Behavioral evidence for memory replay of video episodes in macaque monkeys

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25 **ABSTRACT (148 WORDS)**

26 Humans recall the past by replaying fragments of events temporally. Here, we
 27 demonstrate a similar effect in macaques. We trained six rhesus monkeys with a
 28 temporal-order judgement (TOJ) task and collected 5000 TOJ trials. In each trial, they
 29 watched a naturalistic video of about 10 s comprising two across-context clips, and
 30 after a 2-s delay, performed TOJ between two frames from the video. The monkeys
 31 apply a non-linear forward, time-compressed replay mechanism during the
 32 temporal-order judgement. In contrast with humans, such compression of replay is
 33 however not sophisticated enough to allow them to skip over irrelevant information
 34 by compressing the encoded video globally. We also reveal that the monkeys detect
 35 event contextual boundaries and such detection facilitates recall by an increased rate
 36 of information accumulation. Demonstration of a time-compressed, forward replay
 37 like pattern in the macaque monkeys provides insights into the evolution of episodic
 38 memory in our lineage.

39
 40 Keywords: drift diffusion model framework; event boundary detection; forward
 41 replay-like pattern; naturalistic material; time compression of memory traces;
 42 temporal order judgement

43
 44 **Impact Statement:** Macaque monkeys temporally compress past experiences and use a
 45 forward-replay mechanism during judgment of temporal-order between episodes.

46

47 INTRODUCTION

48 Accumulating evidence indicate that non-human primates possess the ability to
49 remember temporal relationships among events (*1–3*). The apes can remember the
50 movies based on the temporal order of scenes (*4*) and keep track of past time of
51 episodes (*5*), whereas macaque monkeys possess serial (*6*) and ordinal positions
52 expertise for multi-item lists (*7*) and are able to categorize sequences of fractal images
53 by their ordinal number (*8*). However, keeping track of and remembering the
54 positional coding and forming associative chaining (*9, 10*) of lists of arbitrary items
55 might diverge from how a semantically linked, temporally relational representation of
56 real-life events is maintained and utilized.

57 In the human literature, it has been shown that episodes can be replayed
58 sequentially based on learned structures (*11*), sensory information (*12*), and pictorial
59 content (*13*). These findings suggest the possibility that monkeys can rely on a similar
60 mechanism in recalling events that are linked temporally during temporal order
61 judgement (TOJ). However, the extent to which mechanisms of temporal order
62 judgement overlap across humans and monkeys remains undefined. One hypothesis is
63 that the macaques can similarly rely on a scanning model for information retrieval –
64 akin to serial replay of episodes – to perform temporal order judgements (*2, 3*). By
65 this account, following encoding streams of events, the animal performs retrieval
66 through replaying the stream of information in a forward direction. In this way,
67 retrieval time (RT) would be positively correlated to the temporal distance between
68 the beginning of the stream and the target location. This account aligns with recent
69 findings in rodents (*14*) and in humans of memory replay during cued-recall tasks
70 across fragments of video episodes, showing characteristics of replay proceeding in a
71 forward manner and being temporally compressed (*12*). Moreover, a more
72 sophisticated feature of this mechanism is that memory replay is a fluidic process in
73 which subjects are able to skip flexibly across sub-events (*12*). By this account,
74 subjects can omit non-informative parts of episodes and replay a shorter episode
75 (shorter than physical perception) in memory, which contains less information. This

interpretation is supported by other works on mental simulation of paths (15) and video episodes (12). This latter account constitutes a global compression of parts of episodes (that allows skipping across sub-events) and is regarded as substantially superior to a strict forward replay mechanism.

In order to simulate dynamic flow of information as in real-life scenarios, we used naturalistic videos as experimental material to study the mechanism of memory retrieval of event order in the monkeys, which are more realistic than arbitrary items or images that were used in previous studies (1, 16). We used a temporal order judgement paradigm to examine whether and to what extent the pattern underlying memory retrieval conforms to a time-compressed, forward replay mechanism. In each trial, monkeys watched a naturalistic video, which is composed of two clips, and following a 2-s retention delay, made a temporal order judgement of choosing the frame that was shown earlier in the video between two frames extracted from that video (**Figure 1A**). The two frames were either extracted from the same clip or from two different clips of the video. Given that analyses on response latency can provide insights into the extent to which the monkeys' behavior might conform to the two putative replay models outlined above, we looked into the RT data. By applying representational similarity analyses (RSA), the Linear Approach to Threshold with Ergodic Rate (LATER) model and generalized linear models on the RT data, we examined the presence of replay-like behavioral patterns in the monkeys. Specifically, if monkeys recall the frames by their ordinal positions, this would imply a linear increase in their retrieval times. In contrast, if the memory search entails a complex processing of the content determined by their semantically linked, temporally relational linkage within the cinematic footage, we should observe evidence for some non-linear pattern.

Our results showed that macaque monkeys adopt a time-compressed, replay-like pattern to search within representation of continuous information. In addition, by comparing between human and macaque data, we adjudicated between the two aforementioned aspects of the replay models. The results showed a discrepancy between the two species that the monkeys do not compress the cinematic events

globally as effectively as in humans. Finally, we revealed that the monkeys can make use of context changes to facilitate the memory retrieval by an increased rate of information accumulation in a drift diffusion model framework.

RESULTS

Human-like forward replay in macaques

All six monkeys learned to perform the temporal order judgement task with dynamic cinematic videos as encoded content (**Figure 1B** left and **Movie S1**). Note that there are two main kinds of TOJ trials: “within-context” and “across-context” trials (**Figure 1A**). Here, we will be first concerned with the response times (RT) data from “within-context” trials to examine TOJ mechanisms, while RT data from “across-context” trials will be used to test for effects by context changes (event boundary) in subsequent subsections.

We first addressed our main hypothesis by examining changes in RT using only within-context trials. We regressed RT as a function of temporal similarity (TS) for within-context trials and found a significant negative relationship between TS and RT, all $P < 0.001$ (one monkey with $P = 0.02$, **Table S2** upper panel and **Figure S1**). The results were replicated when considering only correct trials or only incorrect trials separately (**Table S2** middle/bottom panels). This suggests that the monkeys are systemically faster in identifying frames that are located earlier in the video. One possibility is that the monkeys perform TOJ relying on some form of memory replay by recalling the events coded at specific ordinal positions in a serial manner. To test this hypothesis, in each trial we explicitly looked at the relationship between RT and the location of the frame within the video which the monkeys have chosen (“chosen frame location”, as indexed by the ordinal frame numbers in the video). By correlating RT as a function of chosen frame location, we indeed found a significantly positive relationship between RT and chosen frame location in all monkeys, all $P < 0.001$ (two monkeys with $P = 0.002$, **Figure 1C** and **Table 1** top panel). The same pattern was replicated when only correct trials (**Table 1** middle panel) or incorrect

135 trials (**Table 1** bottom panel) were included for analysis, suggesting that the putative
 136 retrieval RT patterns are not affected by the memory outcome. This pattern of result is
 137 also replicated using logarithmically transformed RT data, all $P < 0.001$. After taking
 138 individual variability into consideration, we obtained the same result with reciprocal
 139 latency as a function of chosen frame location for the average of all monkeys (**Figure**
 140 **2A**). While the result suggests that the monkeys' judgments are faster to respond to
 141 probe frames that are located at the earlier parts of the videos, it also indicates that the
 142 search does not follow a linear function. This non-linear relationship is important
 143 because it rules out alternative explanations that the main effects are simply resultant
 144 from positional effects. Rather, the non-linear change in slope indicates there are other
 145 factors in play that the monkeys might group (or parse) the content according to the
 146 relational storyline structure, and do not merely recall the frames/items as of their
 147 ordinal positions in a fixed linear manner.

