

CBN-22-98 Hogendoorn
Commentary
MS

**Blurred Lines: Memory, Perceptions, and Consciousness: Commentary on
“Consciousness as a Memory System” by Budson et al (2022)**

Hinze Hogendoorn, PhD

From the Melbourne School of Psychological Sciences, The University of Melbourne,
Melbourne, Australia.

[Corresponding author: Hinze Hogendoorn, PhD, Melbourne School of Psychological
Sciences, The University of Melbourne, Parkville VIC 3010, Australia; email:
hhogendoorn@unimelb.edu.au]

Supported in part by grants (DP180102268 and FT200100246) from the Australian Research
Council.

The author declares no conflicts of interest.

Correspondence: Hinze Hogendoorn, PhD, Melbourne School of Psychological Sciences,
The University of Melbourne, Parkville VIC 3010, Australia (email:
hhogendoorn@unimelb.edu.au).

Running head: Blurred Lines: Memory, Perception, and Consciousness**Abstract**

In the previous issue, Budson, Richman, and Kensinger (2022) put forth the intriguing proposal that consciousness may have evolved from the episodic memory system. In addition to providing a possible evolutionary trajectory for consciousness, I believe that viewing consciousness as an extension of memory in this way is particularly useful for understanding some of the puzzling temporal complexities that are inherent to consciousness. For example, due to neural transmission delays, our conscious experience must necessarily lag the outside world, which creates a paradox for both conscious perception (Do we see the past, rather than the present?) and action (How can we make rapid decisions if it takes so long to become conscious of something?). These paradoxes can be elegantly solved by treating consciousness as a memory system. Finally, the proposal put forth by Budson and colleagues (2022) aligns with the emerging perspective that consciousness, like memory, represents a narrative time line of events rather than any single instant. However, I believe that this conceptualization can be further extended to include not only the past, but also the future. In this way, consciousness can be provocatively viewed as the remembered past, present, and future.

Key Words: consciousness, memory, perception, prediction, awareness

In the target article, Budson, Richman, and Kensinger (2022) develop the argument that consciousness shares a number of critical features with episodic memory; they also propose that over the course of evolution, consciousness may in fact have arisen from the episodic memory system. In support of this proposal, the authors note that both consciousness and episodic memory involve a subjective experience of sensory information, and that both serve to flexibly combine information from prior events in order to plan for the future (Schacter et al, 2007; Suddendorf and Corballis, 2007). However, I think that the most compelling aspects of the proposal relate to the temporal aspects of consciousness: how conscious experience works in real time.

The biology of our brain imposes constraints on what information is available to be experienced when, and these constraints have important implications for how consciousness might be implemented at the neural level. Although many of the implications of these constraints have been identified before (eg, Dennett and Kinsbourne, 1992; Eagleman, 2008; Hogendoorn, 2022; Nijhawan, 2008), the novelty of this proposal is that Budson and colleagues (2022) integrate this literature with an emerging view of consciousness as being closely related to memory (eg, LeDoux and Lau, 2020).

Postdiction and the Timing of Consciousness

Budson and colleagues (2022) identify two key observations about the time course of consciousness that they use to motivate their proposal. The first is the fact that the conscious experience of a given event can be influenced by events that occur later, which is a phenomenon called *postdiction* (Eagleman, 2008; Eagleman and Sejnowski, 2000; Shimojo, 2014). Postdiction is problematic for a view of consciousness as serving purely the present instant because the nervous system has no access to information about future events. However, framing consciousness as a memory system allows new sensory input to alter the

conscious experience of past events. When the experience of an event is affected by sensory input that is detected *after* that event, it is not the instantaneous experience of the event that is changed, but rather the memory of that event. The instantaneous experience (if there ever was one) is overwritten, leaving only the revised memory.

The second observation is that conscious experience takes time to arise, and this necessary delay is problematic for the interpretation that consciousness is causally involved in fast action and decision-making because such actions occur faster than the corresponding conscious experience. A baseball player deciding whether to swing at a ball might report that he consciously made the decision to do so. However, from the moment the ball leaves the pitcher's hand to the moment it reaches the batter, there is insufficient time for the brain to generate a conscious percept of the ball's trajectory, make a decision, and initiate the necessary motor actions. Again, the paradox is neatly solved by framing conscious experience as a memory. Budson and colleagues (2022) argue that when a baseball player swings at a ball, he is not yet conscious of making that decision. The conscious experience is created after the fact: Although he was not conscious of making the decision to swing at the ball at the time, he will nevertheless later have a memory of having made that decision consciously. This illusion of conscious agency is what Wegner (2003) called "the mind's best trick."

