Cognition 157 (2016) 14–23

Contents lists available at ScienceDirect

Cognition

journal homepage: www.elsevier.com/locate/COGNIT

Original Articles

# Mental simulation of routes during navigation involves adaptive temporal compression

Aiden E.G.F. Arnold [a,b], Giuseppe Iaria [a], Arne D. Ekstrom [b,c,d,*]

[a] Department of Psychology, Hotchkiss Brain Institute and Alberta Children's Hospital Research Institute, University of Calgary, Calgary, Alberta, Canada
[b] Center for Neuroscience, University of California, Davis, 1544 Newton Court, Davis, CA, USA
[c] Department of Psychology, University of California, Davis, CA, USA
[d] Neuroscience Graduate Group, University of California, Davis, CA, USA

ARTICLE INFO

*Article history:*
Received 15 January 2016
Revised 3 August 2016
Accepted 17 August 2016

*Keywords:*
Episodic memory
Prospection
Hippocampus
Imagination
Recollection
Virtual reality

ABSTRACT

Mental simulation is a hallmark feature of human cognition, allowing features from memories to be flexibly used during prospection. While past studies demonstrate the preservation of real-world features such as size and distance during mental simulation, their temporal dynamics remains unknown. Here, we compare mental simulations to navigation of routes in a large-scale spatial environment to test the hypothesis that such simulations are temporally compressed in an adaptive manner. Our results show that simulations occurred at 2.39× the speed it took to navigate a route, increasing in compression (3.57×) for slower movement speeds. Participant self-reports of vividness and spatial coherence of simulations also correlated strongly with simulation duration, providing an important link between subjective experiences of simulated events and how spatial representations are combined during prospection. These findings suggest that simulation of spatial events involve adaptive temporal mechanisms, mediated partly by the fidelity of memories used to generate the simulation.



## 1. Introduction

Mentally simulating events is one of our most fundamental cognitive skills, critical to our ability to anticipate and handle future experiences. It underlies flexible goal planning during navigation (Burgess, 2008) and is a central aspect to the constructive nature of episodic memory (Boyer, 2008; Moulton & Kosslyn, 2009; Schacter et al., 2012; Suddendorf, Addis, & Corballis, 2009). Research over the past decade using mental simulation has revealed new aspects of mnemonic processing, including the ability to recapitulate details from past experiences into novel contexts (Hassabis, Kumaran, & Maguire, 2007; Szpunar, Addis, McLelland, & Schacter, 2013) and how these anticipatory future simulations can motivate and guide behavior (Boyer, 2008; Suddendorf & Busby, 2005). Many of these studies have cumulated into a growing consensus (Buckner & Carroll, 2007; Hassabis & Maguire, 2009; Moulton & Kosslyn, 2009; Schacter et al., 2012; Schacter & Addis, 2007; Szpunar et al., 2013) that mental simulation involves a dynamic neurocognitive system dedicated to encoding experiences, extracting features form those memories, and actively combining those features into representations, or mental 'scenes', that are used to optimize behavior. This has led to new perspectives on how aging influences memory, prospection, and mental imagery (Addis, Wong, & Schacter, 2008; Personnier, Kubicki, Laroche, & Papaxanthis, 2010; Schacter, Gaesser, & Addis, 2013), and how these processes are affected by cognitive and neurodegenerative disorders (Addis, Sacchetti, Ally, Budson, & Schacter, 2009; Hassabis, Kumaran, Vann, & Maguire, 2007; Irish & Piolino, 2015; Kwan, Carson, Addis, & Rosenbaum, 2010).

Although past work has shown the utility of mental simulation in experimental (Hassabis, Kumaran, Maguire, 2007; Szpunar et al., 2013), clinical (Addis et al., 2009; Kwan et al., 2010), and real world contexts (Personnier et al., 2010; Schacter & Addis, 2007), critical components of how simulations operate have yet to be empirically evaluated. Early work (Kosslyn, Ball, & Reiser, 1978; Shepard & Metzler, 1971) demonstrated that mental representations based on visually encoded objects retain metric information. This finding has been extended through work with amnesic patients (Hassabis, Kumaran, Vann et al., 2007) and brain imaging (Szpunar, Watson, & McDermott, 2007) to suggest that spatial context acts as a framework to organize features from memory to anticipate future situations (Hassabis & Maguire, 2009). Despite the promising implications of studies on spatial aspects of mental simulations, to our knowledge, no study has investigated their temporal

* Corresponding author at: Center for Neuroscience and Department of Psychology, University of California, Davis, Davis, CA 95618, USA.
*E-mail address:* adekstrom@ucdavis.edu (A.D. Ekstrom).

http://dx.doi.org/10.1016/j.cognition.2016.08.009
0010-0277/

dynamics and how this relates to the constructive nature of memory. Past studies that included temporal components of mental simulations have either (a) limited the simulation to one visuospatial scene, omitting the spatially extended nature of daily experience (e.g. Borst & Kosslyn, 2010; Cui, Jeter, Yang, Montague, & Eagleman, 2007; Personnier et al., 2010), or (b) used temporal extent as an independent variable in task designs, for example, by analyzing detail generation during recall/simulation at different points in the past/future (Addis et al., 2008; Borst & Kosslyn, 2010; Botzung, Denkova, & Manning, 2008). As such, the temporal basis of mental simulations in human remains unknown, despite its critical importance to understanding cognitive processes related to episodic memory and prospection.

