Neural mechanisms of serial dependence in time perception: The impact of prior task and memory processing

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Author note

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Abstract

Our perception and decision-making are susceptible to prior context, as seen in serial dependence where our judgment of stimulus magnitude is biased toward what we experienced in previous trials. While serial bias in the spatial domain has been extensively studied, less is known about it for time perception. Furthermore, it is still debatable whether serial dependence arises during perceptual or post-perceptual stages. To investigate this, we conducted functional magnetic resonance imaging (fMRI) on twenty-one participants performing a timing task, which involved two phases - duration encoding and duration reproduction. Participants had to remember the duration of the green coherent motion and wait for a cue to reproduce the perceived duration. The cue could be either "Response" or "No-response". For the "No-response" cue, participants should only passively view the display. We observed that the reproduction error was positively correlated with the prior duration only when the preceding task was also active reproduction. In contrast, encoding the prior duration without reproduction was insufficient to induce serial dependence. Neurally, we observed activated timing-related networks, such as striato-thalamo-cortical circuits, and performance monitoring networks when the trial sequence implicitly predicted a "Response" trial. Importantly, the hippocampus showed sensitivity to sequential bias and its activation was negatively correlated with the individual's sequential bias following active reproduction trials, indicating that the recycling of prior information in working memory mingles with the present that leads to serial dependence. These findings highlight the crucial role of memory networks in time-related sequential biases at the post-perceptual stage.

Keywords: Serial dependence; Time perception; fMRI; Striato-thalamo-cortical networks; Hippocampus; Working memory

Significance Statement

This study explores the neural mechanisms measured by fMRI underlying time perception and the factors that can influence our time judgments across trials. Our findings reveal that active reproduction of time duration in the previous trial can bias subsequent estimates, resulting in a serial dependence effect. In contrast, passive viewing of a stimulus without reproducing its duration does not produce this effect. At the neural level, we observed increased activity in memory regions like the hippocampus when sequential biases were reduced. Furthermore, we found a negative correlation between hippocampal activation and sequential bias following active reproduction trials. Our findings suggest that the involvement of memory networks mediates how we are influenced by past experiences when judging time.

Introduction

Our experience can influence our perception and decision-making as the past and present often correlate in a relatively short period. Research has shown that our current perception is biased by recent events, referred to as serial dependence (Fischer and Whitney 2014; Cicchini, Mikellidou, and Burr 2018; Glasauer and Shi 2022). The effect has been studied in the context of non-temporal features, such as orientation, color, and motion direction, particularly with a recent paradigm highlighting the influences of the difference between the current and previous stimuli on response biases (Cicchini, Mikellidou, and Burr 2017; Barbosa and Compte 2020; Bae and Luck 2020; Fischer and Whitney 2014). However, less is known about how the subjective duration interacts with the recent past.

There is ongoing debate regarding the underlying mechanisms of serial dependence. Two main perspectives have emerged. The first view proposes that serial dependence is thought to maintain perceptual stability and continuity by integrating past and current information to filter out abrupt noises, serving as a perceptual mechanism (Liberman, Zhang, and Whitney 2016; Whitney, Manassi, and Murai 2022). The second view connects serial dependence to prior task and response-related post-perceptual factors (Fritsche, Mostert, and de Lange 2017; Ceylan, Herzog, and Pascucci 2021; Pascucci et al. 2019; Bae and Luck 2020). For instance, serial dependence is only observed when the current and previous tasks are the same orientation judgments (Bae and Luck 2020), indicating that encoding the previous stimulus was not sufficient but the task-related response in previous trials was essential for serial dependence to occur.

In this latter view, working memory also plays a crucial role in serial dependence, as it involves integrating preceding stimuli with current sensory inputs for decision-making and motor plans (Kiyonaga et al. 2017; Bliss, Sun, and D'Esposito 2017; Bae and Luck 2019; Fornaciai and Park 2020b). Studies have shown serial dependence increases when the memory retention interval increases (Bliss, Sun, and D'Esposito 2017), and decreases when the short-term memory maintenance in the premotor cortex is interrupted with TMS (de Azevedo Neto and Bartels 2021). A recent fMRI

study showed that neural activity in low-level V1 is opposite to behavioral serial dependence, which suggests that the effect emerges in high-level memory or decision-making circuits (Sheehan and Serences 2022). A recent EEG study observed past information (i.e., pitch, category choice, motor response) keep their respective features in memory and are only reactivated by the corresponding features in the current trial, shifting current neural encoding and giving rise to serial biases (Zhang and Luo 2023).

Despite the well-established behavioral traits of serial dependence, more physiological evidence is imperative to clarify the underlying mechanism of serial dependence. A persistent concern that endures is that the current body of research on serial dependence has primarily focused on non-temporal spatial features with a circular scale distribution (e.g., orientation). However, there has been limited investigation into serial dependence in time perception. Previous research demonstrated that time perception is susceptible to various factors, including attention, memory, and temporal context (Holland and Lockhead 1968; Treisman and Williams 1984; Wittmann and Paulus 2009; Shi, Church, and Meck 2013a). For instance, the subjective duration can be biased toward recent history (Nakajima et al. 1992; Burr, Banks, and Morrone 2009; Jazayeri and Shadlen 2010), leading to an underestimation of long durations and an overestimation of short durations, known as central tendency effect. There is only a few studies examining trial-by-trial updating of internal models or priors (serial dependence effect) on timing (e.g., Dyjas, Bausenhart, and Ulrich 2012; Glasauer and Shi 2022), and no neural signature has been linked to it, which leaves an unresolved gap in our understanding.

In this study, drawing on a classic post-cueing paradigm used in serial dependence research (Czoschke et al. 2019; Bae and Luck 2020), we aimed to explore the neural mechanisms underlying serial dependence in time perception using a duration reproduction task (Shi, Ganzenmüller, and Müller 2013; Zang et al. 2022; Shi et al. 2022) with MRI scanning. The task consisted of the encoding phase and the reproduction or passive-viewing phase, with the latter being contingent upon the Response / No-response cue (see Figure 1a). During the encoding phase, participants had to remember the duration of a stimulus, and either reproduce it or passively watch it, based on a post-cue. “Response” and “No-response” trials were randomly intermixed, and participants had to perceive and remember durations on each trial to perform the task accurately. This made it possible to compare

how passive viewing and active reproduction in the previous trial biased the processing of the next stimulus despite the same encoding processing, shedding light on the role of the post-perceptual factor in serial dependence. As time intervals are an open scale, we focused on how the previous stimuli bias current judgments (i.e., serial dependence). To distinguish serial dependence from the central tendency bias (Jazayeri and Shadlen 2010; Shi, Church, and Meck 2013b), we estimated relative errors by measuring the deviation from the mean reproduction for each individual duration and correlated it with the preceding duration.

Our results demonstrate that serial dependence was significant only when the preceding task involved active reproduction, not passive viewing. Using the general linear model (GLM) with fMRI data, we found that striato-thalamo-cortical and performance monitoring networks that were related to prior tasks and time perception. Additionally, we used the normalized response errors as parametric regressor to explore potential brain regions implementing serial dependence. Parametric modulation is a measure of the correlation between neural activity and the normalized response error, which is a way to identify brain regions that have different activity depending on a particular variable (Penny et al. 2011; Mumford 2015). A positive parametric value indicates that brain regions associated with a specific trial type have increased activity when participants have a high response error. On the other hand, a negative parametric value indicates that those regions have a negative correlation between neural activity and the response error, meaning that, the more the subject is biased, the less active those regions are. We observed the hippocampus was directly linked to the serial bias on both prior task and prior duration and its activation during the encoding of durations following passive viewing trials, which led to a reduction of sequential bias. We then further investigated the relationship between hippocampus BOLD activities and the serial dependence effect, revealing a negative correlation between them across participants for trials with preceding active reproduction. These findings highlight the involvement of post-perceptual stages that link sensory representations and responses underlying serial dependence in time perception and underscore the critical role of active timing and memory networks in protecting against sequential biases, indicating the involvement of short-term memory traces from the previous trial on sequential biases.

