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What can we learn from studying replay in humans?

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Noninvasive methods are making it possible to study neural replay in humans. Although focused on alignment with rodent findings, human research often tacitly assumes that replay is linked to conscious, deliberate thought. This assumption represents a missed opportunity to investigate the links between replay and consciousness, as well as cross-species differences more broadly.

When we sleep or rest, the brain does not simply go quiet. It rapidly reactivates sequential traces of past experiences in burst-like moments known as neural replay (Box 1). Decades of research have linked various forms of replay to memory and decision-making, but, until recently, almost all evidence came from studies in rodents. Excitingly, recent methodological advances now allow replay to be probed noninvasively [1,2], opening new possibilities to address questions that are difficult to study in nonhuman animals (hereafter, animals).

These questions came into focus when a journalist approached us to discuss a study reporting replay during brief rest in humans. He asked how people could 'trigger' replay: should they try to think, remember, or not think at all? The journalist assumed that replay involves conscious, deliberate thought—the kind of thought people can voluntarily control. We had no answer and could point to little research seeking one. Yet, it revealed a singular gap in our knowledge: is replay a conscious phenomenon or not? And how might its cognitive function differ between humans and rodents?

Early research on human replay focused on alignment with electrophysiological data from rodents and, reassuringly, confirmed several key consistencies across species, such as its hippocampal localization [1] and reward-dependent direction reversal [2]. However, the field has stopped short of addressing questions that only human research can answer. Does replay cohere with conscious, deliberate thought? Does it play the same role in humans and rodents? How might cross-species replay research shed light on the (dis)continuity in cognition and consciousness across rodents and primates?

So far, we have mostly skirted these issues. Clearly, animal results are measured with greater precision and thus offer an important benchmark. Shared phenomena across species also suggest fundamental neural computations. However, this has led us to tacitly treat replay as something untethered from conscious thought processes, which are difficult to measure in animals. Yet, human brains—and how we study them—are not the same as rodent brains. Some neuroimaging studies, for example, instruct participants to consciously deliberate or retrieve memories, implicitly assuming replay involves intentional thought without ever testing it. We believe this represents a missed opportunity. Rather than ignoring species differences, we should exploit the unique strengths of each approach. Chief among these is that, in humans, we can ask whether replay serves as a proxy for conscious, deliberate thought.

Consider two elegant studies on replay in humans. In one, participants were explicitly instructed to engage in deliberate 'mental construction' and to infer a plan to construct an object from Tetris-like pieces [3]; in another, they were instructed to retrieve an episode associated with a cue [4]. Both papers show that compositional computations and memory retrieval involve replay. But does that mean replay corresponds to the accompanying deliberate mental acts?

There are many reasons to doubt that replay is conscious. Replay is typically faster than conscious thought, can unfold backward, sometimes tracks low-level noncognitive physiological processes, and is often unrelated or only stochastically related to deliberately planned steps [5]. There also is not much evidence to suggest that nighttime replay corresponds to dream experiences [6]. One of our own proposals suggests that conscious vision evolved to keep reality and internal simulations (of the sort indexed by replay) separate. This account predicts that while people are conscious of the relevant aspects of their environment that support model-based planning, replay in both animals and humans should be largely unconscious [7].

However, there is also evidence to the contrary: one intracranial study has, for instance, shown that the hippocampal sharp-wave ripple (SWR) rate rises during self-generated, internally directed thought [8]. Rather than assuming replay does or does not reflect conscious thought, we should therefore test this empirically. Unfortunately, the field has largely avoided questions about how conscious deliberation affects task performance, a tendency Quilty-Dunn and Krakauer have recently called the 'deliberation taboo' [9].

One of our own studies has taken a first step toward testing these hypotheses [10]. Participants performed a motor choice task in which pictures appeared in a probabilistic sequence but were never

Box 1. Neural replay and its diversity

Replay was first described in 1996 by Skaggs and McNaughton, who showed that hippocampal place cells in rats reactivate sequentially during sleep, recapitulating the paths traveled while awake. Today, the term covers a family of related but distinct phenomena, and the distinctions matter for whether, and how, replay relates to conscious experience.

Replay refers to sequential reactivation specifically, as opposed to the broader reinstatement of a prior activity pattern, which need not be ordered; the relationship to awareness may differ for the two. The canonical case is hippocampal, but replay has also been reported in cortex. In human research, cortical replay is in fact the more frequently reported case (a mismatch that complicates cross-species comparison). This is partly rooted in methodological differences: fMRI studies have largely targeted replay in visual and motor cortex, while MEG is spatially less precise and more sensitive to cortical than to subcortical signals.

