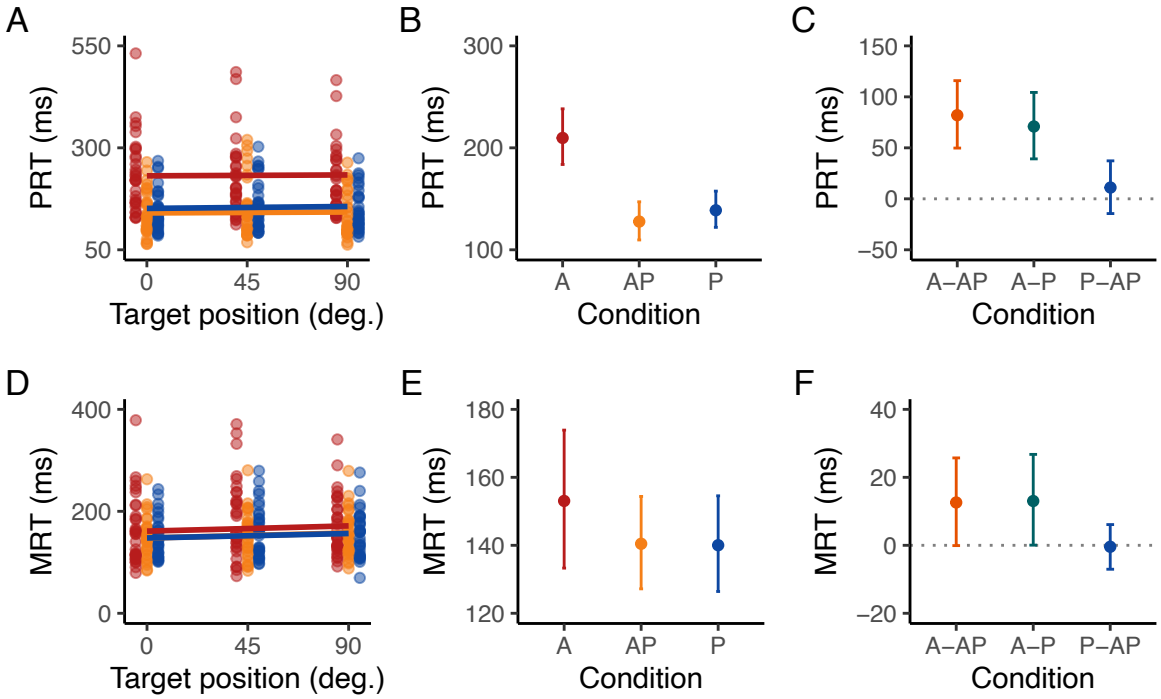

Figure 2: Bayesian model regression estimates. Solid lines show the Bayesian mixed-effects model fits. Each dot represents the average PRT (A) and MRT (D) of a single participant for each condition and target position. B, E) Estimates of the PRT and MRT. The dots represent the model's posterior estimates, and the error bars denote the 95% HDI of the estimates. C, F) Estimates of the differences in PRT and MRT between conditions. The dots represent the estimated difference, and the error bars denote the 95% HDI of the estimates. The grey dotted line represents the points of equality between the compared conditions.

On-line control

The analysis revealed a different standard deviation (SD) pattern between conditions across the three movement phases (Figure 3A). Movement SD was similar across conditions at 5% (SD depth = $\sim$ 13 mm, HDI = $\sim$ 11 mm, $\sim$ 14 mm; SD azimuth = $\sim$ 6 mm, HDI = $\sim$ 5 mm, $\sim$ 8 mm in all conditions) whereas it was higher in A compared to P and AP at 50% (A-P SD depth = 15.9 mm, HDI = 10.6 mm, 21.6 mm; SD azimuth = 18.8 mm, HDI = 14.3 mm, 23.5 mm; A-AP SD depth = 14.7 mm, HDI = 9.2 mm, 20.5 mm SD azimuth = 16.6 mm, HDI = 11.8 mm, 21.6 mm) and at the end of the movement (A-P SD depth = 18.2 mm, HDI = 12.7 mm, 24.4 mm; SD azimuth = 22.2 mm, HDI = 17.3 mm, 27.4 mm; A-AP SD depth = 16.1 mm, HDI = 10.5 mm, 22.2 mm SD azimuth = 20.2 mm, HDI = 15.0 mm, 25.8 mm), with P being similar to AP (Figure 3 B, central and rightmost panels). Additionally, movement SD at 5% was lower in both depth and azimuth direction compared to 50% and 100% (Figure 3C), which showed a similar SD. Taken together, besides confirming a higher variability for actions towards auditory compared to proprioceptive and audio-proprioceptive targets (Camponogara, 2025), the results suggest a different impact of sensory inputs along the movement. Movements are similar between conditions when at the early stage (5%), whereas they differentiated between conditions at 50% of the movement trajectory. Moreover, movements are less variable in the early compared to the late stages.