148 To address the direction and speed of memory reply, reaction times at retrieval
 149 were compared between TOJ frames that are within Clip 1 versus Clip 2. During TOJ
 150 retrieval, frames that were presented in Clip 1 (mean reaction time $\bar{M} = 1.59$ s) were
 151 retrieved significantly faster than the frames that were experienced in Clip 2 (mean
 152 reaction time $\bar{M} = 1.88$ s) (one-tailed $t_5 = -4.533$; $P = 0.003$; Cohen's $d = -0.54$; 95%
 153 CI: $[-\infty, -0.158]$; log(RT): one-tailed $t_5 = -6.473$; $P = 6.558 \times 10^{-4}$; Cohen's
 154 $d = -0.69$; 95% CI: $[-\infty, -0.114]$). These findings again confirm that the replay of
 155 the video takes place in a forward direction.

156 Moreover, since the latency required to responding to the chosen frames is much
 157 smaller than the duration of the videos themselves, the replay of the video must have
 158 been conducted at a compressed speed (i.e., memory replay was faster relative to
 159 perception during video-watching). The difference in reaction time between the very
 160 first frame and the last frame was averaged at 942 ms (range: 468 – 1859 ms). This is
 161 equivalent to 94.2 ms to scan through per second of the video and corresponds to a
 162 compression factor of 10.61 during replay in these monkeys (compression factor for
 163 each monkey: Jupiter = 13.59, Mars = 7.39, Saturn = 14.80, Mercury = 21.37, Uranus =
 164 17.78, Neptune = 5.38, see **Figure 1C**). This is comparable to a compression factor of

165 13.7 observed in humans, corroborating the notion of forward replay and those
166 findings in humans (12).

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168 **Figure 1. TOJ task schema and RT results.** (A) On each trial, the monkey watched
169 a video (8-12s, comprising two 4-6s video clips), and following a 2-s retention delay,
170 made temporal order judgement between two probe frames extracted from the video.
171 The monkeys were required to choose the frame that was presented earlier in the
172 video for water reward. (B) Task performance of six monkeys. Proportion correct for
173 the six monkeys (left); mean reaction times for three trial types (right). Error bars are
174 standard error of the mean (SEM). *** denotes $P < 0.001$. (C) Linear regression
175 analysis of reaction time (RT) as a function of chosen frame location, see also Table 1.
176 (D) Linear regression analysis of RT as a function of chosen frame location for each
177 human participant, see also Table S3. In (C) and (D), black lines and orange lines
178 refer to lists of non-primate and primate videos respectively (with five repetitions
179 collapsed for monkeys and two repetitions collapsed for human participants). All

180 responses in within-context are shown, with cyan and magenta dots denoting whether
181 the chosen probe frames were extracted from either Clip 1 or Clip 2 respectively.

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183 We also ran the same sets of analyses on human participant data for comparison
184 between the two species. Showing a completely opposite pattern, regression analyses
185 on human subjects showed a positive relationship between temporal similarity (TS)
186 and RT for all participants, all $P < 0.01$ (**Table S3** upper panel). These results imply
187 that the more similar the two frames to be judged, the longer time needed for retrieve
188 temporal order information. There was also no observable RT/ chosen frame location
189 slope in the human data (if anything, it shows an opposite trend; see **Figure 1D** &
190 **Table S3** bottom panel). In sum, we found that our monkeys might have performed
191 TOJ of video episodes using a forward search of ordered elements in the mnemonic
192 representation at the time of memory test with a non-linear compression function. By
193 contrasting with **Figure 2A**, it is notable that when reciprocal latency as a function of
194 chosen frame location is analyzed in the humans, as shown in **Figure 2B**, a very
195 different pattern emerges, suggesting some form of mechanistic discrepancy between
196 the species. We will examine these aspects in detail in the next section.

197 We have also run a sliding-window average analysis to illustrate how accuracy
198 varies as a function of the target frames location (**Figure 2C** for monkeys; **Figure 2D**
199 for humans). It is interesting that in both species there is a mild trend that their
200 proportion correct show a little blip right after the beginning of Clip 2. This
201 characteristic might be related to their ability in detecting the boundaries (cf. results
202 and discussion related to **Figure 6**). However, given that we are primarily concerned
203 with using response times as quantitative measures to examine the TOJ mechanisms,
204 we do not speculate further into this aspect.

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Figure 2. Moving average analysis based on reciprocal latency and accuracy for monkeys (left panels) and human participants (right panels). (A) Reciprocal latency for monkeys as a function of chosen frame location for the average of all animals (upper panel) in within-context condition, with results of six individual monkey shown (lower panel). The relationship between chosen frame location and RT follows a non-linear pattern. **(B)** Reciprocal latency for human participants as a function of chosen frame location for the average of all human subjects (upper panel) in within-context condition, with results of individual subject shown (lower panel). In **(A)** and **(B)**, shaded region denotes confidence intervals; the blue line denotes the mean boundary location between Clip 1 and Clip 2 across all trials (116th frame). **(C)** Individual monkey's proportion correct as a function of target frame location in within-context condition. Horizontal blue lines denote chance level accuracy. **(D)** Individual human subject's proportion correct as a function of target frame location in within-context condition.

Table 1. One sample t-tests results of the slopes of RT as a function of chosen frame location for each monkey. The three panels correspond to analyses performed using all trials (top), only correct trials (middle), and only incorrect trials (bottom). Same slope patterns were observed irrespective of correctness.

Monkeys	Mean (SEM)	t-statistics	d.f.	p-value	Cohen's d	95% confidence interval	
						Lower	Upper
Slope of reaction times/chosen frame location tested against zero (all trials)							
Jupiter	0.0015 (0.0017)	6.06	49	<0.001	0.86	0.0010	0.0020
Mars	0.0031 (0.0027)	7.93	49	<0.001	1.12	0.0023	0.0038
Saturn	0.0007 (0.0016)	3.29	49	0.002	0.47	0.0003	0.0012
Mercury	0.0017 (0.0018)	6.77	49	<0.001	0.96	0.0012	0.0022
Uranus	0.0011 (0.0014)	5.12	49	<0.001	0.72	0.0006	0.0015
Neptune	0.0024 (0.0049)	3.34	46	0.002	0.49	0.0009	0.0038
Slope of reaction times/chosen frame location tested against zero (correct trials)							
Jupiter	0.0023 (0.0042)	3.85	49	<0.001	0.55	0.0011	0.0035
Mars	0.0029 (0.0034)	5.98	49	<0.001	0.85	0.0019	0.0038
Saturn	0.0009 (0.0021)	3.03	49	0.004	0.43	0.0003	0.0015
Mercury	0.0018 (0.0026)	4.79	49	<0.001	0.68	0.0010	0.0025
Uranus	0.0012 (0.0021)	4.01	49	<0.001	0.57	0.0006	0.0018
Neptune	0.0030 (0.0070)	2.94	46	0.005	0.43	0.0009	0.0051
Slope of reaction times/chosen frame location tested against zero (Incorrect trials)							
Jupiter	0.0016 (0.0032)	3.49	49	0.001	0.49	0.0007	0.0025
Mars	0.0044 (0.0039)	8.00	49	<0.001	1.13	0.0033	0.0055
Saturn	0.0011 (0.0025)	3.20	49	0.002	0.45	0.0004	0.0018
Mercury	0.0022 (0.0026)	5.96	49	<0.001	0.84	0.0014	0.0029
Uranus	0.0012 (0.0019)	4.52	49	<0.001	0.64	0.0007	0.0017
Neptune	0.0034 (0.0075)	3.15	46	0.003	0.46	0.0012	0.0056

Discrepancy with humans: Compression of replay is local but not global

It has been shown in the humans that memory replay is not a straightforward recapitulation of the original experience. Subjects can skip through their memories on a faster time scale across segments of a video episode than within-segment by skipping flexibly over salient elements such as video boundaries within episodes (12). We propose two possible models with respect to whether the compression is global or not over the whole video. If there is a global compression of the video during replay, the speed to initiate replay for Clip 2 would be sooner than the endpoint of replay for Clip 1 due to the animal being able to skip over the entire Clip 1 to the beginning of Clip 2 (Global-compression model, [Figure 3A right panel](#)). However, if the monkeys are not equipped with the ability of skipping video