Replay events also differ in their oscillatory markers. Some replay events are nested in hippocampal SWRs, which are brief, high-frequency bursts locked to a slower wave. Ripples also occur in the cortex, and human noninvasive methods usually cannot detect SWRs directly. That SWRs occur during non-REM sleep is among the strongest evidence that at least some replay is unconscious.

A final source of variability is the brain state: replay occurs during sleep, during rest, and during brief pauses within tasks. Anatomical origin, oscillatory background, and behavioral state each likely shape how a given replay event relates to ongoing experience.

told about a sequence that could be learned. As is common in these tasks, we found that although only half of the participants could express any awareness of having learned anything in a post-experimental questionnaire, reaction times indicated that virtually everyone learned the sequence implicitly. Using fMRI, we found replay in the visual cortex during short intertrial breaks that reflected the sequence structure and tracked implicit knowledge. Yet, we could not find evidence for a relationship to explicit knowledge. Because our study was underpowered for null results and the awareness measures were limited, strong conclusions are premature. These data and the mixed findings illustrate the kind of questions the field should be asking.

At the same time, we must also acknowledge a deeper complexity: replay is not a singular phenomenon. It occurs across multiple brain regions, timescales, and cognitive states, and any relationship to conscious deliberation is likely specific to particular forms of replay rather than every instance. This complexity is compounded by the fact that such relationships may not be direct. If replay functions as a predeliberative, stochastic sampling mechanism, its effects on behavior and awareness may be delayed. Different non-REM (rapid-eye-movement) sleep stages, for instance, have been linked to subsequent insight, with evidence variously implicating light N1, N2, and slow-wave sleep (e.g., [11]). Notably, such benefits typically emerge only after the nap and with further task experience. Theoretical accounts of memory have similarly suggested that replay might act as a tagging mechanism that influences consolidation processes hours later [5], and other work has suggested replay unfolds in cascades across the cortex [12]. A key challenge, then, is to separate direct accounts, in which hippocampal ripple-linked replay events (or less commonly reported forms of replay) are closely coupled to conscious thought, from indirect accounts, in which replay shapes later cognition without itself giving rise to conscious experience. These ideas remain speculative, but they point to the importance of considering delayed, nonlinear relations between replay and conscious processes.

To better disentangle these phenomena, studies could administer thought probes during rest to capture spontaneous cognition. While thought probes risk disrupting the process they measure, they bring subjective and neural levels into contact in ways that current paradigms rarely do. Another promising approach is to measure metacognitive aspects of decision-making informed by replay (such as decision confidence), given that metacognition appears to be 'consciousness selective' [13], yet remains measurable even in nonhuman animals. If replay is a fast-paced sampling mechanism that invokes many possible scenarios below the threshold of awareness, the confidence of a final decision may reflect the amount of replay preceding it, while the content of the decision reflects longer-term biases in sampling. Separating thought content and confidence could, therefore, prove productive. For instance, conscious replay might even put the system into an optimal state for engaging in unconscious replay.

A broader set of unasked questions concerns differences between species. Much work has focused on hippocampal replay in planning, but the underlying computations likely differ between rodents and primates. Rodents are nocturnal animals with comparatively poor vision and a large hippocampus dominated by spatially selective cells. Primates, in comparison, have better vision, a larger cortex, and a hippocampus far less dominated by spatial computation, which affects their planning process. Other replay-relevant mental processes are likely unique to humans too—such as rumination, which is self-referential, language-mediated, and implicated in mental health disorders. Understanding human replay, therefore, requires building new frameworks that reflect primate-specific affordances and brain organization. Whether these differences fundamentally alter replay remains unknown. However, simultaneously measuring hippocampal and cortical replay alongside deliberative thought and metacognition gives us the tools to find out.

Despite its promise, the study of replay in humans continues to face significant methodological hurdles. Recent work raising concerns about whether MEG-based approaches can reliably detect replay under realistic conditions [14] exemplifies the kind of scrutiny needed to drive further methodological progress.

The journalist's questions we could not answer are, in the end, empirical ones. Do people think during replay? Are they aware of it? Does it shape what they decide to do, or only how confident they are? The tools to begin answering these questions are now within reach, even if they are still maturing. What has been missing is the impetus to ask them.

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