Overview

Neurotypical subjective experience is caused by a hippocampal simulation

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We propose that the phenomenon known to neurologically intact people as 'Subjective Experience' is best understood as the activation of various sites in both extrinsic and intrinsic networks by a brand new *episodic memory engram* (i.e., a complex theta wave coding pattern originating from field CA1 of the hippocampus). Like a media news outlet, the hippocampal complex receives reportage from widely distributed structures around the brain and organizes and binds those reports together into a brand new episodic memory (i.e., a virtual-reality, movie-like, unified, contextualized, but vastly simplified summation of *what just happened*). This memory pattern is then 'broadcast' back to structures across the brain (via bidirectional pathways to and from the entorhinal cortex and perirhinal area) for error correction, to expedite predictive processing, and to inform sites in both extrinsic and intrinsic networks of one unified history. It is the cortical activation by the new episodic memory engram that gives rise to the event of experiencing. Because episodic memory is the only unified and contextualized representation of self-in-the-world in the brain, and because it informs most of the major cortices about 'what just happened,' it is subjectively misinterpreted as the actual interaction of the body/mind with its environment. This misinterpretation offers insight into many of the distinct and mysterious features of neurotypical subjective experience and the pathologies of consciousness. © 2016 Wiley Periodicals, Inc.

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INTRODUCTION

In the quest to find the neural cause of consciousness, the problem is framed by how one defines the phenomenon. Some early theorists (e.g., Descartes[1]) posited consciousness as a command-and-control process, an ersatz 'self' that pilots an unconscious machine: the brain/body.

However, a school of thought that began with Kant[2] views consciousness as a much more modest phenomenon, often called Subjective Experience. To this school, subjective experience is a representation of the self-in-the-world, constructed by the brain for its own internal use. Michael Graziano[3] called subjective experience 'information,' a form of neural representation that helps different brain parts communicate with each other. Bernard Baars[4] likened the role of subjective experience to a 'newscast,' a unified informational structure that includes within it reportage from all over the brain, and which then reciprocally delivers a bound-together big-picture summation of those reports, so the whole brain can share one common story of what is going on.

In this article, we offer an anatomical model for explaining neurotypical subjective experience (NSE), which aligns with the above representationalists and also with a dense constellation of neuroscientific evidence. We believe this model is not only anatomically plausible but is also sufficient to explain the full breadth of conscious experience as well as the numerous pathologies thereof. This model is subjectively counterintuitive and difficult to embrace because it treats the internal experience of self-in-the-world as

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equivalent to memory, but we believe it is elegant from an informational processing standpoint.

In brief, we think that there is good reason to believe that the hippocampal complex (HC) is central to the phenomenon that neurologically intact people know as 'subjective experience.'[5] We see abundant evidence showing the HC is at the apex of a pyramid of reports, receiving final conclusions from sensation, motor, body-state, and cognitive structures from all over the brain.[6,7] The HC has the unique functions to organize all of its input reports on a temporal[8] and spatial lattice[9] and bind them into one united multimodal movie of experience,[10] with a memory version of 'self' at the center of it.[11]

We also see emerging evidence[12,13] that the HC has the reciprocal ability to generate a newscast-like report, which reactivates the various brain structures that contributed to the news, to share one common story of 'what just happened' all around the brain. We believe the activation of brain regions by this reciprocal newscast to be equivalent to NSE.

We expect that this theory will face initial resistance among people who are familiar with the case of H.M., an epileptic patient who lived without a working HC for several decades.[14] We deal extensively with the question of H.M. in section 5: *What Does this Say about H.M. (And Other Patients Like Him)?*

Defining Neurotypical Subjective Experience

We want to be careful with how we use the term 'subjective experience,' because it can have various slightly different meanings. The brain could be said to be experiencing even when it is in deep sleep because neurons are active and processing. However, NSE is a particular kind of experiencing that only takes place during waking and rapid eye movement (REM) sleep.

In this article, we use NSE specifically to mean a neurologically intact person's typical internal unified three-dimensional (3D) virtual-reality movie-like experience of being a mind and body in the world.[15] It is virtual-reality-like in that there is full-surround immersion into the experience, and movie-like in that there is continuity from moment to moment. However, unlike an audio/visual virtual-reality movie, NSE also includes body sensations, motor feedback, emotions, and even qualities of the mind, like thought and the products of our imagination.

