Dopaminergic processes predict temporal distortions in event memory

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Abstract

Our memories do not simply keep time — they warp it, bending the past to fit the structure of our experiences. For example, people tend to remember items as occurring farther apart in time if they spanned a change in context, or 'event boundary,' compared to the same context. While these distortions can sacrifice precise timing, they may serve to help separate temporally adjacent memories. However, the neural bases of this phenomenon are poorly understood. Here, we combined functional magnetic resonance imaging (fMRI; $n = 32$) with eye-tracking ($n = 28$) to test whether the dopaminergic system, known to influence encoding and time perception, predicts time dilation between adjacent events in memory. Participants encoded item sequences while listening to tones that mostly repeated over time, forming a stable auditory context, but occasionally switched, creating an event boundary. We found that boundaries predicted greater retrospective estimates of time between item pairs. Critically, tone switches significantly activated the ventral tegmental area (VTA), a key midbrain dopaminergic region, and these responses in turn predicted greater time dilation between item pairs spanning those switches. Boundaries furthermore predicted a momentary increase in blinks. VTA activation also predicted blinking in general, consistent with the idea that blink behavior is a potential marker of dopaminergic activity. On a larger timescale, higher blink rates predicted greater time dilation in memory, but only for boundary-spanning pairs. Together, these findings suggest that dopaminergic processes are sensitive to event structure and may drive temporal distortions that help disjoin memories of distinct events.

Significance

Meaningful changes in the environment can exaggerate the remembered time between experiences, suggesting a link between temporal distortions and the creation of distinct episodic memories. Here, we combined fMRI and eye-tracking with a paradigm that assessed temporal memory for item pairs encountered within and across task-relevant contexts. We found that contextual changes predicted activation in the ventral tegmental area (VTA) and momentary increases in blinking, both potential markers of dopaminergic activity. VTA activation and more prolonged periods of blinking across boundaries were also associated with greater time dilation in memory. Our findings extend the relationship between dopamine and time perception to episodic memory, revealing how the ebb and flow of experience might bend memories of time to represent discrete events.

Introduction

"[Mechanical time] is unyielding, predetermined. [Body time] makes up its mind as it goes along," remarks physicist and author Alan Lightman (1992, p.32). Indeed, time can seem malleable when we reflect upon the past. For example, experiences from the COVID-19 pandemic are not equally represented in memory. The early lockdown period is often recalled as having passed more quickly than it was originally experienced, potentially driven by a significant lack of variety or novelty (Droit-Volet et al., 2023; also see Rouhani et al., 2023 for similar findings). In contrast, everyday life typically involves frequent shifts in context, or 'event boundaries', which tend to stretch remembered time and promote the separation of experiences into distinct memories. These memory-expanding effects have been reliably demonstrated in laboratory settings, with changes in scenes (Ezzyat & Davachi, 2014), goals (Cowan et al., 2024), and emotional states (McClay, Sachs, & Clewett, 2023; Wang & Lapate, 2024) eliciting time dilation in long-term memory. Yet, despite their central role in human cognition, it remains unclear how the brain uses contextual cues to reshape temporal representations in service of memory organization.

A promising candidate for this process is the ventral tegmental area (VTA), a brainstem nucleus that releases dopamine and modulates episodic memory. Dopamine facilitates encoding and consolidation of behaviorally relevant information over both short (e.g., D'Ardenne et al., 2012) and long timescales (see Clewett & Murty, 2019; Harley, 2004). The VTA responds to a wide variety of salient stimuli, include those that are novel (Duszkiewicz et al., 2019) and carry predictive salience (Shohamy & Adcock, 2010). Neuroimaging studies in humans suggest that phasic VTA activation and dopamine may signal key moments when ongoing predictions fail and it is beneficial to update one's mental model of what is happening (Antony et al., 2021; Zacks et al., 2011). Additionally, midbrain dopamine regulates synaptic plasticity in the hippocampus (Lisman & Grace, 2005; Shohamy & Adcock, 2010), a region that triggers the encoding of new memories and their temporal features (see e.g., Howard & Eichenbaum, 2015). Together, these factors make the VTA well equipped to mediate the influence of event boundaries on the temporal structure of memory.

Alongside its role in memory, dopamine is heavily implicated in time perception. According to the dopamine clock hypothesis (Meck, 1983; 1996), transient increases in dopamine may accelerate a hypothetical internal clock that generates pulses, or 'ticks', that are collected and stored by a memory system to estimate time. The more pulses collected during a fixed interval, the longer that period is perceived to last (Treisman, 1963). Thus, dopamine-induced acceleration of this clock would result in time overestimation (see Fung, Sutlief, & Hussain Shuler, 2022). Other frameworks offer additional nuance; for example, dopamine may modulate this clock based on prediction errors (Mikhael & Gershman, 2019), which are theorized to trigger event segmentation (Zacks et al., 2007) (see Fung, Sutlief, & Hussain Shuler, 2022). However, most research has focused on how dopamine influences time perception as an experience unfolds, using tasks in which participants actively track the duration of an ongoing stimulus or estimate duration immediately after the stimulus ends. Therefore, it remains unclear whether dopamine also helps to encode exaggerated representations of time into long-term memory.

Intriguingly, blink behavior may offer an indirect window into the influence of dopamine and event boundaries on temporal memory distortions. Recent neuroimaging work shows that momentary blinks

correspond with increased activation in dopaminergic regions, including the VTA and substantia nigra (Demiral et al., 2023). Moreover, it has been shown that spontaneous blink rate is altered in individuals with dopamine-related neuropsychiatric conditions like Parkinson's disease (Fitzpatrick et al., 2012) and schizophrenia (Chen et al., 1996) under certain conditions (for review, see Jongkees & Colzato, 2016; Karson, 1983). Like dopamine, blinks also tend to occur around 'breakpoints' in experience, such as punctuation marks in text passages (Hall, 1945), pauses in speech (Nakano & Kitazawa, 2010), and the beginnings of quiz questions on a mentally demanding TV game show (Wyly et al., 2023) (also see Nakano et al., 2009; Nakano et al., 2013). Additionally, one study in humans showed that increased blinking during a short interval was associated with exaggerated estimates of time (Terhune, Sullivan, & Simola, 2016), consistent with the role of dopamine in shaping time perception.

In the current neuroimaging and eye-tracking study, we examined whether dopaminergic processes predict context-driven distortions in memory for time and event structure. Using a well-validated paradigm that indexes event segmentation through retrospective temporal distance ratings, we first sought to replicate prior findings that event boundaries within item sequences lead to time dilation (Buonomano et al., 2023; Clewett et al., 2020; Ezzyat and Davachi, 2014; Cowan et al., 2024). Our main goal was to test whether encountering these boundaries corresponds with changes in indirect measures of dopaminergic processing, including VTA activation and momentary increases in blinking. We also examined whether these transient measures, in addition to blinking patterns across longer periods of time, predicted the later expansion of temporal representations in memory. Together, our findings offer insight into how temporal encoding processes may be shaped by both brief and sustained engagement of the dopaminergic system.

Methods

Participants. Thirty-six participants were recruited from the New York University (NYU) Psychology Subject Pool and the local community. Sample size was estimated using a G*Power 3.1 power analysis (alpha = 0.05, power = 0.80, d = 0.80), based on the pooled temporal memory performance from a very similar event boundary experiment (Clewett, Gasser, & Davachi, 2020). This power analysis yielded a required sample size of 29 participants. To account for attrition, we recruited 36 participants. Participants were required to have normal or corrected-to-normal vision and hearing, to have no metal in their body, and to not be taking beta-blockers or psychoactive medications. All participants provided written informed consent approved by the NYU Institutional Review Board and received monetary compensation for participation.

Four participants were fully excluded from analyses (reasons included falling asleep in the scanner and audio malfunction). Therefore, our final sample size was 32 participants (20 F; M_{age} = 22 years, SD_{age} = 2.7 years). Of this sample, 15 participants identified as Asian, 2 as Black/African American, 4 as more than one race, and 11 as White.