239 segments during the replay process, we would expect a linear increase of retrieval
 240 time with chosen frame location irrespective of the boundary (Strict forward model,
 241 **Figure 3A left**). We tested statistically whether the speed to initiate replay for Clip
 242 2 slowed down compared to that for Clip 1. We divided each video into eight equal
 243 segments and derived cross-correlations computed on pairs of averaged
 244 condition-wise RTs based on chosen frame locations using a representational
 245 similarity analysis. The RT for TOJ between each segment of the video increases
 246 linearly according to their position in encoding (**Figure 3B left**). We tested these
 247 against a hypothetical “Strict forward” model and found significant correlation with
 248 the Strict forward model ($r = 0.66$, $P = 0.009$), but not with the Global compression
 249 model ($r = -0.16$, $P = 0.802$) (**Figure 3B right**). These statistics also remain significant
 250 for the Strict forward model when we divided the video into either 10 ($P = 0.030$) or
 251 14 equal segments ($P = 0.020$). The same patterns are also obtained when considering
 252 correct trials (Strict forward model: $r = 0.37$, $P = 0.040$; Global compression model: r
 253 $= -0.02$, $P = 0.545$) or incorrect trials (Strict forward model: $r = 0.45$, $P = 0.010$;
 254 Global compression model: $r = -0.06$, $P = 0.545$) separately. Contrarily, these
 255 correlational patterns with the Strict forward model are not observed in the human
 256 subjects ($r = -0.11$, $P = 0.703$), but rather we observe a trend favoring the global
 257 compression model instead ($r = 0.39$, $P = 0.069$) (**Figure 3B right**).

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Figure 3. Model comparison using representative similarity analysis. (A) Visualization of two candidate models as RDMs. Pattern of reaction time (rank-transformed values) as a function of increasing chosen frame location underlying the two hypothetical models. The colors of Clip 1 and Clip 2 evolve increasingly with the temporal progression of the video (left); and their respective hypothetical RDMs (right). The reduction in RT indicated by an arrow between Clip 1 and Clip 2 is defined as “offset”; the magnitude of such “offset” is arbitrary but see further analysis in Figure 4. (B) We segmented the videos into eight equal segments and the RDMs contain pairwise Euclidean distances between these different segments for the group average (Monkeys: left; humans: right) and each individual separately (Monkeys: left bottom; humans: right bottom). RDM correlation tests between behavioral RDMs and two candidate RDMs show that the monkeys replay the footage using a Strict forward strategy and show little evidence for the Global compression strategy. Humans show an opposite pattern from the macaques. In the humans (right panels), the Global compression model shows a higher correlation with behavioral RDM (marginally insignificant $r = 0.39$, $P = 0.069$) than with the Strict forward model ($r = -0.11$, $P = 0.703$). Error bars indicate the standard error of the mean based on 100 iterations of randomization. P values are FDR-corrected (***) denotes $P < 0.001$.

285 **Factors modulating the model: “offsets” for search and memory-search RT slope**

286 We defined the reduced RT to initiate replay for Clip 2 as “offsets” in initiating
 287 search in Clip 2 by skipping the non-informative Clip 1 (**Figure 3A**). With respect to
 288 the detailed differences between the two models, one may wonder whether and how
 289 the “offsets” between Clip 1 and Clip 2 might influence the results. Especially for the
 290 Global compression model, changes of this parameter will cause changes in the
 291 RDMs. To address this concern, we simulated an array of RDMs by systemically
 292 varying the offset parameter and produced 11 hypothetical models ranging from an
 293 absolute Global compression model (model 1, most left in **Figure 4A**), to a
 294 Strict-forward model (model 6, middle in **Figure 4A**), and beyond (7th to 11th models,
 295 right in **Figure 4A**). We then tested each individual monkeys’ data with each of these
 296 11 models. The results show that the Spearman correlation values between the
 297 monkey’s data and hypothetical RDMs reach an asymptote of around $r = 0.8$ as the
 298 offset parameter tend to zero, and notably, the correlation values only improve
 299 minimally with increasing offsets (**Figure 4B**, with individual’s RT RDM displayed
 300 as insets). These suggest that the monkeys have processed the video as a holistic
 301 chunk of information rather than taking advantage of skipping the non-informative
 302 first clip when the two probe frames were in Clip 2. *For comparison, we also tested*
 303 *human participant’s data against each of these 11 hypothetical models and found a*
 304 *completely opposite pattern in the humans (**Figure 4C**, with individual’s RT RDM*
 305 *displayed as insets).* Taken together, we reveal a discrepancy between human and
 306 macaque performance in terms of their ability to compress past (irrelevant)
 307 information during TOJ.

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Figure 4. Strict forward model provides better fit to the RT data in monkeys but not in humans. (A) “Offsets” are defined as the magnitude of reduced RT when the frames were in Clip 2. 11 hypothetical models with their reaction time patterns (top) and RDMs (bottom). We systemically varied the “offset” parameter while keeping a constant slope. These models progressively range from an absolute Global compression model (model 1, most left), to a Strict-forward model (model 6, middle), and beyond (7th to 11th models, right). The numerals below the RDMs denote the magnitude of the respective offsets. (B) Each monkey’s data is tested against each of these 11 hypothetical models. The Spearman correlations increase as a function of offset magnitude between Clip 1 and Clip 2 until reaching an asymptote when the offset value is around zero, which corresponds to the Strict forward model (model 6 in **Figure 4A**; see also **Figure 3**). Individuals’ RT RDMs are shown in insets. (C) Each human participant’s data is also tested against each of these 11 hypothetical models. The Spearman correlations decrease as a function of offset magnitude between Clip 1 and Clip 2 until reaching an asymptote when the offset value is around zero. This confirms the hypothetical discrepancy between the two species (see also **Figure 3B**).

We have considered a further factor – slope of RT/chosen frame location – in our model, which might be relevant for the question at hand. To take negative slopes into consideration, we calculated RDM based on the relative differences of each pair of segments. Then, we transformed the vectors “offset” and “slope of RT/chosen frame location” into two arrays and displayed them as three-dimensional mesh/surface plots. In **Figure 5**, in addition to “offsets”, we showed that the correlation between model and monkeys’ data also increase as the slope of RT/chosen frame location increases. In contrast, the correlation values for human data seem to be driven by the “offsets” (cf. **Figure 4C**), and in terms of “slope” going in an opposite direction from the monkeys (cf. **Figure 2A-B**). This visualization converges with other current findings that the slope of RT/chosen frame location does also matter to highlight the cross-species differences (e.g., by contrasting **Figure 1C** vs. **1D**).

Figure 5. Visualization for RDM correlation as modulated by “offset” and “slope” in three-dimensional space (slope, offset, RDM correlation). (A) Monkeys data (B) Human participants data.