The mind subjectively feels like a different kind of thing than the body and the world, but that is an assumption we will avoid. We will instead argue in this article that all elements of perception, including the perception of mind, arise from one unified piece of neural information that is output from the HC (see section 6.1: *The Mind as Representation*).

The three main constituent elements of experience (mind, body, and world) do not need to be equally represented in all activities. In many nonphysical activities, like reading or watching television, the experience of body tends to fade. In deeply immersive mental tasks, like memory recall, social rehearsal, or daydreaming, the outside world fades from awareness, and in flow states or tasks that require strong focus on interacting with the world, the awareness of mind may fade instead. We will argue that the HC organizes, binds and broadcasts the informational output, which gives rise to NSE, but NSE's contents are due to structures upstream of the HC, based on the needs of the moment.

There are two additional elements that add context to NSE: emotions and what William James[16] called 'fringe' senses, which are usually subtle and are shaped by our previous experiences. These are contextual feelings, like familiarity, certainty, and novelty. Along with emotions, fringe senses flavor our other perceptions.

We also need to distinguish between the neural information that activates experiencing and the experiencing itself. In this article, the neural-coded information that activates the experiencing will be called the *episodic memory engram*, whereas we will use NSE to mean the *event* of experiencing. Thus, the theta wave HC output is the episodic memory engram and that engram's activation of relevant target brain structures is NSE.

This article ends with a good deal of speculation as it seeks to sketch out a new framework for considering NSE, but it begins with a (simplified) anatomical model that is based on the latest neuroscience research.

NEWSCAST OF THE BRAIN—THE ANATOMICAL MODEL

In order to explain the HC's role in the brain, we need to first roughly describe the functional organization of the brain as a whole. As a full description of brain function is beyond the scope of this article, we offer an analogy for simplification.

The body can be thought of like a cooperative society in which various populations of cells specialize in their tasks, complementing and assisting each other.[17] Each organ is partially autonomous, with its own local neurons that help guide function.[18] Neurons act as the local governmental administration to this society, providing oversight and communication between various parts.[19]

Body neurons report to the brain, which is analogous to the central government of this society. This central government is in charge of responding to its bodily constituents, resolving issues that cannot be solved locally, like how to coordinate systems together.[19]

The central government is divided into departments and subdepartments, which allow for tasks to be broken down by specialization and handled in parallel to each other.[20] This parallel processing allows for different aspects of a task to be performed by the most relevant departments, but it also demands a robust interdepartmental communication scheme so that these various specialists can collaborate on their processing.[21]

Each department, during a task, receives reports from input neurons, runs its calculations upon that input, and then outputs its own report for other interested departments to work with.[22] These conclusions are usually arrived at through a neuronal form of local democracy: a department-specific vote of how to interpret inputs and what to output.[23]

Within a department, neurons vote like the Iowa caucus system: popular neuronal conclusions amplify the expression of other neurons that agree with them, and inhibit the expression of those that disagree.[24] The vote is roughly winner-take-all, meaning that the department's final conclusion is expressed as an output report, and most contradictory conclusions are soon forgotten.[23]

In the brain, groups of departments that communicate and coordinate extensively with each other are called 'networks.' Networks exist on many scales of function and are divided largely by their areas of concern.[25,26]

Most brain networks can be categorized roughly into two concerns. They are either focused on 'extrinsic' affairs, meaning those that exist outside of the mind (e.g., the body and its immediate interaction with the external environment), or on 'intrinsic' affairs, meaning those that exist entirely in the mind (e.g., imagination[27]).

The intrinsic departments are made up of highly networked structures, primarily at the midline of the cerebrum, that have become collectively known as the default mode network (DMN). It is called 'default' precisely because during imaging studies, it activates when the brain is *not* attending to world-oriented tasks.[28]

The DMN is in charge of mental manipulation of concepts, for tasks like planning, previsualization, reviewing memories, and trying to figure out what is going on in other people's heads.[29] It is focused on figuring out the past, anticipating the future, and extrapolating beyond the current scene.[30] The DMN's relationship to the HC is explored more thoroughly in section 3: *The Hippocampal Complex as Experience Simulator*.