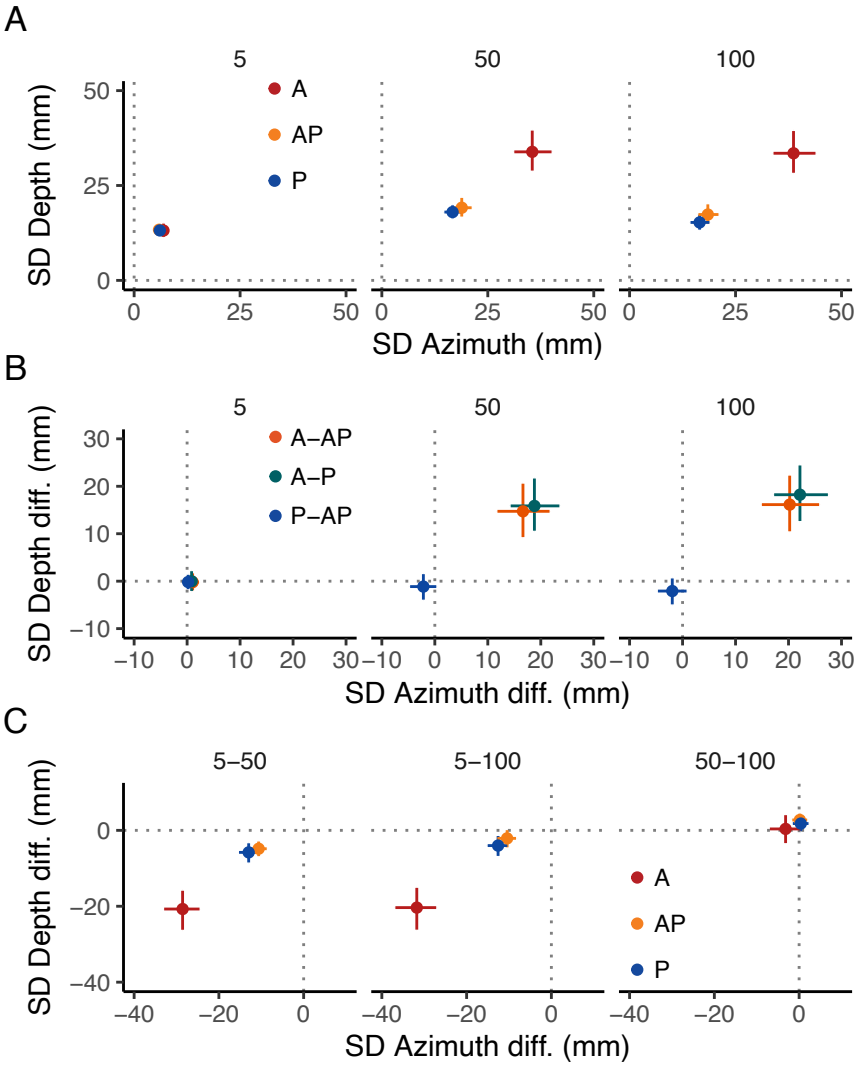

Figure 3: Movement SD A) Estimates of the SD in the azimuth and depth for each movement phase (5%, 50% and 100%). The dots represent the mean, and the error bars denote the 95% HDI of the estimates. B) Estimates of the differences in SD in the azimuth and depth between conditions for each movement phase. The dots represent the mean difference, and the error bars denote the 95% HDI of the differences. C) Estimates of the differences in SD in the azimuth and depth between movement phases for each condition. The dots represent the mean difference, and the error bars denote the 95% HDI of the differences. In panels B and C, the grey dotted line represents the points of equal variability in the depth and azimuth directions.

Effect of Movement Preparation on Online Control

Results showed no effect of PRT on movement, regardless of the movement phase (Figure 4A). Interestingly, MRT affected early online movement execution along the depth direction (Figure 4B), but the magnitude of such modulation was similar across conditions (A depth = 0.095 mm/ms, HDI = 0.06 mm/ms, 0.12 mm/ms; P depth = 0.12 mm/ms, HDI = 0.096 mm/ms, 0.15 mm/ms; AP depth = 0.13 mm/ms, HDI = 0.10 mm/ms, 0.15 mm/ms). This suggests that the initial movement toward the target along the depth dimension is mainly modulated by the timing of motor coordination. As the movement unfolds, movement control is mainly affected by online information, which is used to adjust the movement and guide the final action performance.