Of these 32 participants, five requested to leave the scanner early and thus did not complete all 10 blocks of the task (n = 2 completed 9 blocks, n = 1 completed 8 blocks, n = 2 completed 7 blocks). Finally, four participants' eye tracking data was excluded due to equipment malfunction or poor quality, leaving 28 participants with usable data for all analyses that included blink data.

Materials. Participants viewed 512 grayscale images of everyday objects (Gabrieli et al., 1997; Kensinger et al., 2006), which were resized to 300 x 300 pixels, placed on a gray background, and

luminance-normalized using the MATLAB SHINE toolbox to control for the effect of brightness on pupil behavior. To embed these images within distinct auditory contexts, participants were presented with 1s pure tones (created with Audacity; https://www.audacityteam.org/) in either the left or right ear. The six tone frequencies used ranged from 500-1000 Hz in 100 Hz intervals, were perceptually discriminable, and were sufficiently arousing to facilitate engagement in the task.

Code and data accessibility. The code, experiment materials, and data for this study will be made publicly available on the OSF account of E.M. (osf.io/yt6hm) upon acceptance of this manuscript.

Overview of experimental design. This experiment took place over two days. On the first day, participants completed several questionnaires and a practice task block before completing the full event sequence task in the MRI scanner. The MRI session took approximately 3 hours, with 2.5 hours of scanning. On the second day, approximately 24 hours later, participants returned to perform a surprise item recognition memory test (not described in the current paper).

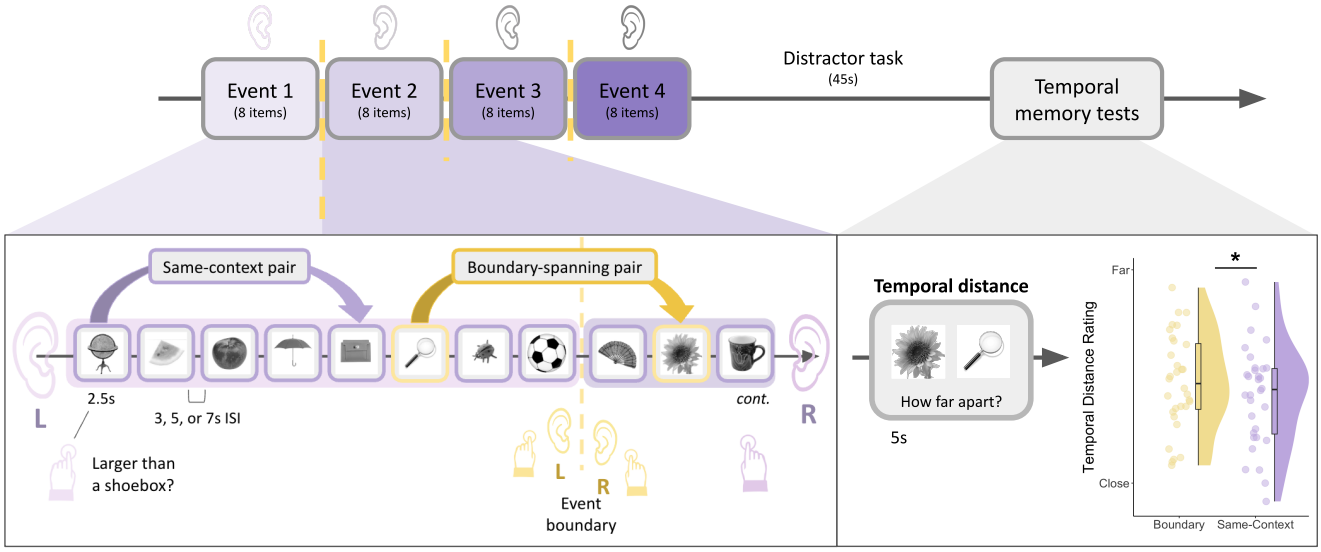

Figure 1. Event sequence encoding task and temporal distance memory test. In each block of the task, participants studied a sequence of 32 neutral object images. Prior to each image, participants listened to pure 1s tones either in their left or right ear during the midpoint of a fixation screen. The side of the tone also cued participants as to which hand they should use to judge whether each object was larger than a shoebox (e.g., left ear = left hand). Critically, the image sequence was divided into four events. Events were defined by a stable auditory context, with the same tone presented to the same ear for 8 successive items. After 8 items, the tone switched to the other ear, representing an event boundary (see dashed yellow line). Additionally, the pitch of the tone changed, as well as the hand required by the participants to make button responses. This pattern continued for the remainder of the 8-item event. After four events and a brief distractor task, participants completed a temporal distance memory test (along with a temporal order memory test discussed elsewhere; Clewett et al., 2024). On each test trial, participants were presented with different pairs of objects from the prior sequence and asked to rate how far apart they thought each pair appeared in time ('very close', 'close', 'far' or 'very far'), despite their equivalent objective distance. Some tested pairs had been encountered in the same context (in purple), while other pairs had been encountered with an intervening boundary (in yellow). In right panel, raincloud plot displays distance memory ratings for boundary-spanning and same-context pairs. Each dot represents averaged data from one participant, with distance memory ratings (1-4) displayed as a continuous variable. Colored boxplots represent 25th-75th percentiles of the data, and the center line represents the median. Statistical significance refers to results from trial-level cumulative link model. *p < .05.

Event sequence encoding task. While in the MRI scanner, participants completed a modified version of an event sequence encoding task that has been shown to elicit reliable event segmentation effects in memory, as indexed by significant time dilation in retrospective distance ratings (Clewett et al., 2020) (**Figure 1**). Our goal was to use these boundary-induced subjective temporal distortions to operationalize whether memories had become separated at context shifts. That is, if item pairs spanning a boundary were remembered as appearing farther apart than item pairs from the same context – despite being the same objective distance apart during encoding – then they were more likely to have become encoded as distinct episodic memories.

In this encoding-retrieval block design, participants were presented with sequences of 32 object images for 2.5s each. For each image, participants made a button press to respond to a simple orienting question ("Is this object larger or smaller than a standard shoebox?"). Additionally, participants were asked to form their own mental narrative of the image sequence to encourage associative encoding (e.g., DuBrow and Davachi, 2013). A jittered ISI (3, 5, or 7s fixation cross) separated each image presentation to optimize deconvolution of the blood-oxygen level dependent (BOLD) signal during the fMRI analyses.

Each item sequence was divided into four auditory 'events' that contained 8 images each. Events were defined by a stable auditory context, in which 1s pure tones played either in participant's left or right ear only, halfway through each jittered ISI. The laterality of the tone also cued participants to use either their left or right hand to make button responses for the object size judgments (left ear = left hand). Thus, the tones not only provided sensory information to elicit perception of stable mental events, but were also task relevant. After the final image in an 8-item event, the tone abruptly switched sides to the opposite ear and changed pitch. Participants were also instructed to switch the hand used to make button responses. This salient change constituted an 'event boundary' in the sequence, marking the end of one event and the beginning of the next. The new context then remained the same for the rest of the 8-item event.

Each item sequence contained three tone switches total, resulting in four stable auditory events. There were 10 encoding-retrieval blocks total across the experiment. The starting ear/hand was counterbalanced across blocks. Pitch changes were pseudorandomized, such that the same frequency (e.g., 500 Hz) was not heard more than once in any given encoding block. To separate the encoding and retrieval tasks and to reduce any recency effects in memory, participants completed a brief arrow detection task (45s) after each encoding block. Participants were presented with 0.5s left-facing (<) or right-facing (>) arrows in the center of the screen, separated by 0.5s ISIs of fixation. They were instructed to indicate which direction the arrow was facing via button press as quickly as possible.

Temporal distance memory test. At the end of each encoding block, participants completed two temporal memory tests: the first for temporal order and the second for temporal distance. Given that our primary focus was on subjective distortions in distance memory, the results from the temporal order memory test are reported elsewhere (Clewett et al., 2024).

In the temporal distance memory test, 14 item pairs from the encoding sequence were presented for a fixed duration of 5s each. Importantly, each of these item pairs had been separated by exactly three images during encoding. Because the objective distance between to-be-tested pairs was

pseudorandomized to always be equivalent (32.5s from onset of the first image to the offset of its pairmate), we were able to measure subjective temporal distortions in memory across conditions.