Context changes (event boundary) increase rate of rise in decision information

We have thus far focused on how the monkeys retrieve the order of frames when information was equated within contexts, but how contextual changes would aid temporal order judgement processes remains to be examined. It was evident that the monkeys retrieved the temporal order of frames with numerally different speeds for the three trial-types, across- vs. within-Clip1 vs. within-Clip2: $F(2, 15) = 2.32$, $P = 0.132$ (Figure 1B, right). Thus, we then compared the latency distribution of

360 within-context and across-context conditions and hypothesized that a context shift
361 would change the rate of rise of information accumulation (shift model) without
362 altering the decision threshold (swivel model) with the Linear Approach to Threshold
363 with Ergodic Rate (LATER) model (**Figure 6A**). We compared across-context and
364 within-context trials specifically and fitted the two types of LATER models separately
365 on each monkey's data (**Figure 6B**), together with an unconstrained model, which
366 supposes the reaction times of two conditions are independent from each other, and a
367 null model, which assumes there is no effect of manipulation. Using the Bayesian
368 information criterion (BIC) as an index of model comparison, the results consistently
369 indicate that the shift model is better than the swivel model in all six monkeys (range
370 of $\Delta\text{BIC} = [14.57, 300.07]$; **Table S1**). These results further indicate that contextual
371 changes do not alter the judgement threshold for decisions (no evidence for a swivel
372 pattern). Within a drift diffusion model framework, the results suggest that monkeys
373 accumulate information for memory decisions at a faster rate when the frames were
374 extracted from two different clips than for frames that were extracted from the
375 same-context clip, signifying a boundary effect in memory in macaque monkeys
376 which parallel closely those established findings in the humans (17). These results
377 suggest that the monkeys adopt a forward search for targets among linearly ordered
378 memory traces and they reach their memory decision threshold more quickly when
379 probe frames are extracted from the two different contexts (across-context condition).

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Figure 6. LATER model fitting of RT in across-context and within-context condition. (A) The LATER model cartoon depicts that a decision signal triggered by a stimulus rises from its start level, at a rate of information accumulation r , to the threshold. Once it reaches the threshold, a decision is initiated. The rate of rise r varies from trial to trial, obeying the Gaussian distribution (variation denoted as green shaded area). (B) Contextual change effect on the distribution of response latency for the monkeys; data from Monkey “Mars” was chosen for larger display. The red and blue dash lines show the best fits (maximum likelihood) of across-context trials and within-context trials respectively.

395 **Confirmatory GLMs for the putative patterns**

396 In order to verify whether the effects are not attributed to the basic stimulus
 397 features such as perceptual differences inherent in the across-context condition. We
 398 then performed several generalized linear models to quantify the effect sizes of several
 399 principal variables. In within-context condition, given that the monkeys would replay
 400 their experience to judge the relative temporal order of probe frames (“replay
 401 hypothesis”), we used temporal characteristics of probe frames, as represented by
 402 chosen frame location (or temporal similarity, which is essentially an inverse of frame
 403 location) as the independent variables. In across-context condition, we included a
 404 perceptual similarity measure based on feature points extracted by the SURF algorithm
 405 (SURF similarity, **Figure S2**) into the generalized linear model to reflect the extent to
 406 which the monkeys could capitalize on using contextual boundaries for TOJ judgment.
 407 The within-context GLM shows that monkey’s RT was indeed significantly faster when
 408 the probe frame was located earlier in the video, $P < 0.001$ (or in equivalent terms,
 409 when two frames were temporally closer, $P = 0.004$), confirming our main finding that
 410 the monkeys adopt a forward scanning strategy for information retrieval (**Figure 7** left).
 411 In contrast, the across-context GLM shows that there was not any significant effect of
 412 the chosen frame location on RT. Rather, the monkeys retrieve their memories
 413 significantly faster for probe frames that are contextually (or perceptually) distinct, $P =$
 414 0.004 (**Figure 7** right). These results are fully replicated when several more regressors
 415 which can potentially affect RT are additionally entered into the design matrix (**Figure**
 416 **S3**).

Figure 7. GLM results on the effects of model variables on reciprocal latency for within-context and across-context condition. The chosen frame location and the temporal similarity are variables associated with the replay hypothesis, whereas the perceptual similarity is with the context hypothesis. In within-context condition, the chosen frame location and the temporal similarity both show significant effects on RT, $P < 0.001$ and $P = 0.004$ respectively, whereas the perceptual similarity does not, $P = 0.844$. We found an opposite effect pattern in across-context condition. The perceptual similarity shows a significant effect on RT, ($P = 0.004$), while the chosen frame location ($P = 0.796$) and the temporal similarity ($P = 0.446$) do not. Effect size (in arbitrary unit, a.u.) denote the beta values. Error bars indicate SEM. *** denotes $P < 0.001$, ** denotes $P < 0.01$, * denotes $P < 0.05$. See also **Figure S3** for a GLM analysis including a full range of variables.

434 DISCUSSION

435 In light of recent reports on neural correlates underlying how humans and
 436 rodents replay their past experiences (*11, 12, 14, 18*), here, we demonstrate parallel
 437 behavioral findings in macaque monkeys with dynamic cinematic material. Previous
 438 reports of macaques succeeding in temporal order judgement indicated their ability in
 439 remembering the order of events (*1, 5, 19*) and even meta-cognitively monitor the
 440 quality of representations of temporal relations among item images (*20*). For example,
 441 Orlov et al. (*8*) suggested that monkeys can categorize stimuli by their ordinal number
 442 to aid recall of order, and Templer et al. showed that monkeys retrieve the temporal
 443 order information based on the order of events rather than elapsed time (*1*). One
 444 possible common mechanism underlying these performances is that monkeys use a
 445 forward search to identify targets in memory representation (*2*). Taking advantage of
 446 the latency data obtained during TOJ on naturalistic materials, we provide new
 447 behavioral evidence in support of the hypothesis proposed by Gower (*2*) that the
 448 monkeys can replay their memory in a serial forward manner. Our analysis further
 449 clarifies that this replay process is conducted in a time-compressed manner.
 450 Notwithstanding task differences, both humans and macaques execute retrieval with
 451 forward replay with a comparable compression factor (factors of ~11 in macaques vs.
 452 ~13 in humans, cf. (*12*), but see also (*13*)).

453 Despite the cross-species similarity, our revelation of a critical discrepancy
 454 between humans and macaques carries an important theoretical implication: humans
 455 can do both local and global compression whereas monkeys are not able to attain
 456 global compression. The implication is that mental time travel is not all-or-none.
 457 There could be multiple layers underpinning the concept of mental time travel, which
 458 entail the ability to relive the past (*21, 22*) and skipping over unimportant information
 459 (*12*). The latter aspect allows humans to recall our memories flexibly far into our past
 460 and suggest powerful computational efficiencies that may facilitate memory storage
 461 and recall. In contrast, we did not find any evidence in the macaques for their ability
 462 of making use of salient boundary cues to skip unimportant details. It thus remains

463 unknown in the current experiment how far back in time monkeys can replay their
464 memories. It has been recently shown that humans can spontaneously replay
465 experience based on learned structures, with fast structural generalization to new
466 experiences by representing structural information in a format that is independent
467 from its sensory consequences (11). The lack of global compression in the monkeys of
468 their video experience implies that the monkeys might not be able to use factorized
469 representations to allow components to be recombined in more ways than were
470 experienced (23).

471 A further caveat is that our monkeys perform their replay-like recall of the videos
472 as an effortful operation to solve a TOJ task whereas most of the extant studies on
473 replay focus on spontaneous replay patterns at rest (11), during sleep (24, 25) or
474 during task-free state (26, 27). While we have argued for the presence of replay-like
475 patterns in the monkey during TOJ, we are aware that replay is a neural phenomenon
476 supported by activity of individual neurons and implicates offline reactivation of
477 sequences of hippocampal place cells that reflect past and future trajectories (28–30).
478 However, by establishing that neither the number of intervening frames nor passage of
479 time per se determines the RT pattern (probably a mixed effect resultant from a
480 combination of both), we ruled out order- or positional- memory as the underlying
481 mechanism supporting TOJ in this task. Our results combined thus provide a novel
482 connection between various kinds of replay(-like) behaviors linking between rodents
483 and humans and provide a primate model for neuronal investigation.

484 We observed one further interesting feature here that the monkeys are able to
485 detect contextual changes to facilitate TOJ. We show that the expedited TOJ in
486 across-context condition was facilitated by contextual details, which in turn results in
487 an increased rate of rise of signal towards memory decision in a drift-diffusion
488 process. Humans studies show that contextual changes lead to segmentation of
489 ongoing information (31, 32). Our results provide evidence consistent with event
490 segmentation in the macaque monkeys and imply that macaque monkeys might be
491 capable of parsing the footage by contextual information, akin to what has been
492 shown in humans (33–36) and rodents (37).