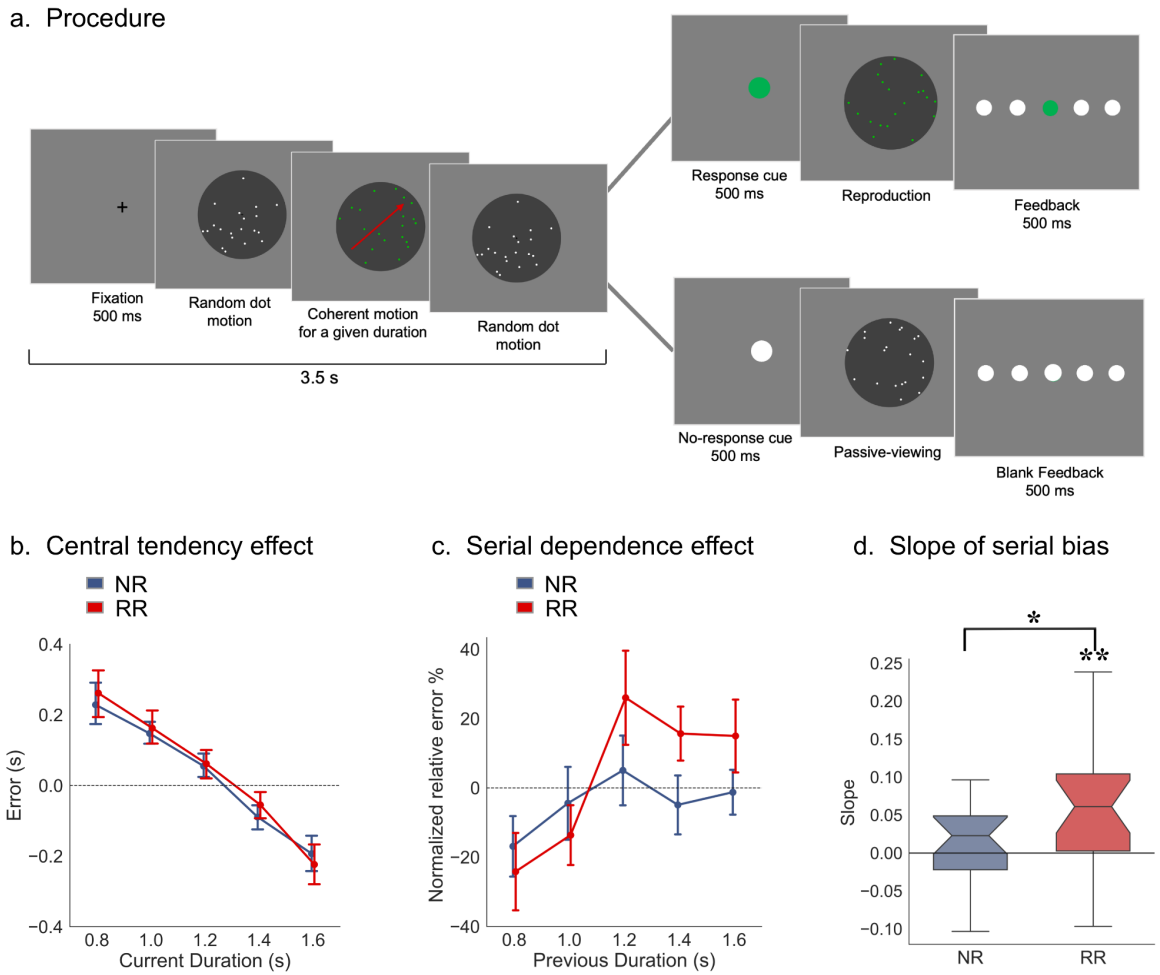

Figure 1 (**a**) Experimental procedure. Each trial consisted of two phases: the duration encoding phase and the duration reproduction or passive-viewing phase, with the latter being contingent upon the Response / No-response cue. The trial started with a fixation, followed by the display of white random dot motion, which then changed to green dots moving coherently in one direction (e.g., in the direction of the red arrow in the illustration, not shown in the actual experiment) for a given duration before reverting back to white random dot motion. The entire presentation of the dots display lasted for 3000 ms. Participants were instructed to remember the duration of the green coherent motion. A cue, either a green ("Response" trial) or white ("No-response" trial) disk, was then shown on the screen, indicating the beginning of the second phase. In the "Response" trials, the green random dot motion appeared, and participants had to press a button when they thought the duration was the same

as the perceived duration in the encoding phase. During "No-response" trials, participants only passively viewed the white random dot motion for the same duration as the coherent movement of the green dots in the encoding phase and were not required to respond. In the end, there was a feedback display featuring five horizontal white disks, with one disk changing color to indicate the accuracy of the reproduction for the “Response” trials. (**b**) The central tendency effect. The reproduction errors (i.e., reproduced duration - actual duration) are shown as a function of the actual duration, separated for the inter-trial type: No-response/Response (NR) and Response/Response (RR) trials. Error bars represent ± SEM. (**c**) The serial dependence effect. The normalized relative errors are plotted on the durations from previous trials, separated for NR and RR conditions. Error bars represent ± SEM. (**d**) Notched boxplots of the serial dependence slope for NR and RR conditions. The box plot depicts the serial dependence effect, measured by the slope, for each condition. The top and bottom of the notched box represent the interquartile range (between 25% and 75%), and the notch in the box is the 95% confidence interval for the median; whiskers exclude outliers. *p <.05,**p <.01.

Results

Behavioral results

The reproduction biases were calculated for the “Response” trials. Overall, reproduced durations were close to the probe durations, resulting in a mean reproduction bias of 35 ms. We excluded trials with large reproduction errors and the outliers were generally rare, on average only 0.89%, ranging individually from 0 to 5 outlier trials. The remaining “Response” trials were categorized into two types depending on the preceding task: (a) “Response” to “Response” (RR) trials that were preceded by a reproduction task, and (b) “No-response” to “Response” (NR) trials that were preceded by a passive viewing task. Given that duration reproduction is affected by both the central tendency effect and the sequential dependence (Glasauer and Shi 2022), we estimated the central tendency and serial dependence effects separately.

The central tendency effect.

We applied a linear regression of the reproduction errors on the current durations (D_n) to obtain the slope (w), and used $1 - w$ as the central tendency index, with 0 indicating no central tendency and 1 strong central tendency (Shi, Church, and Meck 2013b; Cicchini et al. 2012). The results, shown in Figure 1b, indicate a strong central tendency effect - participants overestimated short durations and underestimated long durations. The central tendency effect was quantified through linear regression, revealing significant central tendency biases with mean slopes of -0.540 ($t_{(20)}$ = -9.14, p <.001, d = 1.99) and -0.594 ($t_{(20)}$ = -9.13, p <.001, d = 1.99) for the NR and RR respectively. But the central tendency biases were comparable between the two conditions ($t_{(20)}$ = 1.745, p = .096, BF_{10} = 0.826). Additionally, there was a minor positive general bias ($M \pm SE$: 35 ± 14 ms, $t_{(20)}$ = 2.45, p = .024, BF_{10} = 2.49), which was comparable between the two conditions ($t_{(20)}$ = -1.3, p = .21, BF_{10} = 0.48). That is, the central tendency and the general bias were not influenced by the prior trial task. The lack of a significant difference in the central tendency effect between preceding task types might be primarily due to the same distribution and range of the tested durations for two prior tasks, yielding a consistent long-term representation of the prior durations across tasks. This agrees with previous findings that randomly mixing durations leads to a generalization of the prior across conditions (Roach et al. 2017).