If consciousness arises too slowly to take part in rapid action control and decision-making, then who or what is making those decisions? To answer this question, Budson and colleagues (2022) invoke the dual processing model (Epstein, 1994) that was made famous by Kahneman and Tversky, comprising a fast, automatic, stereotyped, and unconscious *System 1*, and a slow, effortful, and conscious *System 2* (Carruthers, 2017; Kahneman, 2013). Although our conscious experience is enabled by the slower System 2, the majority of our behavior, and especially rapid action initiation, is actually controlled by the unconscious

System 1. In the baseball scenario, the decision to swing at the ball is therefore made unconsciously by System 1, and the conscious experience of making that decision is later created by System 2. In terms of the time course of consciousness, this retroactive conscious experience is consistent with the notion of consciousness as a memory system.

The Evolution of Consciousness

A further innovation of the interpretation proposed by Budson and colleagues (2022) is that it not only addresses some of the temporal wrinkles in our understanding of consciousness, but it also provides a (speculative) account of how consciousness may have arisen over the course of evolution. How consciousness evolved remains a topic of some debate (Gutfreund, 2018; Mashour and Alkire, 2013), in part because trying to identify the evolutionary advantage of consciousness leads to the thorny question of what should be considered the *purpose* of consciousness. This question is difficult to answer because although the various cognitive functions that make up consciousness provide clear survival value, in principle, these functions could evolve without the qualitative subjective experience that characterizes consciousness per se (Gutfreund, 2017, 2018).

Budson and colleagues (2022) approach the question of why consciousness evolved from a different angle. They start with the uncontentious premise that the survival benefit of being able to store information about sensory experiences (ie, memory) is self-evident. In turn, storing richer and richer representations of previous experience provides progressively greater benefit, gradually leading to the evolution of episodic memory. Subsequently, this ability to “call to mind” events from the past could then have developed to allow us to imagine possible future events, thereby providing a scaffold for the ability to understand the consequences of our decisions. This putative evolutionary pathway is at least partially supported by the observation that a number of other animals, such as several species of food-

caching birds, appear to have evolved some capacity for “mental time travel” (Suddendorf and Busby, 2003; Suddendorf and Corballis, 2007). Ultimately, the combination of episodic memory and this understanding of the potential future consequences of our decisions then laid the basis for the complex problem-solving ability that characterizes consciousness today.

In this way, in the proposal presented by Budson and colleagues (2022), consciousness would not need to directly evolve due to its own intrinsic survival benefit—which, as mentioned, is not uncontroversial (Gutfreund, 2018). Instead, the authors present a plausible evolutionary pathway for how consciousness might have evolved from the ability to flexibly combine information from episodic memory. This explanation is also more parsimonious (and frankly more satisfying) than the alternative—that our cognitive capacities evolved on their own evolutionary merit, and that our conscious experience is purely epiphenomenal.

The Neural Basis of (Micro-) Consciousness

Building on the perspective of consciousness as evolving from episodic memory, Budson and colleagues (2022) make a number of important but perhaps understated predictions about the neural underpinnings of both episodic memory and consciousness. Specifically, they propose that consciousness of a particular function or sensory modality is enabled by those cortical areas that are involved in that modality or function. In other words, visual cortex subserves the conscious experience of visual input, motor cortex enables conscious control over motor behavior, and so on.

Budson and colleagues (2022) contrast the predictions of four influential theories of consciousness: recurrent processing theory (Lamme, 2015, 2018), global neuronal workspace theory (Mashour et al, 2020), integrated information theory (Tononi et al, 2016), and higher-order thought theory (Brown et al, 2019). Whereas these theories each implicate specific

brain areas as being especially important for enabling consciousness, Budson and colleagues (2022) argue that there are no specific “consciousness-enabling” brain regions. Instead, they argue on the basis of extensive neuropsychological evidence that modality-specific areas of the cerebral cortex enable the consciousness of corresponding functions.