Accordingly, participants were asked to judge how far apart in time two images appeared. There were four options: 'very close,' 'close,' 'far,' and 'very far.' To replicate previous effects of event boundaries on temporal distance memory, we compared ratings for two types of item pairs: same-context pairs (8 trials per block) and boundary-spanning pairs (6 trials per block). Same-context pairs contained images from the same context during encoding, while boundary-spanning pairs contained images that spanned a change in context (i.e., task-relevant tone switch) during encoding.

We excluded the first same-context item pair from all analyses, because this pair contained the first image in each block. As such, it likely constituted a task-irrelevant event boundary and would therefore produce different behavioral effects than the other same-context pairs. Due to a programming error, one of the boundary pairs from each list also contained an incorrect item. Data for these specific pairs (appearing once per block across 23 participants) were excluded from the analyses. Finally, one block was excluded for 9 participants due to a timing error.

fMRI Acquisition and preprocessing.

fMRI/MRI data acquisition. All neuroimaging data were acquired with 3T Siemens Magnetom PRISMA scanner using a 64-channel matrix head coil. First, participants underwent a high-resolution MPRAGE T1-weighted anatomical scan (slices = 240 sagittal; TR = 2300ms; TE = 2.32ms; TI = 900ms; FOV = 230 mm; voxel in-plane resolution = 0.9 mm^2; slice thickness = 0.9 mm; flip angle = 6°; bandwidth = 200 Hz/Px; GRAPPA with acceleration factor = 2; scan duration: 5m 21s).

Next, participants underwent a T2-weighted functional scan (slices = 240 sagittal; TR = 3200ms; TE = 564 ms; FOV = 230 mm; voxel in-plane resolution = 0.9 mm^2; slice thickness = 0.9 mm; flip angle = 6°; bandwidth = 200 Hz/Px; GRAPPA with acceleration factor = 2; scan duration: 3m 7s). The task audio was also calibrated during this scan to ensure the tones were audible above scanner noise and could be discriminated from one another. Participants could make button presses to request changes in tone volume. Additionally, we collected two fieldmap scans to assist with functional imaging unwarping (1 in anterior-posterior (AP) phase encoding direction and 1 in posterior-anterior (PA) phase encoding direction). Afterwards, we collected a short fast spin echo (FSE) sequence MRI scan that enables visualization of the locus coeruleus (LC). Details are reported elsewhere (Clewett et al., 2024).

After the structural scans were collected, participants underwent separate functional imaging for each of the 10 encoding blocks and the 10 retrieval blocks. Functional scans were collected using a whole-brain T2*-weighted multiband echo planar imaging (EPI) sequence (128 volumes per encoding block; TR = 2000ms; TE = 28.6ms, voxel in-plane resolution = 1.5 x 1.5 mm^2; slice thickness = 1 mm with no gap; flip angle = 75°, FOV = 204 mm X 204 mm; 136 X 136 matrix; phase encoding direction: anterior-posterior; GRAPPA factor = 2; multiband acceleration factor = 2). In each volume, 58 slices were tilted -20° of the anterior commissure-posterior commissure line and were collected in an interleaved order.

fMRI preprocessing. Image preprocessing was performed using FSL Version 6.00 (FMRIB's Software Library, www.fmrib.ox.ac.uk/fsl). Functional images were preprocessed using the following steps: removal of non-brain tissue using BET; B0 unwarping using fieldmap images; grand-mean intensity normalization of the 4D data set by a single multiplicative factor; and application of a high-pass

temporal filter of 100s. No spatial smoothing was applied due to the small size of the VTA and to preserve spatial specificity. Motion correction was performed using the MCFLIRT tool, which produced six motion nuisance regressors. Additionally, fsl_motion_outliers was used to identify volumes with extreme head movements, or frame displacements, using the DVARS option. Both this matrix of outlier volumes and the six motion regressors were as modeled as covariates in the subsequent GLM analyses. Entire blocks with excessive head motion overall (conservatively defined as mean frame displacement > 1 mm) were excluded from analysis, resulting in the removal of one block each from three participants. Each participant's denoised mean functional volume was co-registered to their T1-weighted high-resolution anatomical image using brain-based registration (BBR). Anatomical images were then co-registered to the 2 mm isotropic MNI-152 standard-space brain using an affine registration with 12 degrees of freedom.

Physiological denoising. Eight separate physiological nuisance signal regressors were extracted for the subsequent GLM analyses. First, FSL FAST was used to decompose each participant's high-resolution anatomical images into probabilistic tissue masks for white matter (WM), grey matter (GM), and cerebrospinal fluid (CSF). The CSF and WM masks were thresholded at 75% tissue-type probability to increase their spatial specificity and reduce potential overlap. Following a similar approach to Bartoň et al. (2019), we defined eight 4 mm spheres in representative regions of WM and CSF (four of each type; for exact coordinates, see Bartoň et al., 2019). The eight spheres and WM and CSF anatomical masks were then transformed into each participant or block's native functional space and merged to further increase their spatial specificity. Nuisance timeseries for each of the four WM and four CSF merged masks were then extracted from each block's preprocessed functional data and modeled as nuisance regressors in the GLMs.

VTA region-of-interest (ROI) definition. To create an anatomical mask of the VTA, we used a publicly available probabilistic atlas that was originally created using individual hand-drawn ROIs (Murty et al., 2014). This standard-space VTA mask was thresholded at 75% probability to increase its spatial specificity and then registered into each participant's functional run (i.e., block) of the encoding task.

fMRI analyses.

Generalized linear modeling (GLM) analyses and acquisition of single-trial activation estimates of VTA activation. To estimate VTA activation at the trial level, we conducted Least Squares Separate (LSS) GLM analyses on the unsmoothed functional data from the sequence encoding task. This modeling approach generates unique activation estimates for each stimulus (i.e., tone or image) from the task. Importantly, the repetition or switching of tones carried the critical information about the stability or change in the surrounding context. Thus, using LSS GLM enabled us to isolate the distinct effects of context-relevant tones on brain activation.

Each LSS-GLM contained a total of 64 task-related regressors for each block of the encoding task, because there were 32 tones and 32 images in each block. Each tone was modeled as a 1s stick function and each image was modeled as 2.5s stick function. Both regressors were convolved with a dual-gamma hemodynamic response function (HRF). A total of 64 separate LSS-GLM analyses were conducted for each block of the ten blocks of the task, where one stimulus (image or tone) served as the regressor of interest and all other trials were modeled as a separate regressor. Each LSS-GLM thereby resulted in a unique activation estimate (i.e., beta map) across the whole brain for each stimulus (Mumford et al., 2012; Mumford, Davis, & Poldrack, 2014). To control for noise, a total of 14

nuisance regressors (4 WM, 4 CSF, and 6 motion regressors) were included in each GLM, along with individual nuisance regressors for trials with extreme head movements.

A VTA ROI analysis was performed on the resulting beta maps. The standard-space VTA anatomical mask was transformed into each participant's native run-space for each encoding block and used to extract single-trial VTA parameter estimates (a measure of activation) for each of the 32 tone trials (3 boundary tones, or switches, and 29 same-context tones, or repeats). We excluded noisy datapoints using boxplot outlier removal by participant, resulting in the removal of approximately 3% of the tone-related VTA activation trials across the entire dataset.

Eye-tracking methods.

Eye-tracking. Pupil diameter was measured continuously at 250 Hz during the event sequence task using an infrared EyeLink 1000 eye-tracker system (SR Research, Ontario, Canada). Raw pupil data, segmented by block, were preprocessed using ET-remove-artifacts, a publicly available MATLAB program (https://github.com/EmotionCognitionLab/ET-remove-artifacts). Although this software is typically used to clean pupil timeseries by interpolating over blink events and other artifacts (e.g., Clewett et al., 2024), our primary objective was to identify blink event timestamps and quantify their frequency within different periods of interest.