The serial dependence effect.

To distinguish serial dependence from the central tendency bias, the normalized relative error $RE_{i,k}$ was used to analyze serial dependence (see details in Methods). Then, we applied a linear regression with the normalized relative error to the previous sample duration (D_{n-1}), and took the slope of the linear fit as the sequential bias index (e.g., Glasauer and Shi 2022; Cicchini, Anobile, and Burr 2014; Cicchini, Mikellidou, and Burr 2018). Our results, presented in Figure 1c, show that the normalized relative error increases with the preceding duration, suggesting the sequential bias can be approximated by a linear relation. Thus, to characterize the serial dependence effect, we employed a linear mixed model with Prior Task and Prior Duration as the fixed effects and Subject as the random factor. Our analysis revealed that the normalized relative error was significantly correlated with the preceding duration (slope b = 0.055, 95% CI = [0.024, 0.085], p < .001) for the RR condition. That is,

the sequential bias increased 5.5% with each one-second increase in the preceding duration. However, the linear trend for the NR condition failed to reach significance (slope b = 0.016, 95% *CI* = [-0.014, 0.047], p = .298). The main effect of the Prior Task was not significant (b = 0.008, 95% *CI* = [-0.02, 0.004], p = .191), as relative errors were symmetric around the mean of the preceding duration for both NR and RR conditions (Figure 1c). To determine whether the active reproduction, relative to the passive viewing, in the preceding trial increased the serial dependence on the current reproduction, we compared the slopes of the RR condition to the NR condition, which revealed the slope was significantly larger in the RR condition ($t_{(20)}$ = 2.229, p = .037, BF_{10} = 1.716, see Figure 1d). These results suggest that active reproduction in the preceding trial increased the serial dependence on the current reproduction, whereas passive viewing did not.

To avoid statistical artifacts (Cicchini, Anobile, and Burr 2014), we also tested the serial dependence effect on the durations presented in future trials (n+1), which showed no significance (*ps* > .216). Our behavioral results provide clear evidence that merely passively perceiving an interval is not sufficient to bias subsequent duration estimates.

fMRI Results

Whole-brain analysis

The main analysis was focused here on the effect of prior tasks on the current duration reproduction (i.e., RR and NR). We grouped the preceding durations into two categories: the "Short" (include durations of 0.8 and 1.0 s) and the "Long" categories (include durations of 1.4 and 1.6 s). Therefore, a combination of the factors of the Prior Task (RR or NR) and the Prior Duration (Short or Long) resulted in four conditions, each represented by a separate main canonical hemodynamic response function (HRF) regressor. We further used the normalized relative error $RE_{i,k}$ as an additional parametric regressor for each of the four main regressors to reflect the true modulation of serial bias. The results from the main HRF regressors reflect different brain activations between conditions, while the findings of the parametric regressors reflect the covariate changes of brain activities to the normalized relative errors in duration reproduction. In the following subsections, we

report the results separately for the main HRF regressors and parametric regressors. Once the regions of interest (ROIs) were identified, we proceeded with a comprehensive analysis where all durations were taken into account.

Table 1. Activations associated with the main HRF regressors defined by the two factors Prior Task and Prior Duration

Contrast	Region label	MNI coordinates			Cluster size	T value
Prior Task						
RR > NR	R inferior frontal gyrus	45,	41,	2	109	5.42
NR > RR	R Posterior medial frontal	6,	-1,	53	8003	6.34
	R Thalamus	9,	-22,	5		6.09
	L Precentral gyrus	-30,	-16,	50		7.46
	L Postcentral gyrus	-51,	-19,	53		6.72
	L Precuneus	-9,	-61,	14	259	3.64
Prior Duration						
Long > Short	R Caudate Nucleus	18,	-22,	26	122	4.42
Prior Task* x *Prior Duration	n.s.					

Note: Activations were significant at $p < .001$, with FWE cluster correction at $p < .05$, and n.s. denotes non-significant. R Posterior medial frontal, R Thalamus, L Precentral gyrus, and L Postcentral gyrus were in the same cluster.

Table 2. Activations associated with the parametric regressors defined by the two factors Prior Task and Prior Duration

Contrast	Region label	MNI coordinates			Cluster size	T value
PriorTask	n.s.					
Prior Duration						
Long > Short	L Middle frontal gyrus	-21,	38,	32	124	4.46
Prior Task* x *Prior Duration						
Long (NR > RR)	L Hippocampus	-36	-37,	-7	139	4.09
	R Hippocampus	39,	-31,	-7	305	5.01

Notes: Activations were significant at $p < .001$, with FWE cluster correction at $p < .05$, and n.s. denotes non-significant.