The extrinsic departments, albeit highly internetworked, can also be understood as many smaller networks, each focused on granular subtasks of dealing with the outside world.[31] For example, the extrinsic departments include all the system inputs (i.e., the sensory networks) as well as the attentional system, which decides which inputs to focus on.[32] It also includes the system outputs, i.e., speech and motor systems. For ease of discussion, this article will refer to the sum of all these departments as the Extrinsic Network (EN). Caveat: we acknowledge that the EN label is likely too broad for many purposes in describing this community of networks, but we also believe it is sufficient and useful enough for simplifying this explanation.

Most EN networks are built hierarchically, with more gross calculations performed at earlier (usually more posterior) subdepartments and increasingly refined processing as the reports pass forward up the chain.[7]

The higher levels of the hierarchy also loop back to report to the lower levels. This top–down influence provides error correction and helps to prime the lower areas to reach their conclusions faster.[33,34]

In many departments, the highest arbiter of conclusions is in the prefrontal cortex. Analogous to the Secretary (i.e., head) of a department, the prefrontal area helps arbitrate between conflicting conclusions from earlier in the chain.[32]

Data can be buffered in the brain at many different levels of hierarchy, within a local subdepartment, or in loops along the departmental chain. This buffering provides the individual departments with the opportunity to identify stimuli, contrast current stimulus with stimulus from the moment before, provide predictions, and/or correct errors. These departmental buffers are often referred to as 'working memory' (WM) because they are used during extrinsic tasks.[35]

Historically, WM has been assumed to be a conscious process, but there is now a good deal of evidence that NSE and WM are dissociable (reviewed in Ref 36). WM contents may end up in NSE, but they may also remain out of awareness. Our explanation is that NSE occurs downstream of these EN buffers (and so sometimes includes their contents), but NSE does not occur within them.

Although these EN departments can hold short-term loops and repetitions, there is no place in the EN for the entire multimodal event (world + feelings + thought + action) to be remembered.[9] Event memory is offloaded from all EN departments to another network, the HC.[13]

Among other functions, the HC network is like the historical archive department of the central government. Final conclusions from various sensory, motor, cognitive, and emotional departments are reported to the HC, which organizes and binds those conclusions into a streamlined data packet, known as an *episodic memory engram*, that can be stored for later use.[37]

This episodic memory engram is a low-data scheme of encoding a great deal of sensory and cognitive richness for storage. As the memory is composed of the final conclusions from the various departments, the engram is a complex pattern of pointers, like hyperlinks, which connect back to the cortical areas that gave rise to those conclusions.[38] These pointers are structured temporally and spatially within the HC[9], so that the memory has not only sensation and action but also sequence and a 3D sense of space.[39] We offer a more thorough anatomical description of the formation of a new episodic memory in section 2.2: *Pyramid of Reports: The (Simplified) Anatomy of a New Episodic Memory*.

The HC is also the home of archive retrieval, where old engrams may be reactivated to bring a previous event back to mind. Recall works the memory encoding process in reverse, using the spatiotemporal sequence of pointers to reactivate the various departments around the brain, which originally fed the formation of the memory.[38,40] The more vivid the memory recall, the more the departments and subdepartments are involved in its reconstruction.[41] Thus, the experience of memory recall is a reactivation of the very cortical regions that were active during the original event, giving rise to a sense of re-experiencing.

Memory formation and retrieval show that the HC has a bilateral relationship with the EN. EN activations lead to departmental conclusions, which are sent as reports to the HC. The HC structures these reports into a spatial and temporal scaffolding[9] and then binds them into an episodic memory engram for possible future recall. Upon recall, the HC uses the scaffolding to reinstate space and sequence of the memory and uses the pointers within the engram to reactivate the various departments, thereby creating a new experiencing of the old event.[42]

This article's central hypothesis is that the bilateral relationship between the HC and the other networks is a continual feedback loop. Not only are previous memories fed back to the departments that generated them but so are brand new memories. This immediate reactivation of the various departments by the HC engram is part error correction for the new memory but is also another form of top–down predictive processing, which helps prime the various regions for the next moment's calculations.[9] As in the recall of prior memories, it is the reactivation of the original departments that gives rise to the sense of experience. In our theory, the episodic memory engram carries the information that can give rise to NSE, but NSE only happens upon activation of the receiving structures by that engram.

In this model, we can see the HC not only as the archival and retrieval branch of the central government but also as its newscast. Like a media outlet, the HC receives reports from all over the brain, binds those reports into one story of what just happened, and then broadcasts that news story (i.e., the engram) to reactivate both DMN and EN. That reactivation, we believe, is equivalent to what neurologically intact people commonly know as 'Subjective Experience.'