493 Memory replay is an elaborate mental process and our demonstration of a
 494 time-compressed, forward replay-like pattern in the macaque monkeys provides
 495 insights into mapping the mechanisms and evolution of episodic memory in our
 496 lineage. There are however limitations in their ability in compressing the experienced
 497 past globally, which somehow indicates a form of primordial mnemonic rigidity. This
 498 cognitive discrepancy in our lineage should be further elucidated via
 499 electrophysiological or neuroimaging methods probing into the MTL (18, 26, 38, 39)
 500 and the neocortices (16).

501 **METHODS**

502 **Task performance**

503 The six monkeys performed the task with a significantly above chance level with
504 an overall accuracy at $67.9 \pm 1.5\%$ (mean $\pm$ SD) and with an above chance accuracy
505 for within-context trials, $t_5=14.35$, $p < 0.001$. The human participants performed the
506 task on average at $92.7 \pm 1.2\%$.

507

508 **Subjects**

509 *Macaque monkeys.* Six male rhesus macaques (*Macaca mulatta*) ($5.49 \pm 0.5\text{kg}$)
510 with a mean age of 3.5 years at the start of testing participated in this study. They were
511 initially housed in a group of 6 in a specially built spacious enclosure (max capacity =
512 12-16 adults) with enrichment elements such as a swing and climbing structures until
513 the present study began. The monkeys were then housed in pairs during
514 experimentation period according to their social hierarchy and temperament. They are
515 fed twice a day with portions of 180-g monkey chow and pieces of fruits
516 (8:30am/4:00pm). Water is available *ad libitum* except on experimental days. They are
517 routinely offered treats such as peanuts, raisins and various kinds of seeds in their home
518 cage for forage purpose. The monkeys were procured from a nationally accredited
519 colony located in Beijing outskirts, where the monkeys were bred and reared. The
520 animals are thus ecologically naive to the natural wilderness and should not have had
521 any previous encounter with other creatures except humans and their companion. The
522 room wherein they are housed is operated with an automated 12:12 (7am/7pm)
523 light-dark cycle and kept within temperate around 18-23°C and humidity of 60-80%.

524 *Human subjects.* Seven participants (mean age = 19.57 ± 1.13 , 6 female) took part
525 in the experiment. The participants were recruited from the undergraduate population in
526 East China Normal University. The participants provided informed consent and were
527 compensated 400 RMB for their time. We used the 6 unique video-trials sets and TOJ
528 frames (one unique set per monkey) correspondingly for the human subjects (subject 7
529 re-used set 1).

530 The experimental protocol was approved by the Institutional Animal Care and Use
531 Committee (permission code: M020150902 & M020150902-2018) and the University
532 Committee on Human Research Protection (permission code: HR 023-2017) at East
533 China Normal University. All experimental protocols and animal welfare adhered with
534 the “NIH Guidelines for the Care and Use of Laboratory Animals”.

535

536 **Apparatus and testing cubicle**

537 The testing was conducted in an automated test apparatus controlled by two
538 Windows computers (OptiPlex 3020, Dell). The subject sat, head-unrestrained, in a
539 wheeled, specially-made Plexiglas monkey chair (29.4cm × 30.8cm × 55cm) fixed in
540 position in front of a 17-inch infrared touch-sensitive screen (An-210W02CM,
541 Shenzhen Anmite Technology Co., Ltd., China) with a refresh rate at 60 Hz. The
542 distance between the subjects’ head and the screen was kept at ~20 cm. The
543 touch-sensitive screen was mounted firmly on a custom-made metal frame (18.5cm ×
544 53.2cm) on a large platform (100cm × 150cm × 76cm). Water reward delivery was
545 controlled by an automated water-delivery rewarding system (5-RLD-D1, Crist
546 Instrument Co., Inc., U.S.) and each delivery was accompanied by an audible click. An
547 infrared camera and video recording system (EZVIZ-C2C, Hangzhou Ezviz Network
548 Co., Ltd., China) allowed the subject to be monitored while it was engaged in the task.
549 The entire apparatus was housed in a sound-proof experimental cubicle that was dark
550 apart from the background illumination from the touch screen.

551

552 **Source of video materials and preparation**

553 A collection of documentary films on wild creature was gathered from YouTube.
554 The films were *Monkey Kingdom* (Disney), *Monkey Planet* (Episode 1 – 3; BBC),
555 *Planet Earth* (Episode 1 – 11; BBC), *Life* (Episode 1 – 10; BBC), and *Snow Monkey*
556 (PBS Nature). In total 28 hours of footage was gathered. We applied Video Studio X8
557 (Core Corporation) to parse the footage by camera-cuts into smaller segments.
558 Experimenters then applied the following criteria to manually edit out ~ 2500 unique
559 clips: 1) the clip must contain a continuous flow of depiction of events (i.e., no scene

560 transition); 2) at least one living creature must be included; 3a) at least one of the
561 animals contained must be in obvious motion; 3b) the trajectories of these motion must
562 be unidirectional (i.e., no back and forth motion of the same subject); 4) clips with
563 snakes were discarded. From this library, we then selected 2000 clips (all of 4 s – 6 s)
564 for the final test and a small number of additional clips were also prepared for the
565 training stages. For each individual monkey, the videos assigned to be in an
566 experimental condition would not be used/shown in another condition so that a
567 particular monkey will only view that video repeatedly under the same condition
568 across exposure.

569

570 **Task and experimental procedure**

571 We combined naturalistic material with a temporal order judgement paradigm that
572 is widely used in episodic memory research (*1, 40, 41*). In each trial, the monkey
573 initiated a trial by pressing a colored rectangle in the center of the screen (0.15 ml
574 water). An 8-12 s video (consisting of two 4-6 s clips) was then presented (0.15 ml
575 water), and following a 2-s retention delay, two frames extracted from the video were
576 displayed bilaterally on the screen for TOJ. The monkeys were trained to choose the
577 frame that was shown earlier in the video (see [Movie S1](#)). A touch to the target frame
578 resulted in 1.5 ml water as reward, removed the foil frame, and the target frame would
579 remain alone for 5 s as positive feedback. A touch to the foil frame removed both
580 frames from the screen and blanked the screen for 20 s without water delivery. Since
581 the monkeys could self-start the trials, we did not set an explicit inter-trial interval.
582 Correction trial procedures were not used in the main test.

583 We collected 50 daily sessions of data. Each session contained 100 trials, giving us
584 a 5000 trials per monkey. The 5000 trials contained a break-down of four factors:
585 Boundary (Within vs. Across), Play Order (Normal vs. Reverse), Temporal distance
586 (TDs, 25 levels), and Exposure (R1 – R5), giving out a $2 * 2 * 25 * 5$ within-subject
587 design. The two frames for TOJ could be extracted from same clip (Within) or distinct
588 clips (Across). The 25 levels of TDs ranged between a minimum of 1000 ms
589 (equivalent of 25 frames) and a maximum of 3880 ms (equivalent of 97 frames). Each

TD level increased progressively with 3 frames each step. The 10 lists contained 5 lists of primate animals and 5 lists of non-primate animals (Category: Primate/Non-Primate). The 6 monkeys were counter-balanced in their order of receiving the two kinds of material: three monkeys (Jupiter, Mars, and Saturn) were tested first on Non-Primate lists, whereas the other three (Mercury, Neptune, and Uranus) were tested first on Primate lists. The whole experiment lasted for 68 days. There were three blocks of reset (3 days, 9 days and 6 days) in-between testing days. The task was programmed in PsychoPy2 implemented in Python.