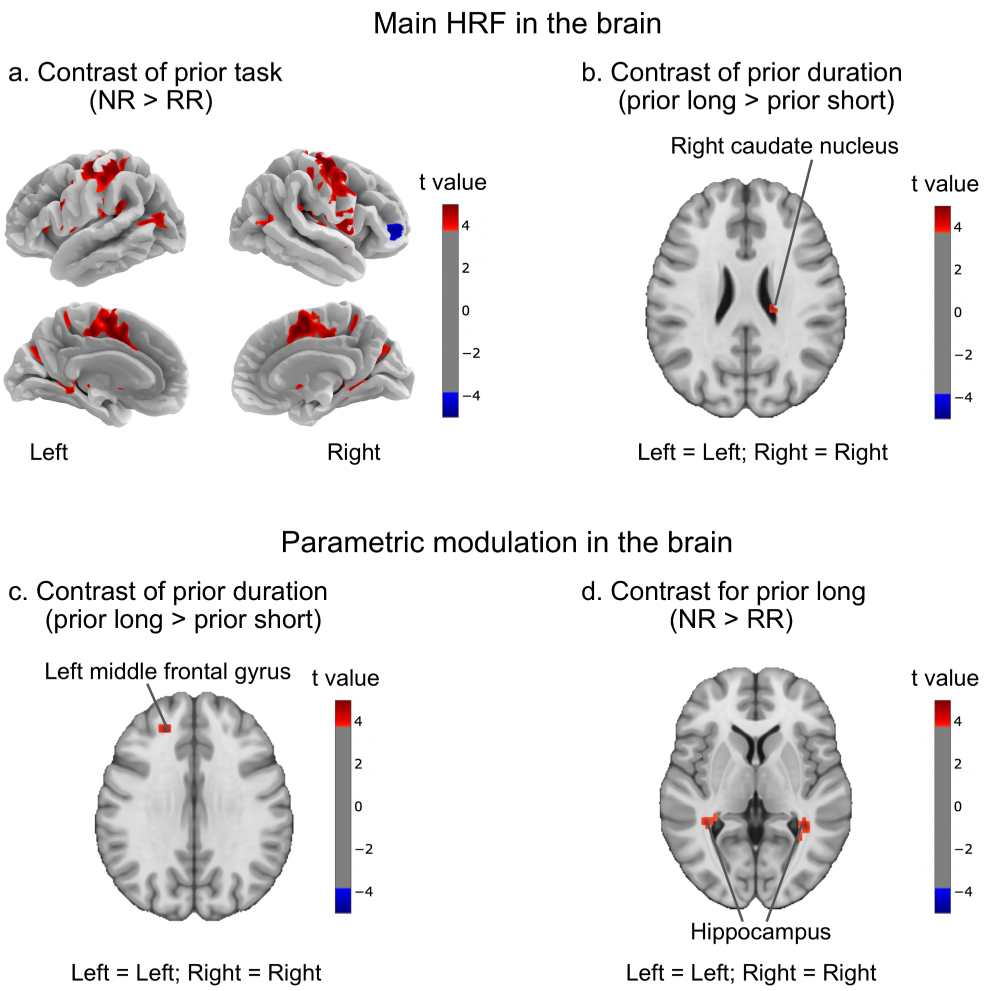

Figure 2. Whole-brain activation results. (**a**) and (**b**) are brain regions activated in the main HRF. (**a**) Whole-brain activation patterns colored in red-blue reflected invoked BOLD signals driven mainly by the prior task. The red-marked regions (the left precentral gyrus, the left postcentral gyrus, the left precuneus, and the right posterior-medial frontal, the right thalamus) were activated more for the preceding No-response (NR) task as compared to the preceding Response task (RR), while the blue-marked region (right inferior frontal gyrus) were activated more for the RR than the NR condition. (**b**) Whole-brain activation patterns colored in red-blue reflected invoked BOLD signals that were driven by the prior duration. The red-marked region (right caudate nucleus) was activated more for the long duration as compared to the short duration. (**c**) and (**d**) are brain regions that show sensitivity to normalized relative error in different conditions. (**c**) Main effect of prior duration for the parametric estimates with the normalized error. The red-marked region (left middle frontal gyrus, MNI coordinates: -21, 38, 32) was activated more with a larger normalized relative error for the

preceding long duration than the short duration. (**d**) The normalized error-dependent differences between prior tasks (NR vs. RR) in the prior long-duration condition were expressed in the hippocampus (MNI coordinates: -36, -37, -7; MNI coordinates: 39, -31, -7). All thresholding was done at $p < .05$ with FWE-corrected at the clustered level. Neurological convention was used (Left = Left and Right = Right).

Main HRF regressors

We conducted contrast analyses using 2 (RR vs. NR) × 2 (Short vs. Long) within-subject ANOVAs. Table 1 and Figure 2a and 2b show the significant regions identified through this contrast analysis. The results show that the right inferior frontal gyrus (RIFG), a region associated with response inhibition (Aron et al. 2007; Hampshire et al. 2010), exhibited greater activation during RR trials compared to NR trials. Conversely, the left precuneus and a large cluster comprising the left precentral gyrus and left postcentral gyrus and the right posterior-medial frontal and the right thalamus were more active during NR trials compared to RR trials.

The RIFG is a critical region for response inhibition and detecting important cues (Aron et al. 2007; Hampshire et al. 2010). The activation of the RIFG for the contrast RR vs. NR is likely due to an Response trial (R) can be followed by Response or No-response trials which require response inhibition. In contrast, for the contrast NR vs. RR, we observed high activation in cognitive control and performance monitoring networks, including the right posterior-medial frontal cortex (Debener et al. 2005) and the left precentral gyrus and left postcentral gyrus, as well as the left precuneus (Ridderinkhof et al. 2004; Fitzgerald et al. 2010). Increased activation in the posterior-medial frontal cortex (Ridderinkhof et al. 2004; Fitzgerald et al. 2010) is believed to be engaged in the cognitive control and performance monitoring that leads to response selection and performance adjustments on subsequent trials (Debener et al. 2005), while the precentral gyrus is the site of the primary motor cortex and the postcentral gyrus which constitutes the primary somatosensory cortex also takes part in motor control of the body (Hari et al. 1998; Dijkerman and de Haan 2007). This was likely due to the activation of the primary motor cortex for those “Response” trials while not for the ‘No-response’

trials. The thalamus plays a key role in the cortico-thalamic-basal ganglia timing circuits (Yin et al. 2022; Mole et al. 2018).

The contrast analysis conducted between the prior short and long durations revealed that the right caudate nucleus, the main component of the dorsal striatum, was more activated when the prior trial was long than short (see Table 1 and Figure 2b). The activity in the dorsal striatum (including the caudate nucleus) is closely related to the representation of temporal information in working memory (White 2009; Teki and Griffiths 2016; Yin et al. 2022; Merchant, Harrington, and Meck 2013). In the current study, preceding long vs. short durations might impact the working memory trace in the following trial, consistent with previous event-related fMRI studies on working memory and time interval demonstrating that activity in the caudate nucleus increased with an increasing number of intervals in the sequence (Teki and Griffiths 2016; Rao, Mayer, and Harrington 2001; Coull and Nobre 2008).

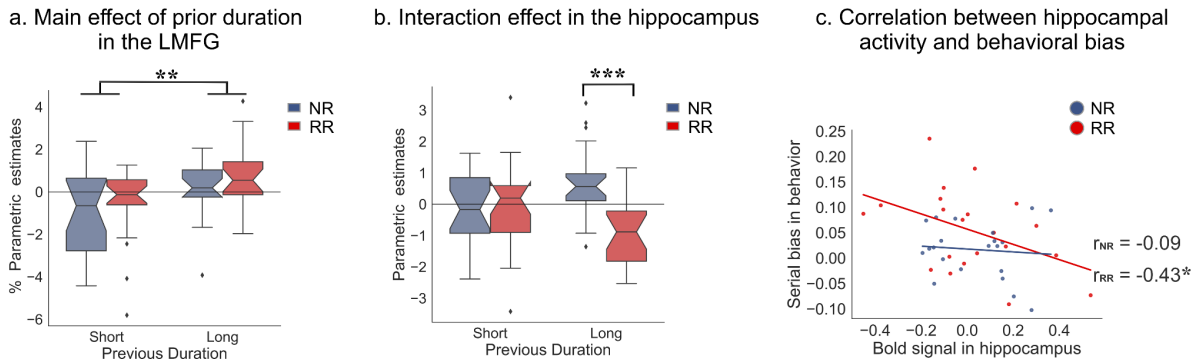

Figure 3. (**a**) Notched boxplots for the mean parameter estimates (β) from the left middle frontal gyrus (LMFG) for the parametric regressor for the prior tasks (NR: No-response; RR: Response), separated for the category of the previous duration (Short vs. Long). The top and bottom of the notched box represent the interquartile range (between 25% and 75%), and the notch in the box is the 95% confidence interval for the median; whiskers exclude outliers. (**b**) Notched boxplots for the mean parameter estimates (β) from the hippocampus for the parametric regressor. (**c**) Correlations between the mean BOLD signal in the bilateral hippocampus (MNI coordinates: -36, -37, -7, including 139 voxels; MNI coordinates: 39, -31, -7, including 305 voxels) and the behavioral bias (slopes of the

linear regression with the normalized errors to the previous sample duration) across participants, separated for the RR and NR conditions. The correlation was significantly negative for the RR condition (r_{RR}= -.43, p < .05), but not for the NR (r_{NG} = -.09). The least-square fit lines are shown. *p <.05, ***p< .001.