What Is Episodic Memory?

The most obvious use of episodic memory is to recall the past, but we can argue that episodic memory is more important in how it prepares the organism for the future.[43] For example, if I experienced a threatening predator on the savanna yesterday, then it helps if I can remember that encounter today, so when I am back in the same area, I can keep an eye out for that predator. I will also remember the feelings I had in the encounter with the predator, which will help keep me activated and aware, as I maneuver through the same territory. I will remember the escape route that allowed me to flee last time, which may save me now if the predator reappears and I can use yesterday's memory to plan out an entirely new route, which bypasses the dangerous area altogether. In these ways, recalled episodic memory, a reflection from the past, is most useful as a way of informing one's present, and planning for one's future.[22]

An episodic memory, as subjectively recalled, is like a spatiotemporal multimodal full-immersion 'movie'[10] that approximates the viewpoint of the original experience. Episodic memory is most obviously like a movie, immediately after a salient event, when it is possible (for most people) to replay a very vivid and detailed reconstruction of what just happened that includes data from all senses (and even emotions), like the playback from a multimodal video camera.

Of course, episodic memory is not nearly as accurate as video. Episodic memories are labile during consolidation and upon recall,[44] which allows for suggestion, assumption, and self-rationalization to alter the story or sensory content[11,45] so that recalled episodes can be very vivid and yet be entirely nonveridical.

In this article, unless stated otherwise, we will use the word 'memory' exclusively to mean 'episodic memory.'

Pyramid of Reports: The (Simplified) Anatomy of a New Episodic Memory

In order to illustrate how sensory data become part of a new episodic memory, we will describe the journey of one moment's visual data from the retina to the HC and beyond.

At the retina, a red-detecting cone activates upon sufficient light of a certain wavelength and sends a report of that activation (via the thalamus) to V1, the first and lowest-definition work center in the visual department.[22]

It is important to distinguish the report from that which it is reporting; e.g., the red-detecting retinal cone does not send anything red to the brain. Rather, it sends a temporally coded data packet,[46] which the brain can interpret as meaning red. So, even the most basic sense datum is a *representation*, a proxy for information from the body and/or environment, which the receiving brain structure decodes into something meaningful.

At V1, the red-cone input is compared to its neighboring inputs, and the result is passed forward on the processing chain, giving rise to blobs, then edges, then shapes, and then eventually objects. Every perceptual subdepartment in the system is dependent upon a *pyramid of reports*[7] from bottom–up sensory inputs, granular data interpreted into increasingly refined conclusions.[9] Each of the various sensation departments receives relatively unprocessed data, performs its computation (albeit also informed by top–down priming loops as described in section 2: *Newscast of the Brain—The Anatomical Model*), and outputs a more sophisticated report, which represents its conclusions.[22]

This pyramid model becomes a lot more complex in the visual system (among others) as distinct aspects of vision are processed in parallel to each other. We will use as our example, the most famous case of parallel visual processing: the split between what's known as the 'ventral stream,' which primarily processes object information (e.g., color, shade, shape), and the 'dorsal stream,' which primarily processes egocentric spatial relations (i.e., the relation between the self/body and objects in the world[47]). These two visual streams communicate throughout their processing, comparing and shaping each other's conclusions,[48] but there is no department in the EN where the representations of objects are fully united with the spatial representation of the environment.[9]

In fact, these parallel processing streams do not come together to form a specific image of the world anywhere in the neocortex, but only come together in the HC for the creation of episodic memory.[49,50] Likewise, the pyramid of reports for *each* perceptual system comes to its respective apex at the HC.[6,7]

The ventral object stream's final conclusions are shared with the HC largely via concept cells. A concept is a mental model, formed from a linked constellation of sensory and/or semantic associations, that represents objects in the world and/or processes in the body/brain.[34] For example, the concept cell for an orange is linked to the sensory input structures that code for the orange's sight, smell, taste, and texture. A concept cell for a person links to structures that code for the sight of their face, the sound of their voice, their name written or spoken, how they smell, and even how I feel about them.[51] In this way, when an object is identified at a distance or in our memory, many associations to that object, which are not themselves part of our sensory input, are nonetheless automatically activated and become a background part of our experiencing of that object.[22]