ET-remove-artifacts located blink events by identifying rapid changes in pupil size, or pupil velocity, following the approach described in Mathôt et al. (2013). The velocity timeseries was computed by applying MATLAB's finite impulse response (FIR) differentiator filter on the raw pupil size timecourse. This method provides a robust estimate of instantaneous rate of change while minimizing noise amplification. For our dataset, we selected FIR filter parameters (Filter Order = 4, Passband Frequency = 10, and Stopband Frequency = 12) to produce a smooth velocity timeseries with trough-and-peak profiles that were identifiable and specific to blink events rather than noise-related data loss.

The algorithm then used MATLAB's "findpeaks" function to locate peaks and troughs in the pupil velocity timecourse. Blink profiles were distinctly identifiable as a contiguous trough followed by a peak in the velocity timeseries. To achieve a high degree of specificity to blink events, we set the Peak and Trough Threshold Factor and Trough Threshold Factor at 8 standard deviations of the velocity timeseries. This threshold is higher than those typically used for cleaning artifacts from pupil timeseries (e.g., Clewett et al., 2024), ensuring that only substantial blink-related troughs and peaks were counted as blink events rather than small and transient velocity changes attributable to other artifacts.

To generate a preprocessed pupil timecourse, the algorithm applied a linear interpolation across identified blink intervals. Artifact intervals exceeding 2 seconds were automatically imputed with NaN (missing data indicator). As mentioned previously, four participants were excluded from eye tracking analyses due to system malfunction or poor overall eye tracking quality, resulting in a total of 28 participants for all blink-related analyses.

Computing local blink counts. Breakpoints in continuous experience have been shown to elicit a momentary increase in blinking (see Nakano et al., 2009; Wyly et al., 2023). Further, blink behavior has also been putatively linked to dopaminergic processes (Jongkees & Colzato, 2016), suggesting that blink behavior may offer a window into neuromodulatory processes that facilitate memory separation at boundaries. To test this idea, we tabulated local blink count in a 1.5s interval immediately after the

onset of each tone. The size of this interval was chosen because the smallest ISI in the current paradigm was 3s – that is, 1.5s on either side of the tone onset. In this way, we were able to capture tone-induced blinks during a brief period that was 'uncontaminated' by the preceding or ensuing images on any trial. To acquire highly conservative estimates of blink behavior that were not confounded by noise or data loss, blink intervals with more than 25% invalid samples were excluded from analyses. As with the VTA data, we also cleaned the trial-level blink responses using boxplot outlier detection within each participant. After these exclusions, approximately 78% of local blink intervals remained per participant, on average.

Computing sustained blink rates between to-be-tested item pairs. We also zoomed out to examine blink patterns across longer, behaviorally relevant windows of encoding to assess more sustained dopaminergic processes. Blink rate was calculated for the 32.5s window between each to-be-tested pair, from the onset of the first item to the offset of its pairmate (encountered four images later). We first tabulated the total blink count during these intervals. As some trials encompassed periods of invalid samples imputed with NaNs, we also calculated the total number of valid datapoints for each of these windows. Blink rate was then computed by dividing the blink count by the number of valid datapoints for each window. Notably, while this approach provided cleaner estimates of blink across a large timeframe, raw blink count produced the same pattern of results reported in this study. Finally, we conducted the same noise-related and by-participant boxplot outlier removal procedure as before, which left approximately 79% of blink windows per participant, on average.

Testing linear relations between the VTA, temporal memory, and blink patterns. To assess trial-level relationships between our key variables, we used linear mixed-effects and cumulative link modeling. Linear mixed-effects modeling was used when the outcome of interest was continuous (i.e., trial-level VTA parameter estimates, post-tone blink count, and prolonged blink rate). Fixed-effect predictors in these models were categorical (i.e., tone type: boundary tone, same-context tone) and/or continuous (i.e., trial-level VTA parameter estimates).

Cumulative link models are the most common type of ordinal regression model, using a similar frequentist approach to linear mixed-effects models (Christensen, 2015; Dunn, 2020). Thus, cumulative link modeling was used when the outcome of interest was ordinal (i.e., trial-level temporal distance memory ratings). Distance memory ratings were ordered from the smallest to largest rating: 'very close,' 'close,' 'far,' 'very far.' Fixed-effect predictors in these models were categorical (i.e., pair type: boundary-spanning pair, same-context pair) and/or continuous (i.e., trial-level parameter estimates, post-tone blink count, and prolonged blink rate).

To meaningfully relate local measures (i.e., VTA parameter estimates and post-tone blink counts) to measures capturing a wider temporal window (i.e., prolonged blink rate and distance memory ratings), we extracted the value associated with one tone between each to-be-tested item pair. For details on the exact positions of the selected tones, which were matched across boundary and same-context pairs, see **Figure S1**.

Analyses were conducted in RStudio (Version 2023.12.1, Posit Team, 2024) using the lme4 (Bates, Maechler, Bolker, & Walker, 2015) and ordinal packages (Christensen, 2023). Each model included random intercepts for participant ID. Continuous predictors were mean centered by participant to reduce the influence of individual differences (see Enders & Tofighi, 2007). This mean centering was

performed separately for each model. Continuous predictors were also *z*-scored as necessary to improve model convergence.

Results

Event boundaries predicted subjective time dilation effects in long-term memory, a behavioral index of event separation. First, we tested how event boundaries influenced temporal distance memory. As expected, boundary-spanning pairs were remembered as having been farther apart than same-context pairs (*ß* = .071, *SE* = .031, *z* = 2.30, *p* = .022). **Figure 1, bottom right panel**), consistent with the idea that boundaries serve to mentally distance contextually distinct episodes in memory.

Event boundaries reliably predicted BOLD activation in the VTA, and these brain responses predicted later time dilation effects in memory. In the next trial-level analysis, we tested our key hypothesis that event boundaries engage VTA activation during encoding (see **Figure 2A** for anatomical mask). Consistent with our prediction, we found that Tone Type significantly predicted VTA activation, such that boundary tones elicited higher VTA activation compared to same-context tones (*ß* = 13.45, *SE* = 2.74, *t*(9281.88) = 4.90, *p* < .001). When examining each Tone Type separately, we found that VTA activation was significantly greater than baseline for boundary tones (*ß* = 30.04, *SE* = 7.47, *t*(31.23) = 4.02, *p* < .001), but not for same-context tones (*ß* = 3.35, *SE* = 2.31, *t*(30.29) = 1.45, *p* = .16) (**Figure 2B/C**).

We next tested if these boundary-related VTA responses predicted increased temporal distance ratings between item pairs spanning those same boundary tones. The results revealed no significant interaction effect of VTA activation and Pair Type (boundary-spanning versus same-context pair) on temporal distance memory (*ß* = .038, *SE* = .032, *z* = 1.19, *p* = .24). However, when analyzing each Pair Type separately, we found that boundary-evoked VTA activation significantly predicted higher temporal distance ratings (*ß* = .097, *SE* = .049, *z* = 1.99, *p* = .046) (**Figure 2D**). In contrast, same-context tone-related VTA activation did not predict temporal distance ratings for the same-context pairs spanning those tones (*ß* = .010, *SE* = .041, *z* = .24, *p* = .81) (**Figure 2E**). Thus, event boundaries appear to engage the VTA in a way that may distort the temporal structure of memory.