Parametric regressors

By using the normalized error, $(R_{i,k} - \bar{R}_k)/\bar{R}_k$, as a parametric regressor to exclude the central tendency and general biases, modulation of the parametric regressors would truly indicate how the sequential bias covaries with BOLD activation. The parametric value of the regressor reflects the strength and linear relationship between brain activity and the normalized error. Given that BOLD activations were analyzed during the encoding phase, while sequential biases were obtained during the late reproduction phase, a positive value indicates that increased brain activity leads to an increase in sequential bias, whereas a negative value suggests that increased brain activity results in a negative change in sequential bias. The contrast results can show which brain regions during the encoding stage are correlated with changes in sequential biases. Table 2 and Figure 2c and 2d show the contrasted results of the parametric regressors according to the 2 (Prior Task: Response vs. No-response) × 2 (Prior Duration: Short vs. Long) factorial analysis.

As seen in Table 2 and Figure 2c, the left middle frontal gyrus (LMFG; MNI coordinates: -21, 38, 32, including 124 voxels) was more positively correlated with the normalized error when the duration of the preceding trial was long vs. short. Figure 3a depicts the parametric values extracted from the left middle frontal gyrus. On average, the parametric value was positive (0.412) when the preceding duration was long, but negative (-0.691) when the preceding duration was short. This suggests that influences of the left middle frontal gyrus activation on normalized error depend on the preceding duration. Specifically, higher activation of the left middle frontal gyrus led to a positive relative error when the preceding duration was long, but a negative relative error when the preceding trial was short. Recall the right caudate nucleus was found to activate more strongly in response to a long preceding duration compared to a short one, and the right caudate nucleus is functionally

connected to the left middle frontal gyrus (Robinson et al. 2012), which is associated with working memory encoding (Dandolo and Schwabe 2019; Nee et al. 2013). Given this association, it is possible that these two regions work together to regulate inter-trial dependence in duration judgments.

Additionally, the analysis revealed a significant Prior Duration × Prior Task interaction in the left and right hippocampus (left MNI coordinates: -36, -40, -7, including 16 voxels; right MNI coordinates: 39, -31, -7, including 25 voxels; with small-volume correction at $p < .05$ FWE corrected). Further analyses revealed the most significant contrast results from the left and right hippocampus between RR and NR conditions when the preceding trial was long, which showed a difference between RR and NR was sensitive to the normalized bias (see Figure 3d, MNI coordinates: -36, -37, -7, including 139 voxels; MNI coordinates: 39, -31, -7, including 305 voxels, Figure 2d). As shown in Figure 3b, on average the parametric values were comparable between NR and RR when the preceding duration was short, but exhibited opposite signs for the preceding long durations. In trials preceded by a long/No-response task, the more active the hippocampus, the higher the normalized errors. Conversely, in trials preceded by a long/Response task the less active the hippocampus, the higher the normalized errors.

We then further conducted a correlation analysis to examine the relationship between the serial dependence effect (using the slope of sequential bias) and the BOLD signal in the hippocampus. The analysis revealed a negative correlation ($r = -.43$, $p = .049$, two-tailed; Figure 3c) for RR trials (for both short and long duration), suggesting more activation in the hippocampus leads to less serial dependence for RR trials. However, there was no correlation for NR trials ($r = -.09$, $p = .69$, two-tailed; Figure 3c), partly because the activation in the hippocampus was generally higher for NR than RR trials (Figure 4a).

ROI analysis on the hippocampus

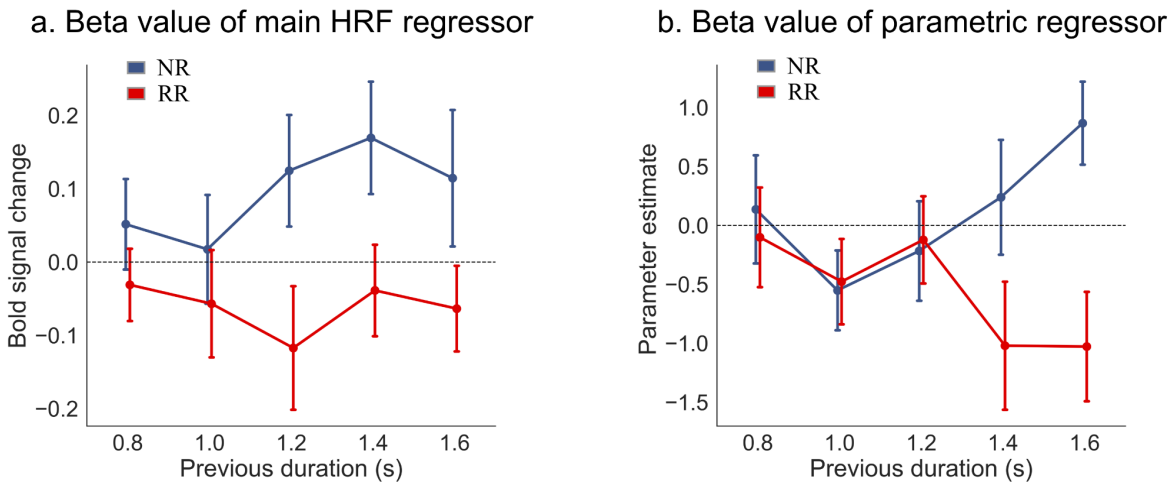

Figure 4. (**a**) BOLD signal change estimated from the hippocampus, plotted as a function of previous duration, separated for the previous task (NR: No-response, RR: Response). (**b**) Mean beta value of the parametric regressor extracted from the bilateral hippocampus (MNI coordinates: -36, -37, -7, including 139 voxels; MNI coordinates: 39, -31, -7, including 305 voxels) plotted as a function of previous durations, separated for the previous task (NR: No-response, RR: Response).

Note that in the whole brain analysis, we observed a large significant activated cluster (consisting of 8003 voxels) in the contrast NR > RR analysis (see Table 1), which included 0.7% (56 voxels) of this cluster that belonged to the hippocampus. To more closely examine the neural activation patterns in the bilateral hippocampus in the cluster we obtained in our ROI analysis (MNI coordinates: -36, -37, -7, including 139 voxels; MNI coordinates: 39, -31, -7, including 305 voxels), we applied a separate GLM on BOLD signals to model the previous tasks (RR vs. NR) with each of the five previous durations (0.8, 1.0, 1.2, 1.4, and 1.6 s) for the individual subject, and extracted the β values from the main and parametric regressors. The β values of the main HRF regressors are shown in Figure 5a. Across all previous durations, the activations were generally higher for NR than for RR trials. Further linear mixed model on the β values with the fixed factors of Prior Duration and Prior Task and participants as a random factor revealed a significant difference between prior tasks (b = 0.16, 95% CI [0.08, 0.233], $p < .001$), but not among prior durations and the interaction between Prior

Task and Prior Duration (all *p*s > .239). On average, trials with preceding passive viewing, compared to trials with preceding active reproduction, had 16% more activations in the hippocampus.

Figure 4b shows that the parametric value decreases with an increase in the previous duration for the RR condition, but increases for the NR condition. A linear mixed model on the parametric values with fixed factors of Prior Duration and Prior Task revealed a significant main effect of Prior Task (b = 0.64, 95% *CI* [0.12, 1.17], p = .016), and a significant interaction between Prior Task and Prior Duration (b = 2.32, 95% *CI* [0.48, 4.17], p = .014). The interaction was due to opposite linear trends observed between the parametric values and the previous duration for the NR and RR conditions: a positive trend for the NR (b = 1.13, 95% CI [-0.18, 2.43], p = .091), but a negative trend for the RR (b = -1.20, 95% CI [-2.50, 0.11], p = .072). Although the individual trends (the slopes of 1.13 vs. -1.20) were marginally significant from zero, the difference between the two (b = 2.32) was significant, particularly for the previous long durations (Figure 4b). Interestingly, for the RR condition, the negative trend of the parametric value with the previous long duration was opposite to the significant positive trend of the serial dependence effect (Figure 1c). This implies that decreased brain activity in the hippocampus was associated with a high normalized error, possibly due to the recycling of prior information in working memory, which results in strong serial dependence (Whitney, Manassi, and Murai 2022; Sheehan and Serences 2022).