The ventral visual system terminates at the object-identifying inferotemporal lobe[52] or the fusiform face gyrus for human faces.[34] In both cases, these structures report their final conclusions to memory by activating concept cells in the HC's perirhinal area (PA).[49]

The PA is an associational hub, with concept cells linking together widely distributed elements of previously learned objects.[53] Among other associations, the PA links together various possible views of the same object so that any recognizable view will activate the object's concept.[54]

Meanwhile, the dorsal (i.e., spatial-relation) visual stream terminates at the posterior parietal lobe of the EN, where it represents an egocentric view of the world,[22] to interact with proprioceptive representations of the body in the somatosensory cortex and cerebellum.[50] This dorsal egocentric spatial representation is also reported to the HC for addition into episodic memory.

Similar to the way that the PA informs object representations, the 'place area' of the HC's parahippocampal cortex (PHC) receives the egocentric spatial representations from the parietal lobe (via the retrosplenial cortex) and associates them with prior semantic concepts of the environment.[55] Just as PA semantic concepts can link various viewed angles of an object, so too can PHC semantic concepts link various viewed angles of the environment. By placing the current egocentric view of the world within a virtual allocentric (i.e., view-independent) cognitive map[56] of what is known about the environment, one can represent this view in memory within the context of the area that it happened (e.g., up ahead, around the corner, is where the reward or punishment was, in my prior experience[6]).

We have been illustrating the pyramid of reports via the major visual streams, but other perceptual streams also arrive at the HC via the PA, so objects and concepts can be associated across modalities before being sent on to the entorhinal cortex (EC) for inclusion in the hippocampus' memory encoding.[6]

PA and PHC conceptual streams converge with other data streams at the EC, the main hub into and out of the hippocampus proper.[57] The EC organizes all incoming data, preparing them for the hippocampus. For example, grid cells in the EC serve to map the XYZ coordinates of a potential scene.[6] The PHC environment data is organized upon this spatial grid to form a 3D layout of the scene,[58] and the PA stream populates the scene with meaningful objects.[9]

Reports of inner activity, like thoughts and feelings, are also included in the formation of memory, giving rise to a remembered self in the middle of the remembered world.[59] Reports of physical arousal arrive at the EC from the amygdala, insula, and other body-state structures, and intrinsic simulational activity (see section 3: *The Hippocampal Complex as Experience Simulator*) like imagination, Theory of Mind, and future planning is generated by structures in the DMN[29,60] and joins the sensory content at the EC hub.[61]

The many pyramids of reports arrive at their mutual summit at the EC,[57] but they remain distinct streams of data until the hippocampus.[62,63] The EC projects three different data streams into the hippocampus: a visuospatial concept stream from the PA and PHC; a body-state stream from insula, amygdala, and olfactory cortex; and a multipurpose stream with afferents from all over the brain.[64]

The hippocampus itself is composed of successive fields: the dentate gyrus (DG), CA3, CA1, and the subiculum (Figure 1).

Field CA1 is the memory-synthesizing engine, and bilateral destruction of CA1 leads to anterograde amnesia, the inability to generate new episodic memories.[65] In CA1, the new memory is spatially constructed and temporally ordered.[66] These are distinct processes, each with their own population of specialist neurons. Place cells in CA1 fire consistently and only in certain places in any known environment,[67] showing that the hippocampus is keeping track of the body in space, so that the memory can accurately encode the precise location of the experience to be remembered.

Just as place cells help map out the locations and movement within a memory, so too do time cells map durations within a memory. For example, a rat that has been conditioned, upon hearing a tone, to