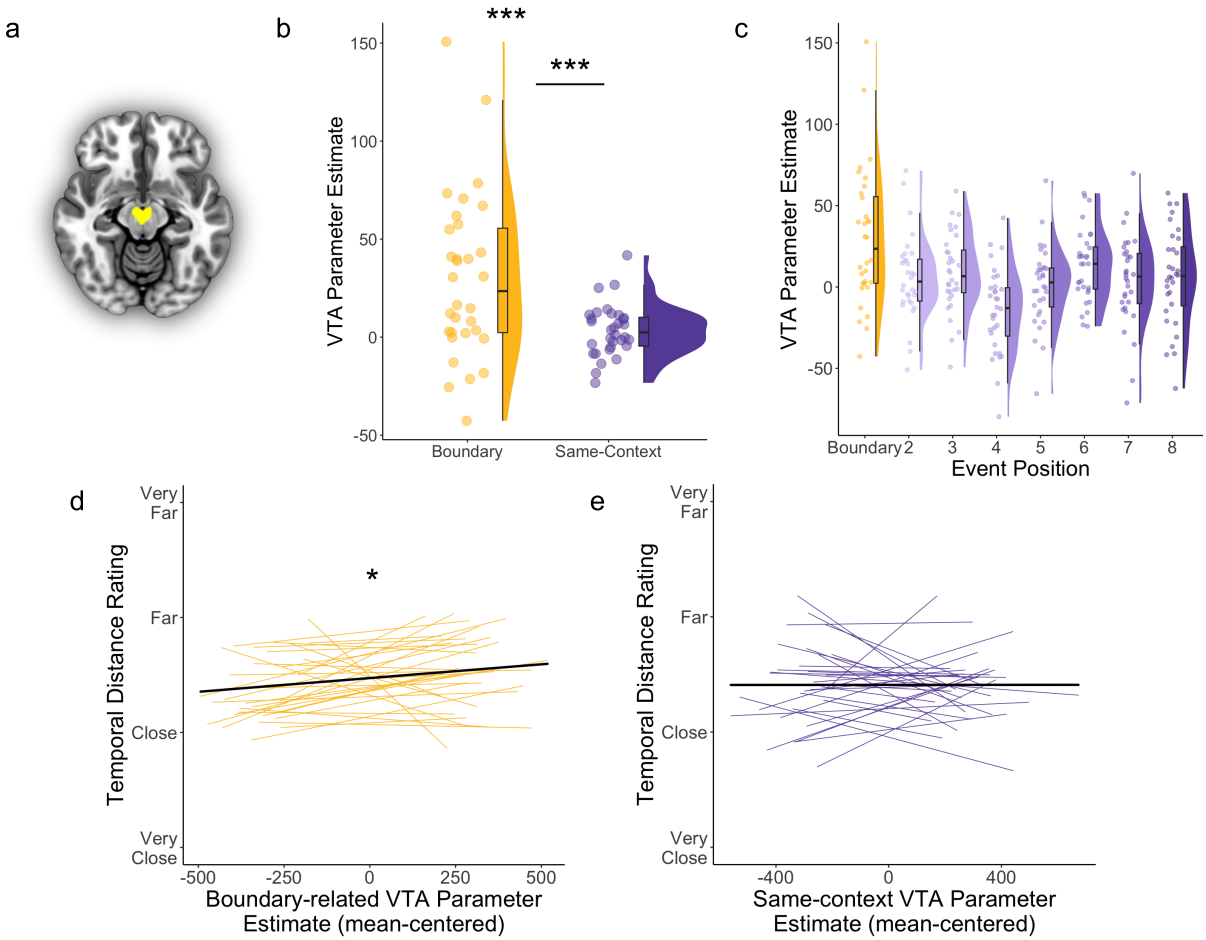

Figure 2. Event boundaries predicted greater VTA activation, and these responses predicted greater time dilation effects in memory. (A) Axial slice of the probabilistic atlas used to identify the VTA (yellow), thresholded at 75% tissue-type probability (Murty et al., 2014). (B) VTA parameter estimates, a measure of brain activation levels, for boundary tones (yellow) and same-context tones (purple). Each dot represents averaged data from one participant. Statistical significance refers to results from trial-level linear mixed effects models. (C) VTA parameter estimates plotted by trial position within the 8-item events during encoding. The first tone in each 8-item event was a boundary trial, when the tone switched from one ear to the other. Same-context tones then played in the same ear and were repeated across items positions 2 through 8 within that stable auditory event. Each dot represents averaged data from one participant. Colored boxplots represent 25th-75th percentiles of the data, and the center line represents the median. (D) Participant-level trendlines plotting the relationship between boundary-related VTA parameter estimates (mean-centered within condition) and temporal distance memory ratings (displayed as a continuous variable). Statistical significance refers to results from trial-level cumulative link model. (E) Participant-level trendlines plotting the relationship between same-context VTA parameter estimates and temporal distance memory ratings. Dark, bold lines represent the average linear trend across participants.***$p < .001$; *$p < .05$.

Event boundaries predicted a momentary increase in blinking. Intriguingly, prior studies have shown that 'breakpoints' in experience are associated with transient increases in spontaneous blinking (see Nakano et al., 2009; Wyly et al., 2023), which in turn has been linked to dopaminergic processes (for review, see Jongkees & Colzato, 2016). We sought to replicate these results in the current paradigm by examining how tone switches predict transient changes in blinking (**Figure 3A/B**). This model revealed a main effect of Tone Type on local blink count ($ß = .12$, $SE = .019$, $t(7461) = 6.07$, $p <$

.001), such that boundary tones were immediately followed by more blinks than same-context tones (**Figure 3C/D**).

Tone-related increases in VTA activation predicted blinking irrespective of contextual stability. To validate the putative link between blink behavior and dopaminergic processes, we next examined trial-level coupling between post-tone blink count and tone-related VTA activation. We found a significant main effect of VTA activation on post-tone blink count ($ß$ = .00025, SE = .00012, $t(7270)$ = 2.08, p = .038), such that greater tone-related VTA activation was associated with higher blink count irrespective of condition (**Figure 3E**). There was no significant VTA-by-tone type interaction effect on post-tone blink count ($ß$ = .00016, SE = .00012, $t(7271)$ = 1.34, p = .18), reinforcing a more general, context-invariant association between phasic VTA activation and blinking.

To verify that blink changes likely resulted from tone-related VTA activation (and not vice versa), we also performed a control analysis focusing on blinks that occurred within the 1.5s period *before* each tone. Pre-tone blink count was not significantly predicted by Tone Type ($ß$ = .017, SE = .020, $t(7410)$ = .83, p = .41) or tone-related VTA activation ($ß$ = .00012, SE = .00013, $t(7224)$ = .95, p = .34). Together, these blink timing-related control analyses provided strong evidence that blinking was triggered by behaviorally relevant changes during a dynamic experience.

Momentary increases in local boundary-evoked blinking behavior were not associated with later temporal distance ratings in memory. Finally, we tested if post-tone blink count was related to later memory separation effects. Contrary to our prediction, there was no main effect of post-tone blink count ($ß$ = .019, SE = .038, z = .50, p = .62) or blink-by-pair type interaction effect on temporal distance ratings ($ß$ = .060, SE = .039, z = 1.54, p = .12; **Figure 3F**).