Discussion

This study investigated neural mechanisms that underlie serial dependence in time perception. We conducted a duration reproduction task with a post-cue to manipulate between active reproduction and passive viewing of durations, aiming to determine where the serial dependence originates. We found a strong central tendency effect in duration reproduction, regardless of the preceding task. However, the normalized reproduced error, measured relative to the mean reproduction of individual durations, depended on the preceding task and duration, showing a positive serial dependence effect only for trials with consecutive reproduction (RR), but not for trials preceded by passive viewing (NR).

Our study seeks to expand upon previous research, which has primarily focused on serial dependence in non-temporal domains (Fischer and Whitney 2014; e.g., Holland and Lockhead 1968). Previous studies have shown that serial dependence requires active retrieval of a recent past (Bae and Luck 2020; Fornaciai and Park 2020a; Ranieri et al. 2022). For instance, a study on motion direction judgment (Bae & Luck, 2020) revealed that serial dependence was only present when the preceding task was identical, as opposed to being different, such as judging the color of the motion stimuli. Our study extends this research by demonstrating that in the temporal domain, simply encoding the previous stimulus was not enough to produce a sequential effect. Instead, serial dependence required the involvement of decisional templates that link sensory representation and responses. Thus, the serial dependence in time perception likely stems from high-level, post-perceptual decisional processes (Ceylan, Herzog, and Pascucci 2021; Bae and Luck 2020; Kiyonaga et al. 2017; Pascucci et al. 2019; Fritsche, Mostert, and de Lange 2017).

At the neuronal level, BOLD signals at the duration encoding phase were enhanced for NR trials relative to RR trials in a cognitive control and response preparation network (Ridderinkhof et al. 2004; Fitzgerald et al. 2010; Dijkerman and de Haan 2007) comprising the right posterior-medial frontal, the left postcentral gyrus, and the left Precueus. Additionally, the right thalamus, a critical component of cortico-thalamic-basal ganglia timing circuits (Yin et al. 2022; Mole et al. 2018), was activated. These differential activations were likely attributed to the passive viewing vs. active reproduction in the previous trial. Following a passive viewing with no response demands, the response preparation network and the cortico-thalamic-basal ganglia timing circuits were more effectively primed for the next upcoming trial. In contrast, the right inferior frontal gyrus (RIFG), a crucial region for response inhibition and detection of important cues (Aron et al. 2007; Hampshire et al. 2010; Hartwigsen et al. 2019), was more active for RR trials than for NR trials. This is because following an active reproduction trial, the next trial could be either Response or No-response trials, which can only be resolved when the post cue appears.

The contrast between the prior long and short durations revealed greater activation in the right caudate nucleus for the prior long duration. The caudate nucleus, a key part of the dorsal striatum, plays a critical role in the striato-thalamo-cortical network (Teki and Griffiths 2016; Rao, Mayer, and

Harrington 2001; Coull and Nobre 2008). Serving as a 'core timer' of the timing system (Meck, Penney, and Pouthas 2008), the caudate nucleus holds temporal 'memories' in its GABAergic medium spiny neurons (MSNs) via dopamine-facilitated long-term potentiation and short-term plasticity mechanisms (Allman and Meck 2012; Kononowicz 2015). Adjustments to corticostriatal synaptic weights by MSNs in the dorsal striatum could tune them to specific time intervals encoded by coincident oscillatory patterns, increasing the likelihood of them firing upon similar intervals in the future (Kononowicz, van Rijn, and Meck 2016; Yin et al. 2022). The observed serial dependence in the present study likely reflects these residual temporal 'memories' left in the MSNs of the caudate nucleus from the previous trial.

Using parametric modulation analysis on the brain activity, which could reflect how the sequential bias covaries with BOLD activations, we found that the left middle frontal gyrus showed greater sensitivity to sequential bias when the prior duration was long compared to short, echoing the activation in the right caudate nucleus for the prior duration contrast. The left middle frontal gyrus is widely recognized to contribute to working memory encoding (Dandolo and Schwabe 2019; Nee et al. 2013) through the fronto-striatal pathway (Teki and Griffiths 2016; Darki and Klingberg 2015). This was evidenced by previous research showing that activity in the caudate nucleus and the frontal cortex systematically increased with an increasing number of intervals in the sequence (Teki and Griffiths 2016; Rao, Mayer, and Harrington 2001; Coull and Nobre 2008), indicating the fronto-striatal pathways underlying time perception (Matell, Meck, and Lustig 2005). Our findings thus suggest that the strong modulation of sequential bias in the left frontal gyrus may be due to the high involvement of working memory encoding and fronto-striatal timing circuits in processing prior long durations.

Furthermore, we observed the hippocampus is sensitive to serial bias when the prior duration was long and the prior task is reproduction. Together with the preparation network that includes the precuneus, the hippocampus was more active for NR trials than for RR trials. Previous research has indicated that the precuneus receives connections from the hippocampal system and is involved in working memory (Ren et al. 2018; Hebscher, Levine, and Gilboa 2018). The increased activation of the response preparation network and hippocampus during NR trials may reflect the process that the previously encoded duration (in the No-response trial) was task-irrelevant, so it needs to be

overwritten with the task-relevant duration in the following Response trial. It may indicate a more efficient encoding of the duration and retention in working memory in the NR trials, preventing inter-trial memory interference and reducing any bias from the past. This could explain why the behavioral results showed less sequential bias in NR trials than in RR trials. In contrast, given the lower activation of the hippocampus during RR trials, the sequential bias was more likely to be influenced by fluctuations in BOLD signals from the hippocampus, with a higher sequential bias for a lower BOLD signal. It is worth noting that we observed a negative correlation between BOLD signals and the strength of sequential biases across participants, but only for RR trials. This correlation was absent for NR trials (Figure 3c). The attenuation in the hippocampus found in the RR condition might be linked to recycling the prior trial information in working memory, which causes serial dependence (Whitney, Manassi, and Murai 2022; Sheehan and Serences 2022). This reduction in neural signal associated with the bias may reflect an optimal allocation of cognition resources to process successive stimuli (Chanales et al. 2017; Hsieh et al. 2014).

The hippocampus and the dorsal striatum collaborate to process temporal expectations based on past experience (van de Ven et al. 2020). Our study indicates that when the hippocampus is actively engaged, sensory encoding of the current duration information held in working memory is effectively protected, resulting in less sequential bias. Other studies have also concurred with the idea that serial dependence is driven by the reactivation of the memory trace during conducting the same task, rather than simply the memory trace itself (Fornaciai and Park 2020a; Ranieri et al. 2022). For example, a recent study using TMS to disrupt the left dorsal premotor cortex, a region critical to short-term memory, during intertrial intervals showed a significant reduction of serial dependence for motion speed judgments (de Azevedo Neto and Bartels 2021), indicating that memory mixing during maintenance is the primary source of serial dependence. An EEG study used an auditory pitch categorization task and adopted the response-cue (High or Low) to dissociate category choice and motor response, it found past information (i.e., pitch, category choice, motor response) keep their respective features in memory and are only reactivated by the corresponding features in the current trial, shifting current neural encoding and giving rise to serial biases (Zhang and Luo 2023). Moreover, a recent fMRI study found a sequential assimilation effect in behavior during a delayed

orientation discrimination task, but repulsive BOLD signals in the early sensory cortex (Sheehan and Serences 2022), suggesting sequential assimilation arises in either memory or decision-making circuits rather than early sensory areas. Similarly, here we observed a negative modulation in the hippocampus by prior reproduction on current encoding, as well as a negative correlation between hippocampus BOLD signals and sequential bias in behavior, further confirming the crucial role of memory in the inter-trial sequential bias.