Here, we ask three fundamental questions about the temporal dynamics of mentally simulated events and evaluate them across two studies. First, following the research of Kosslyn et al. (1978), we investigated whether mental simulations retain temporal information derived from previous experiences in a spatial environment. Our hypothesis is that simulated episodes contain temporal aspects of the experiences the simulation is recapitulated from, albeit in a compressed form. This hypothesis is based in part on findings from place cell recordings in the rodent hippocampus during pre-play/replay events that show temporal compression of route sequences (Davidson, Kloosterman, & Wilson, 2009; Johnson & Redish, 2007; Nádasdy, Hirase, Czurkó, Csicsvari, & Buzsáki, 1999; Skaggs, McNaughton, Wilson, & Barnes, 1996).

Our second question is whether compression of temporal information is a constant or adaptive process. We hypothesize that temporal compression during mental simulation provides an adaptive mechanism to compensate for the speed at which the events used to generate the simulation were experienced. That is, we predicted slower movement speeds during the original experience would lead to greater compression rates during the simulated episode, with faster speeds leading to lower compression rates. Our rationale for formulating this hypothesis originated from theories suggesting that mental simulations offer a form of prospection where features of past experiences are combined into simulations about future events (Schacter, Addis, & Buckner, 2007). We reasoned that an adaptive temporal compression rate would offer an advantage for prospection and prediction by allowing the temporal dynamics of combining past experiences to be adjusted in order to more efficiently simulate future scenarios. We term this the "adaptive" hypothesis of mental simulation.

Our third question pertains to how the temporal flow of a simulation relates to one's ability to construct detailed representations used for mental simulation. If the subjective fidelity of the encoded spatial context from previous experiences facilitates mental simulation, as has been postulated elsewhere (Hassabis, Kumaran, Vann et al., 2007; Szpunar et al., 2007), there may be a statistical relationship between the subjective experience of visuospatial aspects of a simulation and the time it takes to imagine them. However, it is currently unknown how detail generation relates to the temporal flow of simulated episodes. It may be that more vivid and coherent events take longer to simulate. Conversely, more vivid and coherent events might result in faster simulation, consistent with the perspective that environments are represented by a manifold of spatial maps that need to be dynamically organized during navigation (Derdikman & Moser, 2010; McNamara, Hardy, & Hirtle, 1989). Under the multiple spatial maps perspective, simulation speeds depend on how quickly memory systems dynamically organize multiple spatial representations into a coherent representation used to guide navigation. In this case, ratings of subjective experience of simulations, such as vividness and spatial/temporal coherence, would provide a measure of how well the multiple maps are integrated into a task-related spatial representation used for navigation, with less vivid and coherent simulations indicating more effortful and piecemeal integration.

## 2. Methods

### 2.1. Study 1

We first investigated whether there was a systematic relationship between the time to simulate a spatial episode and the actual time to subsequently navigate the same route. For example, would routes that required more time to navigate be simulated at a proportionately faster rate than one that required less time?

#### 2.1.1. Participants

Sample size was determined by previous research investigating preservation of memory features during mental simulations (Borst & Kosslyn, 2010; Hassabis, Kumaran, Maguire, 2007; Schacter et al., 2013). No stopping rule was used. Data from 28 participants were analyzed in Study 1 (13 females, 15 males; mean age = 19.64, *SD* = 1.87). Data from four other participants were collected but not included in the final sample. Two participants were excluded for responding only on the extreme ends of the post-simulation questionnaire (see Section 2.1.2), one participant for mean reaction times (RTs) <1 s on the post-simulation questionnaire, and the fourth did not complete the simulation phase due to feelings of nausea. All participants gave informed consent and the study was approved by the research ethics committee at the University of California Davis.

#### 2.1.2. Procedure

The raw and filtered data for all conditions in this study is available as Supplemental material. Additionally, a Jupyter notebook containing the code for the analysis, results, and supplemental materials are available to view and download on Github (http://bit.ly/1Nxok4I) and all test environments used in the study are freely available for research use (http://bit.ly/1OhQVP3). The study consisted of three phases: an exposure phase, an encoding phase, and a simulation phase. All three phases were conducted in a large virtual city designed using Unity (Unity Technologies, San Francisco, United States). The virtual city consisted of five visually salient landmarks located throughout the environment and a number of non-discreet buildings that were variations of three architectural styles designed to provide limited environmental location information (see Fig. 1 for overview of task and city composition). The layout of the city was selected to be slightly asymmetric so that global cues from the city shape would help prevent participants from feeling lost without providing overt geometric cues about their location.

In the exposure phase, participants were shown a video from a first person perspective of movement along the perimeter of the city. See Fig. 1A for a visualization of the exposure path participants were shown. The video stopped for 5 s at each target landmark (e.g. the grocery store) to show its location. At this point, the experimenter pointed to the location of the landmark on the screen and verbally confirmed that the participant could identify the landmark. See Fig. 1B for images of the target landmarks. The video ended at the same point it started, which was a randomly selected point along the city perimeter and was identical across participants. The exposure phase was designed to provide a sense of scale of the city, as well as provide a consistent base knowledge of the landmark locations across participants.

After the exposure phase, participants underwent the encoding phase. There were a total of 20 trials in this portion of the study. For each trial, participants were cued with an image of a landmark on the center of the screen and asked to rate on a scale of 1–5 their