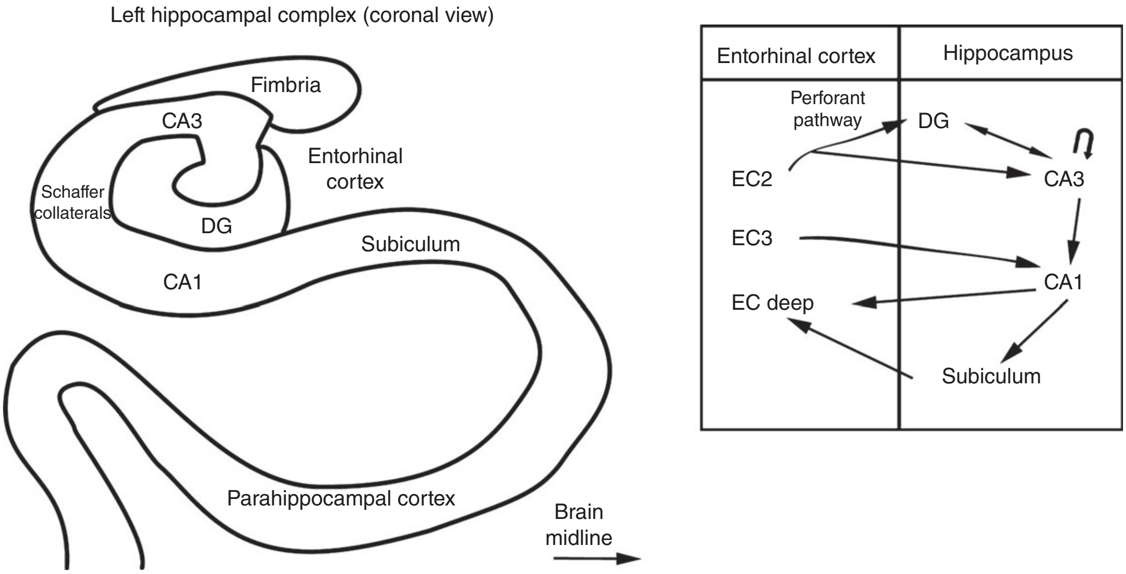

FIGURE 1 | Hippocampal complex anatomy and data flow.

wait 10 s and then push a lever, uses its time cells to keep track of the necessary delay between the tone and the response.[8]

New EC input travels to field CA1 through two hippocampal paths: one quickly (EC directly to CA1) and the other which detours first through the DG and CA3 fields along the way to CA1. The quick EC to CA1 route encodes extrinsic data: the 'what's happening now?' route. The slower route serves to put the current experience in context of previous memories.

The DG and CA3 fields serve complementary functions, relating the current episode to prior ones. CA3 is an autoassociational engine, eliciting previous episodic memories that relate to the current experience. CA3 feeds those memory patterns on to CA1 to help build the context of the ongoing scene. It also sends feedback to the DG to help gate the new incoming data and keep the current patterns separate from the past ones, thereby distinguishing the brand new memory from the old ones that inform it.[68]

Much of the brain's interdepartmental communication is carried out by temporal coding, i.e., information carried in the precise timing of synaptic firing. A piece of vocabulary in this language is called a 'spike train' because it is a coded sequence of activations and pauses. As a temporal code is only comprehensible when compared to a continuous time signal, the spike train is nested within a gamma wave.[69] This wave allows the receiving structure to know when the message begins and ends.

In the HC, the incoming gamma elicits the creation of a slower (~140 ms) theta wave,[46] which can mathematically nest the gamma inputs within it.[70] Theta coordinates the CA1 inputs from EC (up-cycle) versus CA3 (down-cycle)[71] so that each CA1 theta wave includes not only pointers to the EN and DMN departments but also pointers to related memories. The theta wave output from CA1 is what we have been calling the episodic memory engram.

Output from the hippocampus (mostly via the EC) takes four major routes, each with distinct functions.[12] (1) The long-term storage pathway feeds to the mammillary bodies, retrosplenial cortex, and anterior thalamic nuclei.[49] (2) The dopamine pathway feeds to the nucleus accumbens and ventral tegmental area (via the lateral septum) to activate long-term potentiation and the generation of theta.[13] (3) The rostral hippocampal path feeds to the amygdala and nucleus accumbens emotional centers and to the medial prefrontal and orbital-frontal DMN cortices for social self-projection (e.g., 'how do I appear to others?'[60]), emotional analysis of the current or remembered episode, and complex conditioning of behavioral repertoire.[61] (4) The reciprocal sensory loop pathway sends the episode back to the PA and PHC, which then feeds back to the original EN structures that gave rise to this moment's or recalled episodes.[12]

It is on this latter pathway that the episodic memory engram is broadcast back to the EN departments which contributed to the new memory.[13,72] In our model, the reactivation of those departments by the engram is equivalent to NSE.