Importantly, our study indicates that serial dependence in temporal perception requires the involvement of decision templates that link sensory representation and responses. In addition, the parametric modulation model that links measured neural activities to behavioral bias provide neural signatures, such as the hippocampus linking to the bias tuning properties of serial dependence in time perception. The primary exploration is an important step for linking behavior and physiology in serial dependence research of non-spatial domains. While our findings highlight the critical role of memory networks in serial dependence, this does not preclude the involvement of the sensory cortex. Previous literature has shown that serial dependence emerges early in the perceptual processing, and occurred in the visual cortex when exposed to visual stimuli (St. John-Saaltink et al. 2016; Fornaciai and Park 2020a), as well as the premotor cortex during visuomotor integration (de Azevedo Neto and Bartels 2021). Convergent evidence shows that serial dependence could emerge at different stages. However, our study using the post-cue paradigm suggested that the sequential effect in the time domain relies heavily on late decision stages that engage working memory, partly because duration perception requires less perceptual stability. Future work could go further into detail and investigate possible connectivity between cortico-thalamic-basal ganglia timing circuits and memory-related networks underlying serial dependence in time perception.

In summary, our study revealed that serial dependence in duration reproduction is contingent on the task of the preceding trial. Memory and striato-thalamo-cortical networks were actively engaged during reproduction trials preceded by passive viewing, resulting in the absence of sequential bias. In contrast, the hippocampus was less active during trials with consecutive reproduction, leading to prominent sequential biases, which negatively correlated with hippocampal activation across individuals. These findings highlight that serial dependence in temporal perception requires the

involvement of the post-perceptual stage that links sensory representations and responses, and the hippocampus plays a key role in this process.

Materials and Methods

Participants

21 participants (9 females; 12 males; age: *Mean* ± *SD* = 27.24 ± 3.83, range: 23–33 years) were recruited for the two-session MRI experiment[1]. All of them were right-handed and had normal or corrected-to-normal vision and color vision, no history of neurological, psychiatric, or medical disorders, and no symptoms of COVID-19 in the past two weeks. The sample size was determined based on previous studies (Bae and Luck 2020; Fischer and Whitney 2014) that usually found large effect sizes (Cohen's d > 0.753), and with a power of 80% ($1 - \beta$), which yielded a minimum of 19 participants according to G*Power (Erdfelder, Faul, and Buchner 1996). Participants provided their informed consent prior to the experiment and were compensated for their participation for 15 Euro/hour. The study was approved by the ethics committees of the Psychology Department at LMU Munich.

Experimental design and procedure

We adopted a duration reproduction paradigm (Shi, Ganzenmüller, and Müller 2013; Zang et al. 2022; Shi et al. 2022), consisting of an encoding phase and a reproduction phase (see Figure 1). Participants laid down comfortably with their head in the head coil, inside some cushions to fixate the head position and avoid motion. Participants viewed the back projector canvas (diagonal 30 inches) via an adjustable mirror positioned on top of the head coil, with a viewing distance of 110 cm. The task was presented by an MRI-compatible ProPIXX DLP LED projector (Pixx Technologies Inc, Canada).

[1] During scanning, six participants had large head movements (more than 3 mm of displacement measured by 2nd-degree B-spline interpolation or 3° of rotation in any direction) or distortion in the T1 image. We then replaced with six new participants.

Each trial began with a black cross (visual angle of 0.5°) at the center of the display on a light gray background for 500 ms, prompting participants to maintain their fixation on the center. Following this, a tunnel view display (subtended 17.8° visual angle) of white randomly moving dots (20 dots with each diameter of 0.4°, moving at a speed of 1 °/s) appeared for a randomly selected duration between 400 to 600 ms. The white dots then changed to green and moved 100% coherently with a speed of 6°/s in one direction selected between 0 to 360° for a given duration, chosen from 0.8, 1.0, 1.2, 1.4, and 1.6 secs. Immediately after the given duration, the color of the dots changed back to white and moved randomly again at a speed of 1 °/s. When a dot exited the tunnel view, it was regenerated at a random location within the view to maintain dot density. The entire presentation of the tunnel view lasted for 3000 ms. Participants were instructed to remember the duration of the green coherent motion.

Following the encoding phase, a cue was presented in the center for 500 ms that indicates whether participants should perform a reproduction task ("Response") or not ("No-response"). The cue was a color disk (subtended 1.2° visual angle), which could be either green (indicating a Response trial: reproducing the duration) or white (indicating a No-response trial: doing nothing, only passive viewing). For Response trials, immediately following the offset of the cue display, a green random dot motion in a tunnel view (20 green dots with each of 0.4° at a speed of 1°/s) appeared in the center of the screen. Participants had to monitor the elapsed time and press an MRI-compatible ResponsePixx button (Pixx Technologies Inc, Canada) with their right thumb when they perceived the elapsed time as being the same as the duration of coherent movement in the encoding phase. Following the response, a feedback display appeared indicating the response accuracy with a color dot in a horizontal dot array. Each highlighted dot from the left to right five dots corresponded to a range of relative reproduction errors (error/duration): The left most represented below -30%, while the second to fifth dot indicated errors between [-30%, -5%], (-5%, 5%), [5%, 30%], or greater than 30%, respectively. The middle dot was highlighted in green to indicate an accurate reproduction, while the 2nd and 4th dots were highlighted in light red, the utmost 1st and 5th dots in dark red, with the color intensity reflecting the degree of error. The feedback lasted for 500 ms. For the No-response trial, the cue display was followed by a white random dot motion in a tunnel view (20 white dots with each

diameter of 0.4°, moving at a speed of 1°/s), lasting the same amount of time as the coherent movement of the green dots in the encoding phase, and participants didn't need to respond and just passively watched the display. Afterward, a blank feedback display appeared for 500 ms to equate the time with the feedback display in the Response trial. The next trial started after a random interval of 2000 to 3000 ms.

Since we were interested in the impact of the preceding task on the present reproduction, and to ensure equal transitional probability from a No-response to Response trial and from a Response to Response trial while minimizing the number of trials required for MRI scanning (within one hour), we excluded the possibility of a No-response to No-response trial. This yielded a 2:1 ratio of the Response vs. No-response trials while maintaining equal transitional probability (see a similar approach Czoschke et al. 2019).

Prior to the formal scanning, participants received a practice block of 30 trials to familiarize themselves with the task in a sound-reduced and moderately lit chamber, near the scanning room. In the formal MRI study, each participant completed 12 blocks, with each block of 30 trials, among them 20 Response trials and 10 No-response trials. After each block, there was a short 6-second break, and after 6 blocks (comprising a session) a long 7-minute break. During this long break, participants took a rest inside the scanner, and a T1 image was acquired. The whole experiment lasted approximately 60 minutes.