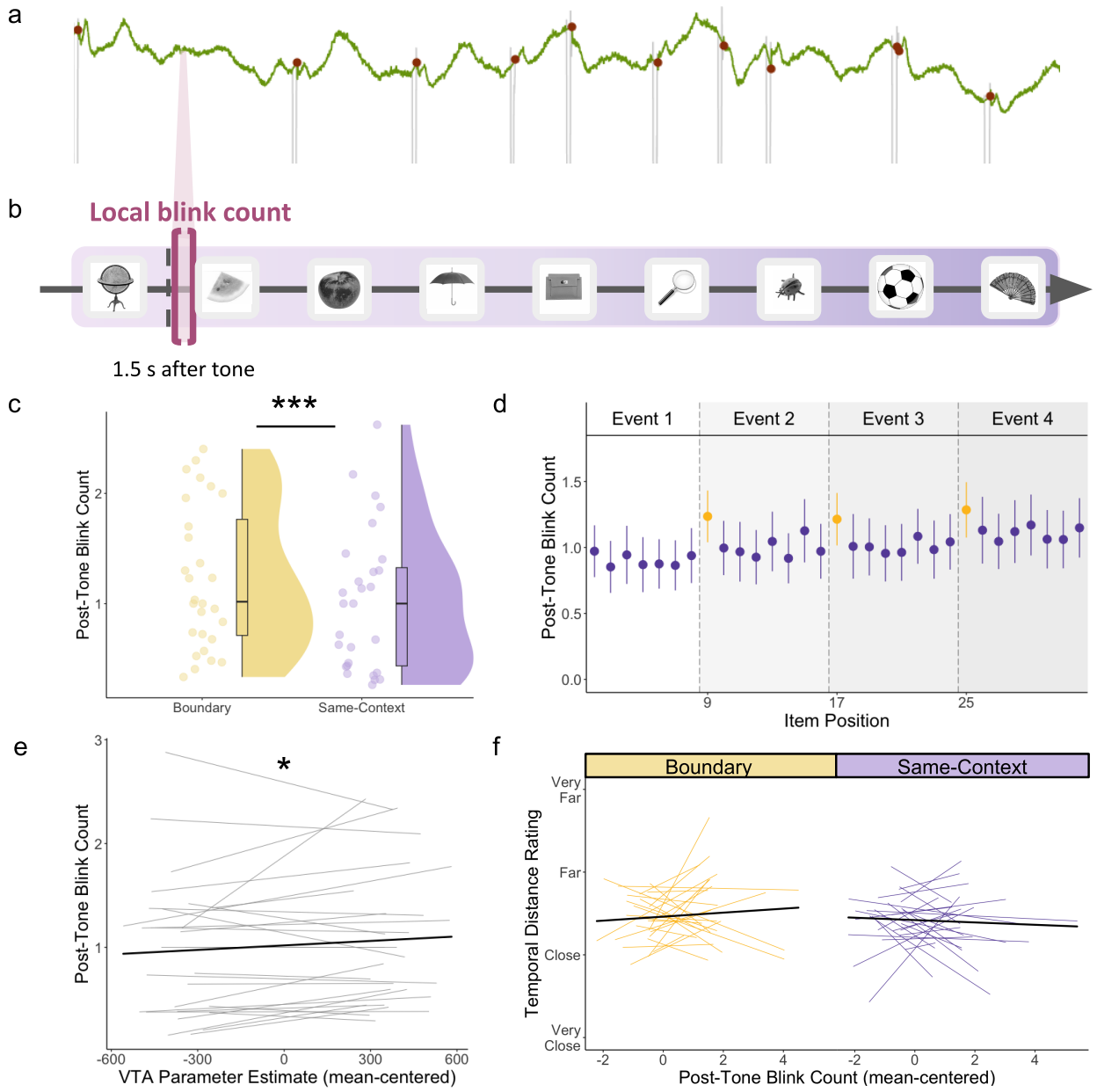

Figure 3. Event boundaries predicted a momentary increase in blinking, and these local changes in blinking were predicted by tone-related VTA activation irrespective of contextual stability or change. (A) Example pupil timeseries for a subset of an encoding block. Green line displays pupil size (in a.u., or arbitrary units) over time. Red circles represent time points when blink artifacts were identified by the pupil preprocessing algorithm based on velocity changes in pupil size. The timeseries is displayed for illustrative purposes and does not strictly align with the trial schematic. (B) A schematic image of the brief post-tone blink period of interest during event sequence encoding. Local blink count was captured in the short 1.5s interval following the onset of each tone (bracketed in pink). (C) An overall comparison between mean blink count after the onset of boundary tones (yellow) and same-context tones (purple). Each dot represents averaged data from one participant. Statistical significance refers to results from trial-level linear mixed effects model. (D) Mean post-tone blink count by item position in each encoding block (2 through 32; first item excluded). Yellow dots represent blink counts after boundary tones, which always occurred every 8 tones (preceding items 9, 17, and 25). Purple dots represent blink counts after same-context tones, which occurred in all remaining positions in the lists. Error bars represent SEM. (E) Participant-level trendlines plotting the relationship between

trial-level VTA parameter estimates (mean-centered) and local post-tone blink count. The dark, bold line represents the average linear trend across participants. Statistical significance refers to results from trial-level linear mixed effects model. (F) Participant-level trendlines plotting the relationship between post-tone blink count (mean-centered) and temporal distance ratings for boundary-spanning pairs (yellow; left) and same-context pairs (purple; right). Local post-tone blink counts are mean centered for each condition separately. The dark, bold lines represent the average trendline across participants, also for each condition separately. ***$p < .001$; *$p < .05$.

Testing relations between more prolonged periods of blinking, VTA activation, and temporal distance memory. Beyond local changes in blinking around boundaries, we examined whether blinking across larger timescales predicted memory and VTA activation. Here, we focused on behaviorally relevant time windows in the task: blink rate between to-be-tested item pairs during encoding (**Figure 4A/B**).

Increased blinking between to-be-tested item pairs was related to tone-related VTA activation and time dilation effects in memory. First, we tested whether boundaries modulated blink rate across these larger time periods. We found that Pair Type (boundary-spanning pair versus same-context pair) did not significantly predict blink rate across the to-be-tested pair windows ($ß = .35$, $SE = .33$, $t(2880.02) = 1.06$, $p = .29$; **Figure 4C/D**).

However, tone-related VTA activation significantly predicted blink rate in the surrounding time window ($ß = .0049$, $SE = .0021$, $t(2793) = 2.36$, $p = .018$), such that greater tone-related VTA activation predicted higher blink rate in general (**Figure 4E**). Like more local changes in blink count, there was no significant VTA-by-pair type interaction effect on sustained blinking behavior ($ß = .00099$, $SE = .0021$, $t(2794) = .48$, $p = .63$), suggesting that momentary VTA activation is coupled with prolonged blinking patterns more generally. Thus, despite differences in their timescales of action, momentary increases in VTA activation were meaningfully embedded within sustained periods of elevated blinking across sequence encoding.

We also found a significant blink-by-pair type interaction effect on temporal distance ratings ($ß = .0062$, $SE = .0020$, $z = 3.10$, $p = .0019$). When analyzing the two pair types separately, we found that blink rate significantly predicted temporal distance ratings for boundary-spanning item pairs ($ß = .010$, $SE = .0030$, $z = 3.38$, $p = .00074$), but not for same-context item pairs ($ß = -.0026$, $SE = .0026$, $z = -1.00$, $p = .32$; **Figure 4F**). This finding suggests that meaningful context shifts predicted stronger coupling between prolonged blinking patterns and the amount of subjective time encoded into long-term memory.