Although Budson and colleagues (2022) do not themselves relate their proposal to the “micro-consciousness” framework that was articulated by Zeki and colleagues at the end of the 20th century (Moutoussis and Zeki, 1997; Zeki and Bartels, 1998, 1999), it nevertheless aligns perfectly with that framework. Over the course of extensive investigations of the macaque and human visual system, Zeki and colleagues noted that visual processing (and sensory processing more generally) is characterized by multiple processing systems operating in parallel on different features (Zeki, 2005). Importantly, they also noted that processing in these different streams happens largely autonomously and takes varying amounts of time to complete, and that there is no final stage where the finished products come together. The authors concluded, like Budson and colleagues (2022), that each individual brain area enables conscious awareness of the feature that it is involved in processing: a micro-consciousness.

Interestingly, Zeki and Bartels (1998) also noted that due to the brain’s asynchrony, the binding of different features into an integrated conscious percept must happen postconsciously, which is akin to saying that it is the memory of the conscious percept that is integrated, rather than the instantaneous percept itself. In other words, when viewing a red ball, because its color and shape are processed at different speeds, we consciously perceive the ball’s roundness and redness at different times. Once both conscious features are available, they are bound into a memory of a red ball, thereby overwriting any earlier memories of unbound features. This interpretation fits neatly with the *after-the-fact* aspect of consciousness when it is framed as evolving from the episodic memory system.

Delineating Consciousness and Memory

As Budson and colleagues (2022) note, due to neural transmission delays, the representation of sensory information in the brain necessarily lags the events in the outside world that are being represented. For simplicity, the authors describe consciousness as lagging behind events in the outside world by a fixed amount of time: ~500 ms. However, this description is an important oversimplification, for two reasons. First, sensory processing (and therefore the conscious perception that it enables) is asynchronous, such that delays are different for different features and modalities (Zeki and Bartels, 1998). Second, this simplification implies that perception at some point is “finished,” as if the version of events that was being processed is now finalized. In turn, the idea of perceptual processing being finished implies a point at which perception (fluid and revisable) becomes memory (a definitive version of events). This idea is intuitively appealing, but it is contradicted by the observation that postdictive effects can extend well beyond the 500-ms window (Shimojo, 2014). Indeed, the phenomenon of false and implanted memories shows that postdictive effects can extend many years into the past—a time line that most would call memory, and few would call perception (Loftus and Palmer, 1974).

Several authors have previously noted that episodic memory and consciousness are closely related (eg, Brown et al, 2019; Gardiner, 2001; von Helmholtz, 1867). But is it actually possible to delineate episodic memory from consciousness (Hogendoorn, 2022; LeDoux and Lau, 2020; Tulving, 1985a, 1985b)? From a temporal angle, I would argue that there is no hard boundary between the two. Because postdiction has no clear temporal limit (although see Herzog et al, 2016, 2020), there is no single moment at which the present becomes the past, and therefore no hard line separating consciousness from memory. Rather, I would argue that conscious perception forms a continuum with episodic memory, with the

only difference between the ends of that continuum being the *when* of what is being experienced.

Framing consciousness and memory as equivalent also brings together what have heretofore been argued to be distinct memory subsystems, including sensory (or iconic) memory, short-term or working memory, and long-term episodic memory. It is interesting to note that working memory is considered to be closely related to attention (eg, Oberauer, 2019), which in turn is closely related to (or even synonymous with [Cohen et al, 2012]) conscious perception. Allowing consciousness to include the experience of both the past and present erases the delineations between these putatively different constructs, leaving a continuum of represented information that extends from the past to the present (and even the future, see later). Viewed in this way, calling to mind information from the past (ie, memory recall) would be no different than calling to mind information from the present (ie, conscious perception).

Consciousness as Trajectory Estimation

Although we are used to thinking of memory as representing sequences of events that unfold over a temporal extent, conscious perception is typically thought of as representing a single moment. An interesting consequence of framing consciousness and memory as equivalent is therefore that the present no longer has an inherently privileged status. In turn, this idea neatly aligns with an idea that was first articulated by Grush (2005): Our consciousness does not represent successive single instants, but instead represents a trajectory—in other words, like memory, it represents a time line, or narrative (Hogendoorn, 2022). For example, when we view a ball in flight, our conscious experience is not built up out of successive still frames of the ball in successive positions. Instead, consciousness represents a trajectory: We consciously experience the arc of the ball through the air rather

than successive individual positions. Conscious experience at any given instant therefore not only contains information about the present; it contains information from a range of time points.