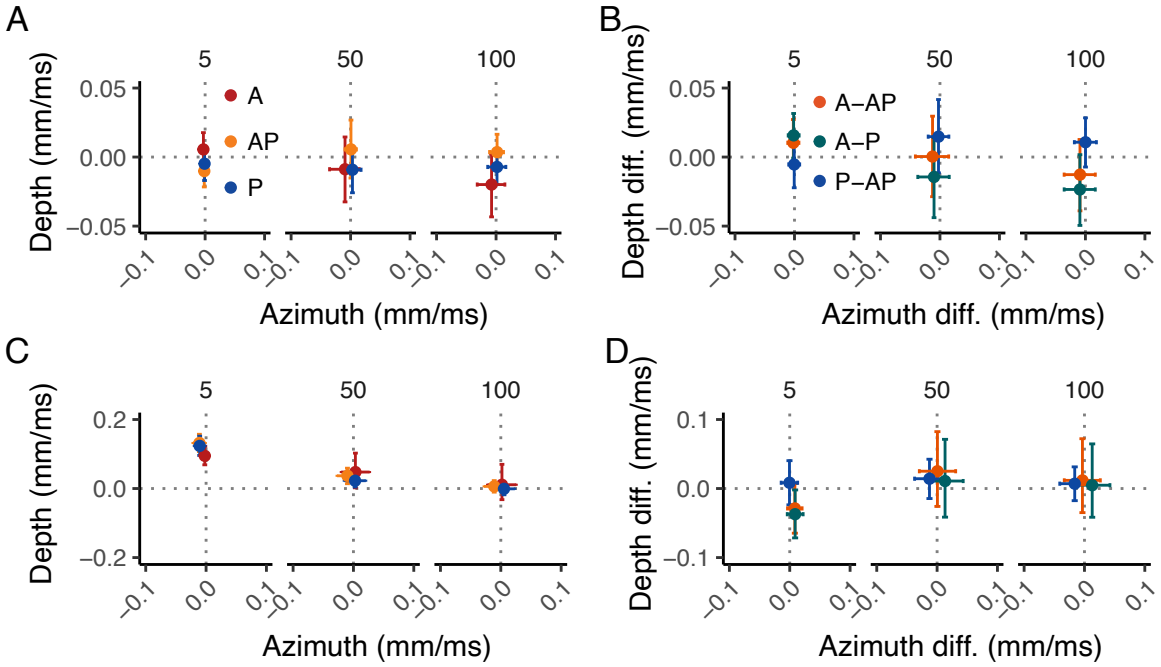

Figure 4: A, C) Effect of PRT (A) and MRT (C) on online control for each movement phase (5%, 50%, and 100%) in azimuth and depth. The dots represent the mean, and the error bars denote the 95% HDI of the estimates. B, D) Estimates of the differences between conditions of the effect of PRT (B) and MRT (D) on movement performance in azimuth and depth between each movement phase. The dots represent the mean, and the error bars denote the 95% HDI of the differences. In panels A and C, the grey dashed line represents the points of null effect (i.e., flat slope), whereas in panels B and D, the points of equal slope values in the depth and azimuth directions.

Discussion

This study aimed to investigate the sensorimotor integration process of non-visual target-related sensory information within the movement preparation and online control phases of a reaching movement. To this aim, we asked participants to reach auditory, proprioceptive, and audio-proprioceptive targets, while recording their movement kinematics and muscle activation through EMG. Movement kinematics were used to investigate online control (movement variability) at 5%, 50%, and 100% of the movement time, whereas EMG was used to investigate two main components of movement preparation: the PRT, indexing of the sensory encoding, and MRT, indexing the pattern of motor coordination during movement preparation. Results showed a modulation of the sensory encoding phase according to the available sensory information, with longer PRT in the auditory than in proprioceptive and audio-proprioceptive conditions, which were similar. In contrast, the motor coordination phase was almost unaffected by the target-related sensory information. This corroborates previous EEG studies showing different preparatory activity when presenting non-visual targets before action performance (Bianco et al, 2020a), and extends these findings by showing an effect of target-related sensory information on the central but not peripheral component of movement preparation. Moreover, it suggests that integrating target-related sensory information within motor commands primarily occurs during the sensory encoding phase. In contrast, the motor coordination phase is primarily involved in shaping the kinematic parameters

of the forthcoming movement (Harris and Wolpert, 1998). Additionally, the results demonstrated a pivotal role of target-related proprioceptive information in movement preparation during multisensory target reaching, underscoring the relevant role of proprioception in defining target positional information (Camponogara and Volcic, 2021b, 2022) even before movement onset.