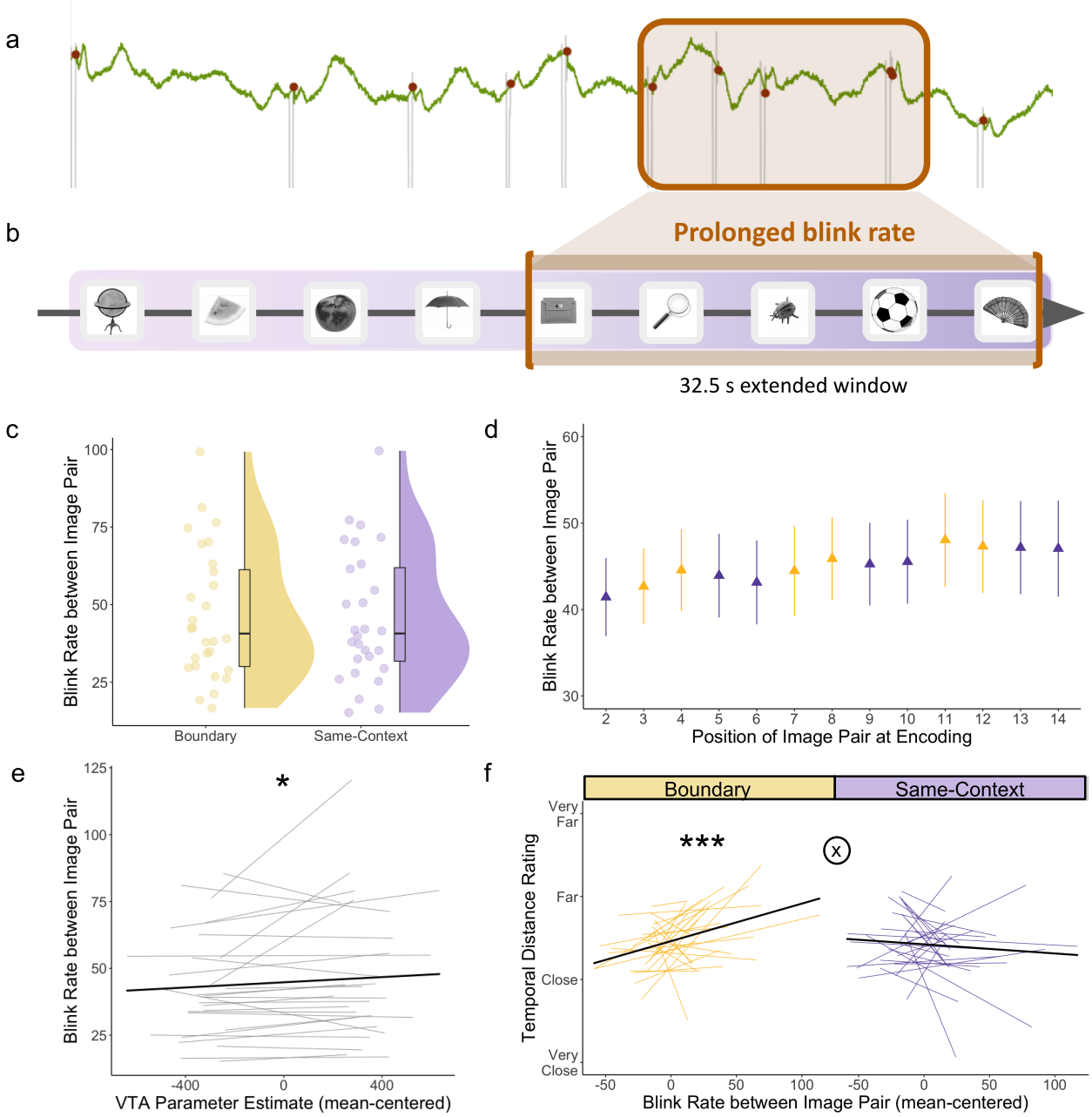

Figure 4. Event boundary-evoked VTA activation predicted greater sustained blinking between to-be-tested item pairs, and this blink pattern predicted later time dilation specifically between boundary-spanning item pairs in memory. (A) Example pupil timeseries for a subset of an encoding block. (B) Schematic of blink window of interest during event sequence encoding. Prolonged blink rate was captured during each 32.5s window between the onset and offset of to-be-tested item pairs (bracketed in orange). To calculate blink rate, the number of blinks was divided by the number of usable eye tracking datapoints in the time windows of interest. (C) An overall comparison between mean blink rate between to-be-tested images spanning an event boundary (yellow) or from the same context (purple). Each dot represents averaged data from one participant. (D) Mean blink rate during these longer time windows, plotted by item pair position at encoding (14 tested pairs total; first pair excluded). Yellow triangles represent boundary-spanning item pairs, while purple triangles represent same-context item pairs. In order of pair presentation at encoding, the boundary-spanning pairs were the 3rd, 4th, 7th, 8th, 11th, and 12th item pairs. Error bars represent SEM. (E) Participant-level trendlines plotting the relationship between trial-level VTA parameter estimates (mean-centered) and more sustained blinking patterns between to-be-tested item pairs. The dark, bold line represents the average linear

trend across participants. Statistical significance refers to results from trial-level linear mixed effects model. (F) Participant-level trendlines plotting the relationship between prolonged blink rate (mean-centered) and temporal distance ratings for boundary-spanning pairs (yellow; left) and same-context pairs (purple; right). Blink rate was mean-centered for each condition separately. The dark, bold line represents the average trendline across participants, also for each condition separately. Statistical significance refers to results from trial-level cumulative link models. The circled "X" symbol represents a significant condition-by-blink rate interaction effect on temporal distance ratings with $p < .01$. ***$p < .001$; *$p < .05$.

Testing the specificity of blink and distance memory measures to the dopaminergic system. Recent findings from this same dataset showed that pupil-linked arousal and locus coeruleus (LC), a key hub of the brain's arousal and noradrenergic system, were associated with boundary-related impairments in temporal order memory, an objective measure of memory separation (Clewett et al., 2024). An important open question, then, is whether our current findings on subjective temporal memory are linked to arousal-related neuromodulation more generally. According to theoretical frameworks of event segmentation (Zacks & Sargent, 2010), both these catecholaminergic systems are well positioned to elicit a global updating signal when event transitions occur. However, it is possible that they contribute to memory separation in different ways: the noradrenergic system via changes in objective temporal order memory accuracy and the dopaminergic system via subjective distortions in temporal memory (Rouhani et al., 2024).

To test this idea, we ran the same mixed effects modeling analyses as above, but with tone-related LC activation rather than VTA activation as the predictor of interest. The LC was visualized in each participant using neuromelanin-sensitive MRI, a technique that is sensitive to the magnetic signature of neuromelanin and water content in LC neurons. For details about these sequences and procedures for hand-drawing each participant's LC ROI mask, see Clewett et al. (2024). There were no significant relationships across any of these analyses, including models relating LC activation to temporal distance ratings, local blink count, and prolonged blink rate (all ps > .05).

Conversely, to examine whether VTA activation specifically predicted temporal distance memory and not order accuracy, we ran a generalized linear mixed effects model that included tone-related VTA activation as a fixed-effect predictor of order accuracy (correct = 1, incorrect = 0). Importantly, unlike the LC (Clewett et al., 2024), there was no main or pair type-related interaction effect of VTA activation on temporal order memory ($p > .05$).

Taken together, these results first suggest that blinks are indeed closely tied to dopaminergic activity as opposed to arousal processes more generally. Further, they suggest that dopaminergic processes may enhance memory separation by modulating subjective representations of time in memory, whereas the noradrenergic system may modulate objective memory accuracy for temporal order.

Discussion

Segmenting continuous experience into distinct events helps structure memories in ways that support adaptive behavior. One way this structure might be achieved is through the subjective 'stretching' of remembered time across an abrupt change in context, such as a shift in location, goal, or mood (for review, see DuBrow, 2024; Clewett et al., 2019, 2020; Ezzyat & Davachi, 2014; Cowan et al., 2024). Although these subjective distortions can belie the actual passage of time, they may serve a functional role in delineating boundaries between events in both perception and memory. In the current

neuroimaging study, we replicated this time dilation effect in memory and found that context shifts, or event boundaries, elicited transient increases in ventral tegmental area (VTA) activation – a key hub of the dopamine system – and blinking. VTA activation was associated with both momentary and sustained increases in blink rate, supporting a putative link between blink behavior and dopaminergic activity. Finally, stronger VTA responses and elevated blink rates at boundaries predicted greater time dilation between item pairs spanning those same boundaries. Together, these converging results suggest that dopaminergic signaling may contribute to the mnemonic separation of distinct events by expanding the temporal gap between them.

Our findings help bridge separate lines of research linking dopamine to episodic memory and temporal processing. We first showed that context shifts predicted stronger activation of the VTA, consistent with prior work showing that dopamine flags novel and salient stimuli (Duszkiewicz et al., 2019; Shohamy & Adcock, 2010). Context shifts also predicted brief increases in blinking, aligning with studies showing that blinks tend to occur near event transitions, including punctuation marks in text passages or breakpoints in everyday conversations (Hall, 1945; Wyly et al., 2023; Nakano et al., 2009; but also see Nakano et al., 2013 for an alternative interpretation). Moreover, VTA responses to boundary tones, which signaled task and perceptual switches, predicted transient increases in blinking. This finding aligns with recent evidence that discrete blinks are associated with fMRI activation in dopaminergic regions, including the VTA and substantia nigra (Demiral et al., 2023). Overall, these results support the idea that VTA activation and blinks mark transition points in experience.

Why might dopaminergic processes be engaged at event boundaries? One possibility is that dopamine facilitates the rapid updating of event models during sudden or unexpected changes in the environment. Supporting this view, prior neuroimaging work shows that dopaminergic brain regions – such as the substantia nigra and basal ganglia – are activated when participants make predictions about the next few seconds of videos depicting everyday activities (e.g., gardening). When these intervals contain an event boundary, participants tend to make less accurate predictions (Zacks et al., 2011). Dopamine may signal high prediction error at event boundaries, indicating that a new mental representation of the world is needed to represent unfolding events more accurately (Zacks et al., 2011; also see Zacks et al., 2007). It has also been shown that VTA activation relates to moments of surprise in more naturalistic settings, such as watching videos of basketball games (Antony et al., 2021). However, given that the structure of our task was largely predictable, we speculate that it is unlikely that prediction errors and surprise accounted for boundary-related patterns of VTA activation in the current sequence paradigm.