Viewing consciousness (like episodic memory) as representing a time line of events rather than individual instants has even broader implications. Specifically, I have previously argued that if conscious awareness represents information from a range of time points (including the past and present), this framework could equally represent information for future time points (Hogendoorn, 2022). Because sensory information about future events is obviously unavailable to the brain, these representations would be activated by prediction mechanisms, which in turn would solve some of the problems that result from neural transmission delays (Blom et al, 2020; Ekman et al, 2017; Feuerriegel et al, 2021; Hogendoorn, 2020). In this sense, I would argue that it is possible to extend the proposal put forth by Budson and colleagues (2022) even further, allowing memory (and therefore consciousness) to represent not only the past, but also both the present and the future. In this way, viewing consciousness through a “memory lens” (LeDoux and Lau, 2020) unifies the entire time line of experience.

CONCLUSION AND FUTURE DIRECTIONS

Budson and colleagues’ (2022) proposal that consciousness evolved from episodic memory is both insightful and provocative. To my mind, its key contribution is that it fits with some of the challenging temporal complexities of consciousness that many other models of consciousness simply do not address. Furthermore, although not explicitly mentioned in the paper, the proposal is also consistent with previous models of visual “micro-

consciousness” (eg, Zeki, 2005), as well as with the emerging perspective that consciousness and memory are closely related (eg, LeDoux and Lau, 2020).

One new question that the proposal raises relates to the idea of a local, modality-specific neural substrate for consciousness. The idea that consciousness is enabled by local processing in modality-specific brain regions has substantial empirical support and theoretical appeal. However, one of the key phenomena for which such a model provides no explanation is the multimodal nature of our experience: If consciousness of individual modalities or features is enabled by distinct neural circuits, how is the experience of integrated features enabled? Is there a sense in which “it all comes together”(Dennett and Kinsbourne, 1992)?

Anatomically, the temporoparietal junction is often implicated in multimodal processing (eg, Sepulcre et al, 2012), but it is unclear whether this area would serve conscious or unconscious processing. Alternatively, LeDoux and Lau (2020) proposed that integrated consciousness might be enabled by the prefrontal cortex “re-representing” unconscious information from modality-specific cortical areas. Finally, the hippocampus is well-known to replay sensory information, and this hippocampal replay has been implicated in both memory consolidation (Carr et al, 2011) and decision-making (Denovellis et al, 2021; Ólafsdóttir et al, 2018). The neural locus (if there is one) of multimodal consciousness therefore needs further investigation.

Finally, Budson and colleagues’ (2022) perspective on consciousness as evolving from episodic memory fits with other recent literature arguing that memory and consciousness might be more closely related than typically thought. For example, LeDoux and Lau (2020) suggested that consciousness emerges from the integration of sensory input with a context of episodic memory, whereby the embedding of new information into our experiential narrative produces conscious experience. Complementary to this idea, I recently argued that conscious experience should be thought of as a narrative time line that

encompasses memory (of the past), perception (of the present), and prediction (of the future) as different time points on a continuum (Hogendoorn, 2022). In both of these accounts, the key new feature of consciousness is its narrative nature, which of course is the classical feature of episodic memory.

One new question that arises if memory and consciousness are conceived of as merely different points on a time line is why we nevertheless experience what is happening *now* differently from what has happened in the *past* (or indeed what is expected to happen in the *future*). Perhaps one point or short range of time is experienced as *now*, but whatever marks that point as the present would then need to shift as time passes. The experience of a given event would then similarly change as time passes—from perceiving an event to remembering having perceived that event. How different features of an experience gradually evolve as they move from the remembered (predicted) future to the remembered present, and ultimately, the remembered past, is an exciting area for further research, and I believe that Budson and colleagues (2022) have provided the framework to structure our thinking as we continue investigating these fundamental questions.