The analysis of movement variability at 5%, 50%, and 100% of the reach duration confirmed an effect of sensory information on online control, but only at its late stages (50% and 100% of the movement). Confirming our previous study's results (Camponogara, 2025), movement variability was higher in the auditory compared to proprioceptive and audio-proprioceptive conditions, and similar between proprioceptive and audio-proprioceptive conditions. Movement variability was lower at 5% compared to 50% and 100% of the movement, which were similar to each other. These results suggest that initial movement control is insensitive to the target-related sensory information. To further understand this process, we examined the relationship between movement preparation (sensory encoding and motor coordination) and online control. We found no effect of the sensory encoding phase on online control at any point during execution. However, motor coordination affected online control at the 5% of the movement time, regardless of the sensory condition. This confirms that initial action performance is mainly affected by the coordination of motor commands of the reaching limb, rather than the target-related sensory information (Harris and Wolpert, 1998; Churchland et al, 2006a,b; Sutter et al, 2021; Churchland and Shenoy, 2024). In contrast, as the action unfolds, online control becomes modality-dependent.

The insensitivity to available sensory information during motor coordination and at 5% of movement time, and the modality-specific sensory encoding and mid-movement online control of the action, aligns with prior research investigating the time course of sensory processing during movement. In these studies, tactile stimuli are applied while participants perform a reaching movement. Typically, tactile sensitivity is diminished during these actions, a phenomenon known as tactile suppression (Voudouris and Fiehler, 2017; Gertz et al, 2018; Klever et al, 2019; Voudouris et al, 2019; Voudouris and Fiehler, 2021). Notably, tactile suppression is strongest (i.e., tactile stimuli are perceived less) before the movement onset (Voudouris and Fiehler, 2017; Gertz et al, 2018; Klever et al, 2019; Voudouris et al, 2019; Voudouris and Fiehler, 2021; Colino et al, 2017; Colino and Binsted, 2016), and in early movement execution (Kilteni and Ehrsson, 2022; Cemeljic et al, 2025; Colino et al, 2017; Colino and Binsted, 2016) with a specific modulation within the movement preparation stage: tactile suppression is weaker (i.e., tactile stimuli are perceived more) approximately 200 ms before movement onset than at 100 ms prior (Colino et al, 2017; Colino and Binsted, 2016). This temporal pattern closely aligns with the time window of the PRT and MRT observed in our study. Our results are also further corroborated by previous studies examining the time dynamics of EEG beta-band activity (the brain's signature of movement preparation) before and after the movement onset (Jasper and Penfield, 1949). These studies have shown that beta-band activity modulates according to target uncertainty during the target presentation phase (i.e., the sensory encoding phase), whereas it is similar across target uncertainties slightly before and after the response's onset (i.e., the movement coordination phase and early online control) (Tzagarakis et al, 2010).

The observed sensorimotor temporal dynamics are also in line with Woodworth's classic two-stage model of movement control in visual target reaching (Woodworth, 1899). This model posits an initial impulse phase, corresponding to early movement execution and reflecting motor preparation processes, followed by a limb-target control phase, during which online sensory information is used to refine and guide the movement (for review, see Elliott et al (2010)). Our results extend these findings in the non-visual domain by demonstrating that the initial impulse phase (i.e., early online control) is less sensitive to non-visual target-related sensory input compared to the limb-target control phase (i.e., late online control), which, instead, modulates according to the target-related sensory information. Thus, sensory input is crucial at the early stages of movement preparation for encoding forthcoming sensory information, and again during mid-movement for fine-tuning motor control. In contrast, the phases immediately preceding movement initiation (motor coordination phase) and immediately after it (early online control) mainly depend on the planned motor commands, making them less sensitive to the upcoming sensory information. Additionally, the results suggest a functional independence between the sensory encoding phase and online action control, with motor coordination mediating the transition between these two phases.

Taken together, our results suggest that reaching performance toward non-visual targets is governed by four distinct phases (Figure 5). The first involves the sensory encoding, which is influenced by the available target-related sensory modalities. The second phase corresponds to the motor coordination, which is insensitive to further incoming target-related sensory information and triggers the initiation of movement. A third phase marks the transition from the movement preparation to early online control. This phase is independent from the available target-related sensory information, but is shaped by the preceding motor coordination phase. Notably, the effect of motor coordination (second phase) on the early online control (third phase) is consistent across different non-visual sensory modalities. This suggests that sensory inputs play a limited role during the shift from motor preparation to the initial control of movement, and that such transition primarily depends on the motor commands governing the reaching limb. Lastly, the fourth phase is characterized by a shift from early to late online control, during which available sensory information is integrated to refine and adjust the movement trajectory. Interestingly, action variability stabilizes by the midpoint of the movement duration, indicating that, in non-visual target reaching, most fine-tuned adjustments occur around halfway through the action.