598

599 **Data analysis, temporal and perceptual similarity, and model comparison**

600 *Representational similarity analysis (RSA)*

601 To create RDMs for the representational pattern of response time, we evenly
602 divided each video into eight segments based on chosen frame location and averaged
603 the response times within each segment for each monkey individually. For each
604 matrix, we then computed the Euclidean distance of average response time for each
605 pair of the segments. In order to show the relative distance among all pairs of
606 segments intuitively, we further transformed the matrix by replacing each element
607 with the rank number in the distribution of all the elements, and linearly scaled into
608 [0,1]. To compare similarity between response times patterns and the candidate
609 models, we computed Spearman correlation between the model and group averaged
610 RDMs with 100 randomized iterations. The statistical threshold was set at $p < 0.05$
611 (FDR corrected).

612

613 *LATER (linear approach to threshold with ergodic rate) modelling*

614 The observations that the brain needs longer time than it requires for nerves to
615 transport information and that trial-by-trial RTs vary considerably have stimulated
616 researchers to make use of distribution of reaction times for examining mental
617 processes (37). Latency, as an indicator of decision processes, provides a source of
618 insight into the underlying decision mechanisms (34–36). The Linear Approach to
619 Threshold with Ergodic Rate (LATER) model is a widely used model that taps into

these processes (42). The LATER model stipulates that the winner signals that reach threshold faster would trigger the decision, resulting in shorter latency. Accordingly, changing the rate of rise would cause the line to “shift” along the abscissa without changing its slope. In contrast, lines plotted by latency distribution would “swivel” around an intercept when the threshold changes (43) (**Figure 4A**). To explore the underlying mechanisms of different experiment conditions, we plotted the reciprocal of reaction time as a function of their z-scores, on account for making the distributions follow Gaussian distribution (44). Hence, we fitted the main component for each condition. The main component is a ramp to the threshold with rate of rise r . The distance between start level S_0 and threshold S_T is defined as θ , and rate of rise r follows a Gaussian distribution of mean, μ , and standard deviation, σl .

For model comparison, we fitted four different models to the data. The “null” model fits reaction times of both conditions with the same parameters, implying no effect of manipulation. The “Unconstrained” model set all the parameters to be free, which supposes the reaction times of two conditions are independent from each other. The “Shift” model only allows the slope of main component μ to change according different conditions, on the assumption that the manipulation will change the rate of rise. The “Swivel” model only allows θ to change according different conditions, on the assumption that the subject set different thresholds for different conditions.

639

640 *Generalized linear models (GLM)*

We ran generalized linear models to compare the effect sizes of independent variables to the dependent variable. The mean (μ) of the outcome distribution Y depends on the independent variables X, through the following formula:

$$644 \quad E(Y) = \mu = g^{-1}(X\beta),$$

where Y is a distribution of outcomes, β is unknown parameters to be estimated, g is a link function (Gaussian function). The dependent variable (Y) is reciprocal latency, and independent variables are as follows: a binary regressor indicating whether the video includes primate content or not, a binary regressor indicating that a video is played forward or backward, the five repetitions of the video-trials, physical

location of the selected probe (left or right), time elapsed within session, chosen frame location, temporal similarity, perceptual similarity (SURF), and temporal distance. To reduce the effect of behavioral noise of monkeys on the analysis, we included only correct trials in these GLM analyses and excluded trials with RT longer than 10 s or shorter than 0.7 s.

Model comparison

To obtain the best fit among these models, we used Bayesian Information Criterion (BIC) as a criterion for model selection among these four models. The formula for BIC is: $BIC = -2(\log L) + \text{numParam} * \log(\text{numObs})$, where L is the maximum likelihood for the model, numParam and numObs represent the number of free parameters and the number of samples respectively. We computed ΔBIC as the strength of the evidence, which indicates to what extent the selected model is superior to other models. Different ranges of ΔBIC show different level of evidence: The value of ΔBIC larger than 2 shows a positive evidence, the value of ΔBIC larger than 6 indicates a strong evidence (56).

Temporal similarity

For each trial, we calculated temporal similarity (TS) as an index of the discriminability of probe frames. Temporal similarity between two probe frames extracted from the video is calculated by the ratio of two frames' temporal separation between their occurrence in the video and the time of testing. Temporal similarity of any two memory traces can be calculated as: $TS = \text{delay2} / \text{delay1}$, where $\text{delay2} < \text{delay1}$ (45).

Perceptual similarity

RGB-histogram is computed as the Sum-of Square-Difference (SSD) error between image pairs for the three color channels (RGB). For each color channel the intensity values range from 0 to 255 (i.e., 256 bins), we first computed the total number of pixels at each intensity value and then computed the SSD for all 256 bins for each

680 image pair. The smaller the value of the SSD, the more similar 658 the two images
681 (image pair) was. In the case of the HOG similarity, we constructed a histogram of
682 directions of gradient over fixed sized grid across the entire image. A vector is
683 generated from each grid cell and correlated with HOG features from another image.
684 Besides, Speeded Up Robust Features (SURF) (46) uses Box Filter which is
685 calculated in parallel using integral images (47) to approximate
686 Laplacian-of-Gaussian (LoG). Wavelet responses in both horizontal and vertical
687 directions are used to assign orientation in SURF. The first step in SURF consists of
688 fixing a reproducible orientation based on information from a circular region around
689 the interest point. A descriptor vector is generated around the interest point using
690 integral image, which is compared to descriptor vectors extracted from a compared
691 image to find a match. The Euclidean distance is used to measure the similarity between
692 two descriptor vectors from two images.

693

694 *Data preprocessing*

695 Trials with RT longer than 10 s (1.45%) or faster than 0.7 s (2.47%) were
696 excluded from the analyses. Both correct and incorrect trials were entered for all
697 analyses, except those reported in the GLMs. For Neptune, data of one day of primate
698 list 5 (exposure 4) and two days of primate lists 4 and 5 (exposure 5) were lost due to
699 machine breakdown and thus only 4,700 trials are included for Neptune.

700

701

702 **Funding:** This research received funding from National Key Fundamental Research
703 Program of China (973 Program) Grant 2013CB329501 (Y-d Z.), Ministry of
704 Education of PRC Humanities and Social Sciences Research Grant 16YJC190006
705 (S.C.K.). **Author contributions:** Conceptualization, S.Z., L.W. and S.C.K.;
706 Methodology, S.Z., L.W., J.S., S.W.L., K.A., and S.C.K.; Investigation, S.Z., L.W.,
707 and Y.C.; Data interpretation: S.Z., L.W., J.S., S.W.L., Y-d.Z., and S.C.K.; Writing –
708 Original Draft, S.Z. and S.C.K.; Writing – Review & Editing, S.Z. and S.C.K.; Funding
709 Acquisition, Y-d.Z., and S.C.K.; Supervision, S.C.K. **Competing interests:** Authors
710 declare no competing interests. **Data and materials availability:** All data is available
711 at Dryad (doi: [10.5061/dryad.3r2280gcc](https://doi.org/10.5061/dryad.3r2280gcc)) and codes are available upon request.