REFERENCES

- Blom T, Feuerriegel D, Johnson P, et al. 2020. Predictions drive neural representations of visual events ahead of incoming sensory information. *Proc Natl Acad Sci U S A*. 117:7510–7515. doi:10.1073/pnas.1917777117
- Brown R, Lau H, LeDoux JE. 2019. Understanding the higher-order approach to consciousness. *Trends Cogn Sci*. 23:754–768. doi:10.1016/j.tics.2019.06.009
- Carr MF, Jadhav SP, Frank LM. 2011. Hippocampal replay in the awake state: a potential substrate for memory consolidation and retrieval. *Nat Neurosci*. 14:147–153. doi:10.1038/nn.2732
- Carruthers P. 2017. *The Centered Mind: What the Science of Working Memory Shows us About the Nature of Human Thought*. Oxford, UK: Oxford University Press.
- Cohen MA, Cavanagh P, Chun MM, et al. 2012. The attentional requirements of consciousness. *Trends Cogn Sci*. 16:411–417. doi:10.1016/j.tics.2012.06.013
- Dennett DC, Kinsbourne M. 1992. Time and the observer: the where and when of consciousness in the brain. *Behav Brain Sci*. 15:183–201. doi:10.1017/S0140525X00068229
- Denovellis EL, Gillespie AK, Coulter ME, et al. 2021. Hippocampal replay of experience at real-world speeds. *Elife*. 10:e64505. doi:10.7554/eLife.64505
- Eagleman DM. 2008. Prediction and postdiction: two frameworks with the goal of delay compensation. *Behav Brain Sci*. 31:205–206. doi:10.1017/S0140525X08003889
- Eagleman DM, Sejnowski TJ. 2000. Motion integration and postdiction in visual awareness. *Science*. 287:2036–2038. doi:10.1126/science.287.5460.2036
- Ekman M, Kok P, de Lange FP. 2017. Time-compressed preplay of anticipated events in human primary visual cortex. *Nat Commun*. 8:15276. doi:10.1038/ncomms15276

- Epstein S. 1994. Integration of the cognitive and the psychodynamic unconscious. *Am Psychol.* 49:709–724. doi:10.1037/0003-066X.49.8.709
- Feuerriegel D, Blom T, Hogendoorn H. 2021. Predictive activation of sensory representations as a source of evidence in perceptual decision-making. *Cortex.* 136:140–146. doi:10.1016/j.cortex.2020.12.008
- Gardiner JM. 2001. Episodic memory and autothetic consciousness: a first-person approach. *Philos Trans R Soc Lond B Biol Sci.* 356:1351–1361. doi:10.1098/rstb.2001.0955
- Grush R. 2005. Internal models and the construction of time: generalizing from state estimation to trajectory estimation to address temporal features of perception, including temporal illusions. *J Neural Eng.* 2:S209–S218. doi:10.1088/1741-2560/2/3/S05
- Gutfreund Y. 2018. The mind-evolution problem: the difficulty of fitting consciousness in an evolutionary framework. *Front Psychol.* 9:1537. doi:10.3389/fpsyg.2018.01537
- Gutfreund Y. 2017. The neuroethological paradox of animal consciousness. *Trends Neurosci.* 40:196–199. doi:10.1016/j.tins.2017.02.001
- Herzog MH, Drissi-Daoudi L, Doerig A. 2020. All in good time: long-lasting postdictive effects reveal discrete perception. *Trends Cogn Sci.* 24:826–837. doi:10.1016/j.tics.2020.07.001
- Herzog MH, Kammer T, Scharnowski F. 2016. Time slices: What is the duration of a percept? *PLoS Biol.* 14:e1002433. doi:10.1371/journal.pbio.1002433
- Hogendoorn H. 2020. Motion extrapolation in visual processing: lessons from 25 years of flash-lag debate. *J Neurosci.* 40:5698–5705. doi:10.1523/JNEUROSCI.0275-20.2020
- Hogendoorn H. 2022. Perception in real-time: predicting the present, reconstructing the past. *Trends Cogn Sci.* 26:128–141. doi:10.1016/j.tics.2021.11.003