An alternative, more plausible explanation for boundary-evoked dopaminergic activity is that it signals contextual novelty during dynamic experience. It has been theorized that the VTA releases dopamine into the hippocampus in response to ‘common novelty’ – that is, stimuli that are novel under current conditions but not completely new (Duszkiewicz et al., 2019). Following this logic in the current study, each context change was relatively novel within its local temporal context (i.e., block), because the tone switches occurred infrequently and introduced a pitch that was unique to a given block. Thus, dopamine might signal a kind of common novelty at these transitions within sequences, marking the end of one meaningful event and the start of the next.

Consistent with our key hypothesis, we also found that higher boundary-related VTA activation predicted greater time dilation effects in subsequent memory, with individuals remembering item pairs as being encountered farther apart in time if they spanned a boundary. This finding aligns with prior

research showing that dopaminergic processing relates to changes in internal representations of time. For example, studies in humans have found that encountering salient oddball stimuli, linked to dopamine signaling (Bunzeck & Düzel, 2006), can lead individuals to overestimate the duration of those stimuli (see Failing & Theeuwes, 2016; Gupta, 2022; Ongchoco, Wong, & Scholl, 2023). However, we note that this effect of VTA activation on time dilation did not differ between conditions, so we cannot draw strong conclusions about specificity – the possibility that this coupling only occurs at event boundaries.

The time dilation we observed aligns with existing conceptual frameworks of temporal processing, including the dopamine clock hypothesis and contextual-change hypothesis of remembered duration. According to these models, both dopamine (Meck, 1983; 1996; see Fung, Sutlief, & Hussain Shuler, 2022) and the number of contextual changes stored in memory (Block, 1992, Block & Zakay, 1996) serve to expand internal representations of time. One intriguing possibility is that boundary-induced VTA activation and dopamine release boost encoding of local context changes, constructing more memories of salient experiences. As a result, there is a greater amount of episodic information and details available at retrieval, leading to overestimations of retrospective time. Future work could test this idea by examining whether boundary-induced VTA activation relates to increases in local source encoding processes, as boundaries have been shown to reliably enhance source memory for concurrent information (Clewett et al., 2020; Cowan et al., 2024; McClay et al., 2023). We suggest that these dopamine-mediated temporal distortions may occur via modulation of hippocampal activity, given its well-known role in supporting the storage and retrieval of temporal and source information (see Howard & Eichenbaum, 2013).

On a larger timescale, we observed that prolonged periods of blinking across boundaries predicted remembered time. This relationship was stronger for periods spanning contextual change versus contextual stability, suggesting that boundary-specific features like contextual novelty and task relevance might be critical for shaping memories of time in a meaningful way. Indeed, our analytical approach to the blink data was novel in that prior eye-tracking studies have either measured discrete blinks after individual stimuli (e.g., Terhune, Sullivan, & Simola, 2016) or longer periods of spontaneous blinking offline or during rest. In particular, this spontaneous blinking may be relatively noisy and not necessarily tied to meaningful changes in behavior. For example, spontaneous blink rate has been linked to dopaminergic processes in non-human primates and humans with neuropsychiatric disorders (for review, see Jongkees & Colzato, 2016). Our current study assessed blinking during a behaviorally relevant time window during memory encoding, perhaps leading to a stronger and more meaningful coupling between blinking and dopaminergic activity. One possibility, then, is that blinking may better track dopamine dynamics online and over longer periods of time, potentially explaining some of the mixed findings in the blink-dopamine literature (see Blin et al., 1990; Demiral et al., 2022, 2023; Jongkees & Colzato, 2016; Strakowski et al., 1996; Strakowski & Sax, 1998),

There are several limitations in the current study that warrant consideration. First, fMRI cannot establish a causal link between dopaminergic processing and time dilation in memory, nor can it directly assess neurotransmitter activity (see Hauser, Eldar, & Dolan, 2017). Second, while we used a highly specific, data-driven algorithm to locate blink artifacts, examining electrical activity near the eye offers a more direct method of detecting blinks (Cruz et al., 2011). Third, there are mixed findings concerning the existence or strength of an association between blink rate and dopaminergic processing. Some studies challenge the relationship between certain measures, such as striatal dopamine synthesis capacity, and blink rate (Sescousse et al., 2018; van den Bosch et al., 2023; also see Dang et al., 2017). Additional

factors that could influence blink rate include the activity of other neuromodulators like serotonin (see e.g., Gunduz et al., 2024), as well as inattentiveness or fatigue (see Maffei & Angrilli, 2018). However, because event boundaries typically elicit an increase in attention (Heusser et al., 2018), it is unlikely that the effects we observed were solely or predominantly driven by fatigue or time-on-task effects (Stern et al., 1994; Maffei and Angrilli, 2018). Future studies should examine how relations between blinking and cognitive processing may be altered under different conditions, including whether blinking is measured online or during rest.

In summary, our findings revealed that different indirect markers of dopaminergic processing are related to time dilation effects in memory. We speculate that these subjective time distortions are highly adaptive, because they might serve to increase the representational distance between adjacent episodes in memory. These results are an important first step towards unraveling the complex role of dopamine activity in shaping everyday memory organization. Still, additional techniques are needed to assay neuromodulatory activity more directly and at a higher temporal resolution (e.g., Bang et al., 2023). Ultimately, these findings will promote a deeper understanding of how internal representations of time mold the complexity of our experience into a meaningful record of past events.

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Supplementary Figures

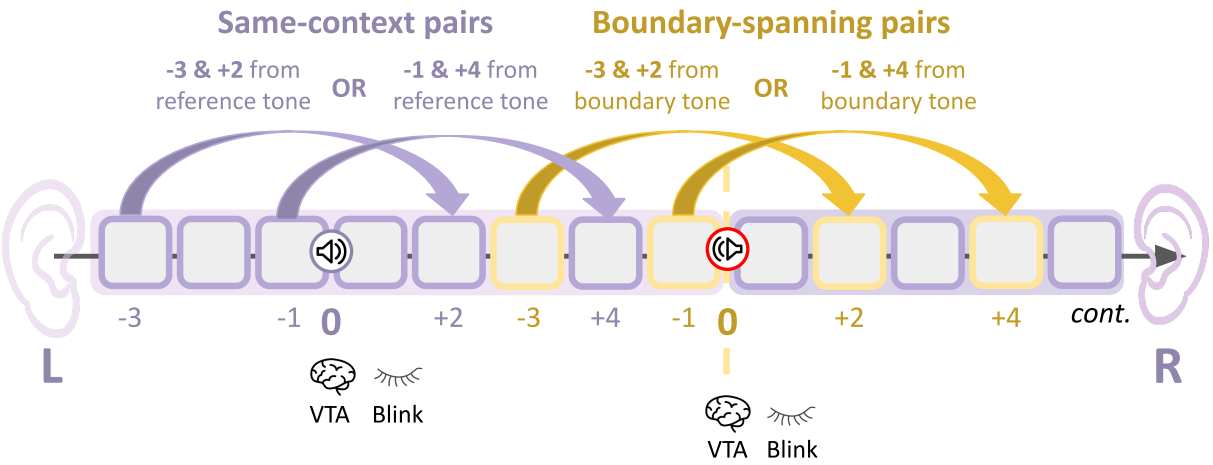

Figure S1. Example analysis schematic for event sequence. Several analyses examined how indirect measures of brief dopaminergic processes during encoding (i.e., tone-related VTA activation or local blink count) predicted larger-scale outcomes (i.e., memory for temporal distance or blink rate between to-be-tested pairs). For these analyses, one intervening tone was selected for each to-be-tested pair in the event encoding sequence. Arrow connections represent to-be-tested pairs, including same-context pairs (purple) and boundary-spanning pairs (yellow). For boundary-spanning pairs, the selected tone was the tone switch that denoted an event boundary (red circle). Depending on the particular boundary-spanning pair, the to-be-tested items fell either 3 positions before (-3) and 2 positions after (+2) the tone switch or 1 position before (-1) and 4 positions after (+4) the tone switch. For same-context pairs, the selected tone (purple circle) matched these positions (i.e., -3 and +2 or -1 and +4).