Hippocampal Output as 'Newscast' of the Brain

Earlier models of brain function segregated perception from memory, but very recent research is uniting the two into one functional perceptual/mnemonic system, with the hippocampus at the top of the pyramid. Barense et al.[73] demonstrated that the HC is involved in even low-level perceptual tasks like figure/ground separation. Nadel and Peterson wrote (Ref 9, p. 1250): "The hippocampus is just the last in a set of mostly posterior brain systems organized in a rather similar way to represent the world as we experience it in all its sensory richness…," and "there is every reason to believe that an approach requiring extensive bidirectional, dynamical interactions is at least biologically plausible…." Aggleton[12] illustrated those bidirectional pathways, and Bosch et al.[74] demonstrated that hippocampal feedback reaches and affects even the very early visual departments, among others.

In our model, the immediate hippocampal feedback of a brand new episodic memory is the equivalent of a central government newscast. Many departments contribute reportage to the HC, and the newscast is then fed back to all departments[13] for error correction, predictive priming, and for sharing one unified story of 'what just happened.'

Of course, it is not appropriate to think of the various departments of the brain as 'watching' the newscast of episodic memory. Instead, those departments are *activated* by the episodic engram[41] (in the same way that the visual cortex does not 'watch' the outside world but is rather activated by it).

In the EN, that newscast activation serves to inform ongoing sensory processes by priming their predictions of the next moment's input.[9] The color of red is interpreted now within the ongoing scene (e.g., the gestalt image of a fire engine racing down the street with its lights spinning and siren wailing). This top–down influence drives the interpretation of new reports as they travel up the pyramid. The HC newscast, because it represents the gestalt—the complete scene of self-in-the-world—drives predictive top–down processes all over the EN.[34]

In the DMN, by contrast, the HC newscast activates the analysis of the ongoing scene in order to elicit proper emotional response, social self-awareness, and behavioral repertoire.[61] The DMN also uses the HC as a virtual staging ground for its future-planning simulations (see section 3: *The Hippocampal Complex as Experience Simulator*).

We hypothesize that NSE is equivalent to the process of the EN and DMN being informed/activated by the HC's brand new episodic newscast, still vivid and full of detail.

THE HIPPOCAMPAL COMPLEX AS EXPERIENCE SIMULATOR

Simulation is the process of building a model that approximates real-world phenomena and then using that model to create and test potential scenarios before trying them out on the world.[42]

The Holodeck of the Brain

The importance of the HC in generating and recalling memories has long been known. Recent imaging work shows that the HC, in conjunction with the DMN, is also involved in the creation of virtual scenes that have not actually happened.[43]

This new understanding of the HC began with Eleanor Maguire's lab[75] testing a former taxi cab driver with a damaged HC to see if he maintained his ability to navigate. They found that the control subjects could visualize the route (a virtual tour of London) and thus plan their driving decisions, but the subject with a damaged HC had a very difficult time engaging in this sort of previsualization or with comparing his current virtual view with his previously experienced views.

Maguire's colleague Demis Hassabis[76] extended that research by testing patients with adult-onset complete bilateral hippocampal damage (AOCBHD) and finding that they were greatly impaired in their ability to form imaginary scenes, whether their prospective future or purely fantastical scenes. The patients were not completely unable to imagine because their DMN structures were intact, but they could not create rich visual scenes in their minds' eyes. Hassabis and Maguire's work provided the foundations of our understanding of the HC as an experience generator rather than just a memory encoder.

Subsequent fMRI studies (reviewed in Refs 29,60) have shown that the above and other scene-simulation imagination tasks (e.g., daydreaming) involve a common neural signature of activation of both the HC and the DMN. One possible reading of this is that the DMN initiates and guides the simulational task,[77] activating conceptual models in the PA and PHC to be brought into the EC and hippocampus for scene generation and manipulation.

Even Theory of Mind, the simulation of other people, seems to involve the HC[78] engaged with most of the same DMN structures.[29] In this case, the simulation is populated with personality models that we create of other people in order to be able predict their actions and responses.[79]

Hassabis[80] compared the simulational role of the HC to virtual reality, a fake environment for the sake of safely pretesting scenarios, but one should not think of it as a person wearing VR goggles on his head. We prefer the analogy of the Holodeck as introduced on 'Star Trek, the Next Generation.' The Holodeck is an empty space, devoid of features, within which 3D models of virtual environments can be instantly constructed and populated with virtual objects and people. In the Holodeck of our imagination, dynamics are simulated as proxies for physics and personalities. We even imagine ourselves in these scenes, suggesting that the perceived body and the self/personality are also models that can be manipulated.