712

713 REFERENCES

- 714 1. V. L. Templer, R. R. Hampton, Cognitive mechanisms of memory for order in
715 rhesus monkeys (*Macaca mulatta*). *Hippocampus*. **23**, 193–201 (2013).
- 716 2. E. C. Gower, Short-term memory for the temporal order of events in monkeys.
717 *Behav. Brain Res.* **52**, 99–103 (1992).
- 718 3. D. P. Charles, D. Gaffan, M. J. Buckley, Impaired Recency Judgments and
719 Intact Novelty Judgments after Fornix Transection in Monkeys. *J. Neurosci.* **24**,
720 2037–2044 (2004).
- 721 4. N. Morimura, T. Matsuzawa, Memory of movies by chimpanzees (*Pan*
722 *troglydotes*). *J. Comp. Psychol.* **115**, 152–158 (2001).
- 723 5. G. Martin-Ordas, D. Haun, F. Colmenares, J. Call, Keeping track of time:
724 Evidence for episodic-like memory in great apes. *Anim. Cogn.* **13**, 331–340
725 (2010).
- 726 6. H. S. Terrace, L. K. Son, E. M. Brannon, Serial expertise of rhesus macaques.
727 *Psychol. Sci.* **14**, 66–73 (2003).
- 728 7. S. Chen, K. B. Swartz, H. S. Terrace, Knowledge of the Ordinal Position of
729 List Items in Rhesus Monkeys. *Psychol. Sci.* **8**, 80–86 (1997).
- 730 8. T. Orlov, V. Yakovlev, S. Hochstein, E. Zohary, Macaque monkeys categorize
731 images by their ordinal number. *Nature*. **404**, 77–80 (2000).
- 732 9. V. L. Templer, R. P. Gazes, R. R. Hampton, Co-operation of long-term and
733 working memory representations in simultaneous chaining by rhesus monkeys
734 (*Macaca mulatta*). *Q. J. Exp. Psychol.* (2019),
735 doi:10.1177/1747021819838432.
- 736 10. N. M. Long, M. J. Kahana, Hippocampal contributions to serial-order memory.
737 *Hippocampus*. **29**, 252–259 (2019).
- 738 11. Y. Liu, R. J. Dolan, Z. Kurth-Nelson, T. E. J. Behrens, Human Replay
739 Spontaneously Reorganizes Experience. *Cell*, 1–13 (2019).
- 740 12. S. Michelmann, B. P. Staresina, H. Bowman, S. Hanslmayr, Speed of
741 time-compressed forward replay flexibly changes in human episodic memory.
742 *Nat. Hum. Behav.* **3**, 143–154 (2019).

- 743 13. G. E. Wimmer, Y. Liu, N. Vehar, T. E. Behrens, R. J. Dolan, Episodic memory
744 retrieval is supported by rapid replay of episode content. *bioRxiv*, 758185
745 (2019).
- 746 14. D. Panoz-Brown *et al.*, Replay of Episodic Memories in the Rat. *Curr. Biol.* **28**,
747 1628–1634.e7 (2018).
- 748 15. K. Bonasia, J. Blommestein, M. Moscovitch, Memory and navigation:
749 Compression of space varies with route length and turns. *Hippocampus*. **26**,
750 9–12 (2016).
- 751 16. Y. Naya, H. Chen, C. Yang, W. A. Suzuki, Contributions of primate prefrontal
752 cortex and medial temporal lobe to temporal-order memory. *Proc. Natl. Acad.*
753 *Sci.* **114**, 13555–13560 (2017).
- 754 17. J. M. Zacks, B. Tversky, Event Structure in Perception and Conception.
755 *Psychol. Bull.* **127**, 3–21 (2001).
- 756 18. T. J. Davidson, F. Kloosterman, M. A. Wilson, Hippocampal Replay of
757 Extended Experience. *Neuron*. **63**, 497–507 (2009).
- 758 19. Y. Ninokura, H. Mushiaki, J. Tanji, Representation of the Temporal Order of
759 Visual Objects in the Primate Lateral Prefrontal Cortex. *J. Neurophysiol.* **89**,
760 2868–2873 (2003).
- 761 20. V. L. Templer, E. K. Brown, R. R. Hampton, Rhesus monkeys metacognitively
762 monitor memories of the order of events. *Sci. Rep.* **8**, 11541 (2018).
- 763 21. T. Suddendorf, D. R. Addis, M. C. Corballis, Mental time travel and the
764 shaping of the human mind. *Philos. Trans. R. Soc. B Biol. Sci.* **364**, 1317–1324
765 (2009).
- 766 22. E. Tulving, Memory and consciousness. *Can. Psychol. Can.* **26**, 1–12 (1985).
- 767 23. T. E. J. Behrens *et al.*, What Is a Cognitive Map? Organizing Knowledge for
768 Flexible Behavior. *Neuron*. **100**, 490–509 (2018).
- 769 24. K. Louie, M. A. Wilson, Temporally structured replay of awake hippocampal
770 ensemble activity during rapid eye movement sleep. *Neuron*. **29**, 145–156
771 (2001).

- 772 25. A. K. Lee, M. A. Wilson, Memory of Sequential Experience in the
773 Hippocampus during Slow Wave Sleep. *Neuron*. **36**, 1183–1194 (2002).
- 774 26. D. J. Foster, M. A. Wilson, Reverse replay of behavioural sequences in
775 hippocampal place cells during the awake state. *Nature*. **440**, 680–683 (2006).
- 776 27. M. P. Karlsson, L. M. Frank, Awake replay of remote experiences in the
777 hippocampus. *Nat. Neurosci.* **12**, 913–918 (2009).
- 778 28. B. E. Pfeiffer, D. J. Foster, Hippocampal place-cell sequences depict future
779 paths to remembered goals. *Nature*. **497**, 74–79 (2013).
- 780 29. S. P. Jadhav, C. Kemere, P. W. German, L. M. Frank, Awake Hippocampal
781 Sharp-Wave Ripples Support Spatial Memory. *Science (80-.)*. **336**, 1454
782 (2012).
- 783 30. H. F. Ólafsdóttir, D. Bush, C. Barry, The Role of Hippocampal Replay in
784 Memory and Planning. *Curr. Biol.* **28**, R37–R50 (2018).
- 785 31. J. P. Magliano, J. Miller, R. A. Zwaan, Indexing Space and Time in Film
786 Understanding. *Appl. Cogn. Psychol.* **15**, 533–545 (2001).
- 787 32. B. M. Hard, B. Tversky, D. S. Lang, Making sense of abstract events: Building
788 event schemas. *Mem. Cogn.* **34**, 1221–1235 (2006).
- 789 33. S. DuBrow, L. Davachi, The influence of context boundaries on memory for
790 the sequential order of events. *J. Exp. Psychol. Gen.* **142**, 1277–1286 (2013).
- 791 34. I. Sols, S. DuBrow, L. Davachi, L. Fuentemilla, Event Boundaries Trigger
792 Rapid Memory Reinstatement of the Prior Events to Promote Their
793 Representation in Long-Term Memory. *Curr. Biol.* **27**, 3499–3504.e4 (2017).
- 794 35. Y. Ezzyat, L. Davachi, What constitutes an episode in episodic memory?
795 *Psychol. Sci.* **22**, 243–252 (2011).
- 796 36. S. C. Kwok, E. Macaluso, Exogenous features versus prior experiences
797 modulate different subregions of the right IPL during episodic memory
798 retrieval. *Sci. Rep.* **5**, 11248 (2015).
- 799 37. D. Panoz-Brown *et al.*, Rats Remember Items in Context Using Episodic
800 Memory. *Curr. Biol.* **26**, 2821–2826 (2016).

- 801 38. M. P. Karlsson, L. M. Frank, Awake replay of remote experiences in the
802 hippocampus. *Nat. Neurosci.* **12**, 913–918 (2009).
- 803 39. K. Diba, G. Buzsáki, Forward and reverse hippocampal place-cell sequences
804 during ripples. *Nat. Neurosci.* **10**, 1241–1242 (2007).
- 805 40. J. R. Manns, M. W. Howard, H. Eichenbaum, Gradual Changes in
806 Hippocampal Activity Support Remembering the Order of Events. *Neuron.* **56**,
807 530–540 (2007).
- 808 41. S. C. Kwok, E. Macaluso, Scale invariance of temporal order discrimination
809 using complex, naturalistic events. *Cognition.* **140**, 111–121 (2015).
- 810 42. I. Noorani, R. H. S. Carpenter, The LATER model of reaction time and
811 decision. *Neurosci. Biobehav. Rev.* **64**, 229–251 (2016).
- 812 43. B. A. J. Reddi, R. H. S. Carpenter, The influence of urgency on decision time.
813 *Nat. Neurosci.* **3**, 827–830 (2000).
- 814 44. I. Noorani, R. H. S. Carpenter, Full reaction time distributions reveal the
815 complexity of neural decision-making. *Eur. J. Neurosci.* **33**, 1948–1951
816 (2011).
- 817 45. G. D. A. Brown, I. Neath, N. Chater, A Temporal Ratio Model of Memory.
818 *Psychol. Rev.* **114**, 539–576 (2007).
- 819 46. H. Bay, A. Ess, T. Tuytelaars, L. Van Gool, Speeded-Up Robust Features
820 (SURF). *Comput. Vis. Image Underst.* **110**, 346–359 (2008).
- 821 47. P. Viola, M. J. Jones, Robust Real-Time Face Detection. *Int. J. Comput. Vis.* **57**,
822 137–154 (2004).