These findings provide further support for the sensorimotor integration framework proposed by Camponogara (2023). It is well established that, during movement preparation, sensory estimates of the future state of the reaching hand are integrated into the motor plan to generate predictive representations of the forthcoming movement. During online control, these predictions are refined through the integration of incoming sensory inputs (Diedrichsen et al, 2010). According to the model proposed by Camponogara (2023), motor preparation involves the integration of proprioceptive (or haptic) estimates of the reaching hand with the available target-related sensory information (Friston et al, 2011; Sandbrink et al, 2023; Camponogara, 2023, 2025). At the

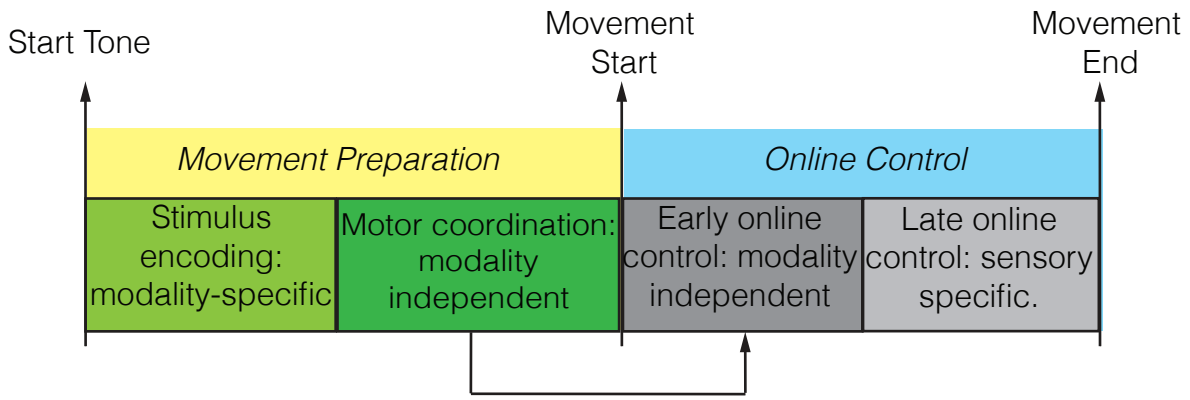

Figure 5: Representation of the four phases of movement control. Target-related sensory information is mostly relevant during the stimulus encoding phase of movement preparation and late online control. In contrast, it is less relevant during the motor coordination phase of movement preparation and the early online control. Motor coordination affects movement variability at the early stage of movement. This effect is modality-independent.

movement onset, the release of motor commands is primarily guided by proprioceptive (or haptic) estimations of the future state of the reaching hand. As movement unfolds, these predictions are continuously updated with real-time sensory information from both the reaching hand and the target (Camponogara, 2023). Our results further suggest that, within movement preparation, particularly during sensory encoding, proprioceptive information from the reaching hand and target-related sensory information are integrated with motor commands. This sensory information may be accumulated over time during the sensory encoding phase to define when transitioning to the motor coordination phase and subsequently initiate movement (Servant et al, 2021; Dendauw et al, 2024). The phase immediately preceding movement onset, along with the early phase of online control, is predominantly governed by motor coordination mechanisms that are relatively insensitive to target-related sensory information (Harris and Wolpert, 1998). As it progresses, movement is dynamically adjusted through the integration of upcoming sensory information from the reaching hand (proprioception) and the target, enabling fine-tuned control of the action.

In conclusion, our results indicate a modulation of the sensory encoding, but not the motor coordination phase during movement preparation for actions directed toward non-visual targets. Moreover, target-related sensory information appears to be primarily integrated during the later stages of movement execution. Notably, the sensory encoding did not influence movement variability at any point during the action, whereas motor coordination modulated the movement variability at 5% of the movement duration; this effect was modality-independent. These findings suggest that, in auditory and proprioceptive target reaching, target-related sensory inputs are primarily involved in determining the timing of action initiation and in refining control during later phases of movement. In contrast, sensory information plays a limited role during motor command coordination and in the early stages of action execution.

CRediT author statement

Ivan Camponogara: Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Data Curation, Writing - Original Draft, Writing - Review and Editing, Visualization, Supervision, Funding acquisition.

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Additional information

Competing interests The authors declare no competing interests.

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