- Kahneman D. 2013. *Thinking, Fast and Slow*. New York, New York: Farrar, Straus and Giroux.
- Lamme VA. 2018. Challenges for theories of consciousness: seeing or knowing, the missing ingredient and how to deal with panpsychism. *Philos Trans R Soc Lond B Biol Sci*. 373:20170344. doi:10.1098/rstb.2017.0344
- Lamme V. 2015. The crack of dawn: perceptual functions and neural mechanisms that mark the transition from unconscious processing to conscious vision. *Open MIND*. 22(T). doi:10.15502/9783958570092
- LeDoux JE, Lau H. 2020. Seeing consciousness through the lens of memory. *Curr Biol*. 30:R1018–R1022. doi:10.1016/j.cub.2020.08.008
- Loftus EF, Palmer JC. 1974. Reconstruction of automobile destruction: an example of the interaction between language and memory. *J Verbal Learn Verbal Behav*. 13:585–589. doi:10.1016/S0022-5371(74)80011-3
- Mashour GA, Alkire MT. 2013. Evolution of consciousness: phylogeny, ontogeny, and emergence from general anesthesia. *Proc Natl Acad Sci U S A*. 110:10357–10364. doi:10.1073/pnas.1301188110
- Mashour GA, Roelfsema P, Changeux JP, et al. 2020. Conscious processing and the global neuronal workspace hypothesis. *Neuron*. 105:776–798. doi:10.1016/j.neuron.2020.01.026
- Moutoussis K, Zeki S. 1997. Functional segregation and temporal hierarchy of the visual perceptive systems. *Proc Biol Sci*. 264:1407–1414. doi:10.1098/rspb.1997.0196
- Nijhawan R. 2008. Visual prediction: psychophysics and neurophysiology of compensation for time delays. *Behav Brain Sci*. 31:179–198. doi:10.1017/S0140525X08003804
- Oberauer K. 2019. Working memory and attention—a conceptual analysis and review. *J Cogn*. 2:36. doi:10.5334/joc.58

- Ólafsdóttir HF, Bush D, Barry C. 2018. The role of hippocampal replay in memory and planning. *Curr Biol.* 28:R37–R50. doi:10.1016/j.cub.2017.10.073
- Schacter DL, Addis DR, Buckner RL. 2007. Remembering the past to imagine the future: the prospective brain. *Nat Rev Neurosci.* 8:657–661. doi:10.1038/nrn2213
- Sepulcre J, Sabuncu MR, Yeo TB, et al. 2012. Stepwise connectivity of the modal cortex reveals the multimodal organization of the human brain. *J Neurosci.* 32:10649–10661. doi:10.1523/JNEUROSCI.0759-12.2012
- Shimojo S. 2014. Postdiction: its implications on visual awareness, hindsight, and sense of agency. *Front Psychol.* 5:196. doi:10.3389/fpsyg.2014.00196
- Suddendorf T, Busby J. 2003. Mental time travel in animals? *Trends Cogn Sci.* 7:391–396. doi:10.1016/S1364-6613(03)00187-6
- Suddendorf T, Corballis MC. 2007. The evolution of foresight: What is mental time travel, and is it unique to humans? *Behav Brain Sci.* 30:299–313. doi:10.1017/S0140525X07001975
- Tononi G, Boly M, Massimini M, et al. 2016. Integrated information theory: from consciousness to its physical substrate. *Nat Rev Neurosci.* 17:450–461. doi:10.1038/nrn.2016.44
- Tulving E. 1985a. Ebbinghaus's memory: What did he learn and remember? *J Exp Psychol Learn Mem Cogn.* 11:485–490. doi:10.1037/0278-7393.11.3.485
- Tulving E. 1985b. Memory and consciousness. *Canadian Psychology/Psychologie Canadienne.* 26:1–12. doi:10.1037/h0080017
- von Helmholtz H. 1867. *Handbuch der physiologischen Optik.* Leipzig, Germany: Voss.
- Wegner DM. 2003. The mind's best trick: how we experience conscious will. *Trends Cogn Sci.* 7:65–69. doi:10.1016/S1364-6613(03)00002-0

Zeki S. 2005. The Ferrier Lecture 1995 Behind the seen: the functional specialization of the brain in space and time. *Philos Trans R Soc Lond B Biol Sci.* 360:1145–1183.

doi:10.1098/rstb.2005.1666

Zeki S, Bartels A. 1998. The asynchrony of consciousness. *Proc Biol Sci.* 265:1583–1585.

doi:10.1098/rspb.1998.0475

Zeki S, Bartels A. 1999. Toward a theory of visual consciousness. *Conscious Cogn.* 8:225–

259. doi:10.1006/ccog.1999.0390