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Supplemental Information

Figure S1. Relationship between temporal similarity and reciprocal latency for within-context trials. Reciprocal latency as a function of temporal similarity for the average of all monkeys (upper panel) and individual monkeys (bottom panel). Temporal similarity between two frames is mathematically the inverse of their respective frame locations in the video, see Methods. **Related to Figure 2A.**

840

841

842

843 **Figure S2. GLM results on the effects of image similarity measures on reciprocal**
844 **latency for within-context and across-context condition.** Difference of distribution
845 in RGB- histogram, HOG similarity and SURF similarity were tested. The SURF
846 similarity measure was significantly correlated with RT in the across-context condition
847 ($P = 0.0015$). **Related to Figure 7.**

848

Figure S3. Full GLM analysis including a number of variables that might affect reciprocal latency. The nine regressors include a binary regressor indicating whether the video category is primate or non-primate (video category), a binary regressor indicating that a video is played forward or backward (play order), the repeated exposure of the trial (1 – 5) (exposure), the physical location of the selected probe on screen (left or right) (touch side), time elapsed within session (elapsed time; to rule out fatigue or attentional confounds), chosen frame location, temporal similarity, SURF similarity as a perceptual similarity measure (perceptual similarity) and temporal distance between two probe frames. The results confirm that chosen frame location is the most significant regressor in within-context trials while perceptual similarity is the most significant regressor in across-context trials. *** denotes $P < 0.001$, ** denotes $P < 0.01$, * denotes $P < 0.05$. **Related to Figure 7.**

869

870 **Table S1.** LATER model fitting results of six monkeys. For ease of comparison, we
 871 computed the respective Δ BIC to index the strength of evidence for each model. Note
 872 that the model with the lowest BIC is the winning model. In all 6 monkeys, the shift
 873 model was superior to the other three models. **Related to Figure 6.**

874

Condition		BIC				delta_BIC			
		null	two fits	swivel	shift	null	two fits	swivel	shift
Across VS Within	Jupiter	-67157.39	-67603.99	-67543.25	-67615.23	457.83	11.24	71.98	0
	Mars	-63948.06	-65937.89	-65769.84	-65948.72	2000.65	10.82	178.88	0
	Saturn	-61307.14	-61929.72	-61853.77	-61938.70	631.56	8.98	84.93	0
	Mercury	-63904.96	-64047.31	-64042.94	-64057.52	152.56	10.20	14.57	0
	Uranus	-67652.66	-67850.84	-67841.34	-67864.67	212.01	13.83	23.34	0
	Neptune	-56695.53	-58327.76	-58037.15	-58337.23	1641.70	9.47	300.07	0

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Table S2. For monkeys: One sample *t*-tests results of the slopes of RT as a function of temporal similarity. The three panels correspond to analyses performed using all trials (top), only correct trials (middle), and only incorrect trials (bottom). Same slope patterns were observed irrespective of correctness, in consistency with the analyses on slopes of RT as a function of chosen frame location for each monkey. **Related to Table 1.**

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Monkeys	Mean (SEM)	t-statistics	d.f.	p-value	Cohen's d	95% confidence interval	
						Lower	Upper
Slope of reaction times/temporal similarity tested against zero (all trials)							
Jupiter	-0.59 (1.04)	-3.99	49	<0.001	-0.56	-0.88	-0.29
Mars	-1.15 (1.18)	-6.86	49	<0.001	-0.97	-1.48	-0.81
Saturn	-0.24 (0.69)	-2.46	49	0.020	-0.35	-0.43	-0.04
Mercury	-0.52 (0.73)	-5.02	49	<0.001	-0.71	-0.73	-0.31
Uranus	-0.44 (0.64)	-4.93	49	<0.001	-0.70	-0.62	-0.26
Neptune	-1.03 (1.94)	-3.65	46	<0.001	-0.53	-1.60	-0.46
Slope of reaction times/temporal similarity tested against zero (correct trials)							
Jupiter	-0.63 (1.45)	-3.06	49	0.004	-0.43	-1.04	-0.22
Mars	-1.01 (1.44)	-4.98	49	<0.001	-0.70	-1.42	-0.60
Saturn	-0.29 (0.80)	-2.58	49	0.013	-0.36	-0.52	-0.06
Mercury	-0.46 (0.89)	-3.64	49	<0.001	-0.51	-0.71	-0.20
Uranus	-0.46 (0.70)	-4.64	49	<0.001	-0.66	-0.66	-0.26
Neptune	-1.01 (2.69)	-2.56	46	0.014	-0.37	-1.80	-0.22
Slope of reaction times/temporal similarity tested against zero (Incorrect trials)							
Jupiter	-0.63 (1.40)	-3.17	49	0.003	-0.45	-1.02	-0.23
Mars	-1.31 (1.70)	-5.43	49	<0.001	-0.77	-1.79	-0.82
Saturn	-0.25 (0.28)	-1.39	49	0.169	-0.20	-0.61	0.11
Mercury	-0.55 (1.40)	-2.81	49	0.007	-0.40	-0.95	-0.16
Uranus	-0.42 (0.90)	-3.29	49	0.002	-0.47	-0.68	-0.16
Neptune	-1.27 (3.42)	-2.55	46	0.014	-0.37	-2.27	-0.27

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Table S3. For human participants: One sample *t*-tests results of the slopes of RT as a function of temporal similarity (upper panel) and the slopes of RT as a function of chosen frame location (bottom panel) against zero. **Related to Figure 1D.**

Subjects	Mean (SEM)	t-statistics	d.f.	p-value	Cohen's d	95% confidence interval	
						Lower	Upper
Slope of reaction times/temporal similarity tested against zero							
Subject 1	1.54 (1.17)	5.87	19	<0.001	1.31	0.99	2.09
Subject 2	2.10 (1.84)	5.10	19	<0.001	1.14	1.24	2.96
Subject 3	2.28 (1.56)	6.55	19	<0.001	1.55	1.55	3.01
Subject 4	2.12 (1.30)	7.32	19	<0.001	1.51	1.51	2.73
Subject 5	1.01 (1.05)	4.30	19	<0.001	0.52	0.52	1.50
Subject 6	0.51 (0.80)	2.87	19	0.010	0.41	0.14	0.89
Subject 7	1.31 (1.77)	3.29	19	0.004	0.48	0.48	2.14
Slope of reaction times/chosen frame location tested against zero							
Subject 1	0.0004 (0.0038)	0.44	19	0.667	0.10	-0.0014	0.0021
Subject 2	-0.0005 (0.0034)	-0.71	19	0.487	-0.16	-0.0021	0.0010
Subject 3	-0.0027 (0.0040)	-2.99	19	0.008	-0.67	-0.0045	-0.0008
Subject 4	-0.0018 (0.0024)	-3.35	19	0.003	-0.75	-0.0029	-0.0007
Subject 5	-0.0001 (0.0027)	-0.09	19	0.931	-0.02	-0.0013	0.0012
Subject 6	-0.0003 (0.0020)	-0.65	19	0.521	-0.15	-0.0012	0.0006
Subject 7	-0.0009 (0.0047)	-0.84	19	0.410	-0.19	-0.0031	0.0013