MRI data acquisition and preprocessing

All MRI data were acquired using a 3-Tesla Siemens Prisma MRI scanner (Siemens, Erlangen, Germany), equipped with a 32-channel head coil. Functional MRI images were obtained using a blood oxygenation level-dependent (BOLD) contrast-sensitive gradient-echo EPI sequence. A total of 3000 to 3300 volumes of fMRI data, depending on the duration of the experiment, were acquired for each participant through two sessions. The following parameters were used: TR = 1000 ms, multi-band factor = 4, TE = 30 ms, flip angle = 45◦, FOV = 210 × 210 mm, voxels size = 3 × 3 × 3 mm, slices number = 48, slice thickness = 3 mm. In addition, structural MRI images (T1 weighted) were acquired from the sagittal plane using a three dimensional magnetization prepared rapid

gradient-echo (MPRAGE) pulse sequence with the following scanning parameters: TR = 2500 ms, TE = 2.22 ms, flip angle = 8◦, FOV = 256 × 256 mm, voxel size = 0.8 × 0.8 × 0.8 mm, slice thickness = 0.8 mm.

The analyses and visualization of imaging data were performed with SPM12 (Ashburner et al. 2014) and Nilearn - 0.9.2 (Abraham et al. 2014). The functional images were first preprocessed with realignment, reslicing, and slice time correction. Then, the head movement correction was done by using affine transformation in a two-pass procedure and aligning individual functional images to their mean image using 2nd degree B-spline interpolation. Participants who had head movements more than 3 mm or rotations greater than 3° were excluded from further analysis, which yielded the exclusion of six participants in total, five for large head motion and one for T1 image distortion. We then replaced them with six new participants. The mean image of each participant was then spatially normalized to a 3mm standard Montreal Neurological Institute (MNI) template using the "unified segmentation" approach, and the resulting deformation field was applied to the individual functional images. The normalized fMRI images were then smoothed with a 6 mm full-width-at-half-maximum (FWHM) Gaussian kernel to improve the signal-to-noise ratio and compensate for residual anatomical variations.

Statistical analyses

Behavioral analysis

The reproduction biases, the difference between the reproduced duration and the physical duration, were calculated for the Response trials. To exclude trials with large reproduction errors due to accidental button presses or inattention, we applied the three-sigma rule to exclude those outliers. Then, we categorized the remaining Response trials into two types depending on the preceding task: (a) Response-Response (RR) trials that were preceded by a reproduction task, and (b) NoResponse-Response (NR) trials that were preceded by a passive viewing task.

Given that duration reproduction (D_r) is affected by both the central tendency effect and the short-term serial dependence (Glasauer and Shi 2022), we estimated the central tendency and serial

dependence effects separately. The central tendency effect results from the integration of the prior (D_p) and the current duration (D_n), which can be approximated using linear regression when the prior is assumed to be unchanged (Shi, Church, and Meck 2013b; Cicchini et al. 2012):

$$D_r = wD_n + (1 - w)D_p .$$

Thus, here we applied a linear regression to obtain the slope (w), and used $1 - w$ as the central tendency index, with 0 indicating no central tendency and 1 strong central tendency.

To assess the serial dependence of time perception, we first eliminated the general bias by subtracting the mean reproduction for each sample duration from the trial-level reproduced duration, then normalized the error in a relative term for each subject:

$$RE_{i,k} = (D_{i,k} - \bar{D}_k)/\bar{D}_k ,$$

where $\bar{D}_k$ is the mean reproduction at duration D_k, $D_{i,k}$ the reproduced duration at trial i of a given Duration D_k, $RE_{i,k}$ the normalized relative error. Second, given that duration is an open-scale measure, we applied a linear regression with the normalized relative error to the previous sample duration (D_{n-1}), and took the slope of the linear fit as the sequential bias index (e.g., Glasauer and Shi 2022; Cicchini, Anobile, and Burr 2014; Cicchini, Mikellidou, and Burr 2018). A positive slope indicates that the current estimation is attracted towards the previous duration (henceforth referred to as the "serial dependence effect"), while a negative slope indicates that the current time estimation is repulsed from the previous duration.

For statistical analyses, we applied linear mixed model analysis, repeated measures ANOVA, and simple t-tests according to the data structure. Linear mixed models are robust to sphericity violations and do not inflate Type I errors (Singmann and Kellen 2019) and they can accommodate the covariant factor (duration) in addition to the fixed effects addressed by ANOVA. The p-values reported for the mixed models were calculated using the maximum likelihood estimation.

fMRI statistical analysis

There were three types of inter-trial transitions: No-response to Response (NR), Response to Response (RR), and Response to No-response (RN). Given that the third type (RN) trials yielded no behavioral response, the main analysis was focused here on the Response trials (i.e., RR and NR). To boost the power of the first-level fMRI analyses, we grouped the preceding durations into two categories: the "Short" and the "Long" categories. The "Short" category included durations of 0.8 and 1.0 s, and the "Long" categories were 1.4 and 1.6 s, with the middle duration of 1.2 s being excluded. Once the regions of interest (ROIs) were identified, we proceeded with a comprehensive analysis where all durations were taken into account.

At the first-level analysis with individual participants, BOLD responses obtained from the smoothed images were time-locked to the onset of the target duration and modeled using a canonical hemodynamic response function (HRF) with a box-car function to represent the duration of the coherent movement. A combination of the factor of the Prior Task (RR or NR) and the categorical Prior Duration (Short or Long) resulted in four conditions, each represented by a separate main HRF regressor. To reflect the true modulation of sequential bias, we used the normalized relative error $RE_{i,k}$ as an additional parametric regressor for each of the four main regressors, similar to previous studies (Penny et al. 2011; Mumford 2015), four parametric modulators in total. Additionally, six head movement parameters were added as nuisance regressors to control head motion artifacts (Lund et al. 2005). The data were high-pass filtered at 1/128 Hz. For each subject, 8 condition-specific contrast images were created (for each trial type and parametric modulator).

The respective contrast images for the main HRF regressors and the parametric regressors were subjected to the second-level analysis with flexible factorial design, separately. In the flexible factorial design, Prior Task and Prior Duration were created as within-subject factors and Participant as a random factor. The 2 (Prior Task: Response vs. No-response) × 2 (Prior Duration: Short vs. Long) ANOVAs allowed us to determine the unique contributions of each factor to brain activity, and how they might interact with each other to affect neural processing. We conducted a whole-brain analysis to determine the candidate brain regions involved in the main effects of Prior Task and Prior Duration,

as well as their interaction, by using planned t-contrasts. All contrasts were thresholded at $p < .001$, with FWE cluster correction at $p < .05$. We focused on brain regions that showed sensitivity to the modulation of brain activity by the normalized relative deviation. Parameter estimates were extracted from the statistically significant clusters and averaged across the voxels in the individual-level analyses.

To gain further insight into activation patterns, a separate general linear model (GLM) was applied to the fMRI time series, similar to the model designed above, except all individual durations were included (0.8, 1.0, 1.2, 1.4, and 1.6 s). Thus, we have 2 (Prior Tasks) × 5 (Prior Durations), 10 conditions in total. Each condition had one main HRF regressor and one parametric regressor using the normalized relative error. β values of individual main regressor as well as parametric modulator were calculated from the significant voxels detected above (a sphere with a diameter of 10 mm) for individual participants. To assess the changes in the BOLD signal and the parametric modulation in the brain activity, a linear mixed model analysis with Prior Task and Prior Duration as the fixed effects and Subject as the random factor was applied to the β values of the main regressor as well as the parametric modulator.

We then conducted Spearman's correlation ($\alpha = 0.05$, two-tailed) to assess the relationship between the magnitude of the serial dependence effect in behavior and the BOLD activity of interest. The slope of the linear regression with the normalized relative error depending on the previous sample duration was operationalized to indicate the magnitude of the behavioral serial dependence effect. The BOLD response was measured as the β values of the main regressors in the designated regions detected above.

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