Dreams are, of course, simulated experiences, and they are also generated in the Holodeck of the HC. Most episodic memory consolidation happens early in the sleep cycle, and many subjects, awakened from early slow-wave sleep, report dreams with fresh episodic content. During REM sleep, the EN undergoes extensive consolidation, rewiring connections between procedural and semantic traces. This seemingly random stream of cortical activity arrives at the HC, which confabulates an experience out of it. Prefrontal executive function is (usually) offline during REM sleep, so there is no reality check.[81]

Memory Recall as Simulation

If the HC serves as a Holodeck for these various kinds of simulations, then perhaps, memory generation and playback should be considered forms of simulation as well. The simulational aspect of episodic memory is most obvious during recall, when the previous episode is reconstructed from the sparse hyperlink pointers contained in the engram.

One fitting analogy for the low-data engram is a player piano roll,[82] a mnemonic device that has no music recorded upon it but which, when played back upon the instrument, activates the appropriate keys to reconstruct the original tune.

The 'player piano' relationship between the sparse memory engram and the sensory cortices of the EN is high-lit in patients with hemispatial neglect (i.e., the inability to experience half of their visual field of view because of cortical damage). These patients also suffer the same visual neglect in the recall of scenes, even those which were committed to memory, premorbidity. Bisiach and Luzzatti[83] tested hemispatial neglect patients on their ability to mentally picture the Piazza del Duomo in Milan, which the patients were familiar with prior to their brain damage. If asked to imagine facing the cathedral and describe the scene, they could only bring to mind the details to their right. When asked to imagine the square from the other side of it, they could only bring to mind the opposite side of the square, the one they had just previously neglected. We know the memory engrams themselves were still complete because the entire scene could be recalled, just not all at once.

This is a translational error, the inability for the playback cortices to reconstruct the original episode, rather than an indication of an incomplete episode. The episodic memory index, as it was committed to memory before the cortical damage, has pointers to reactivate the entire scene, but only the intact cortical regions can be employed in recreating that experience. In the 'player piano roll' metaphor, this is like a breakdown between the mapping roll and all the keys to the left of piano center. Even though the entire song is mapped onto the roll, only the right hand's contribution to the tune can play back. Hemispatial neglect reveals the simulational aspect of memory recall because it shows that the recall is entirely dependent on reconstruction.

Memory Generation as Simulation

As even the most basic sense report is a representation of meaning rather than the meaning itself (e.g., a report signifying redness is not itself red), every step along the processing path is some form of representation, an interpretation of the pyramid of reports thus far.

Another piece of evidence that the HC generation of a brand new memory is a simulation is that: unlike most other amnesiacs, patients with AOCBHD do not confabulate.[84] By contrast, when patients with frontal lobe amnesia are prompted to recall an event that is not retrievable, they will often spontaneously generate a memory-like story, which is not reflective of their actual history but which they present with full confidence.[85] The ability of the brain to create false memories displays that the HC can easily simulate experiences that never happened but that cannot necessarily be distinguished from veridical recall. The fact that AOCBHD patients do not create false memories shows that the HC is needed for their simulation.

Another piece of evidence comes from Chadwick, et al.'s[86] study that shows that patients with AOCBHD do not extend the boundaries of the visual input that comes in. In their study, controls and patients with hippocampal damage were presented two photos of an unoccluded object in front of a background and asked whether the second presentation was a closer or wider view or was the same as the first photo. In fact, all the presentations were of the exact same photo, with no differences, but in most cases, the control group confidently decided that the second presentation was a closer shot than the first one. This shows that they consistently remembered the photo with more environment around the object than was actually in the photo. The researchers explain this as the hippocampus automatically extending the boundaries of the first presentation in the control subjects' memories, making the object seem smaller in comparison. Paradoxically, the patients with AOCBHD were more accurate in their judgments, usually confidently deciding that the presentations were the same.

(Of course, this study may sound odd in that the AOCBHD amnesic patients were asked to compare these images to 'memory,' but as stated in the section 2: *Newscast of the Brain—The Anatomical Model*, the EN cortices do have short-term WM buffers in the various modalities, including vision,[87] and this is presumably how the AOCBHD patients were able to hold onto their mental image of the presented photos. The time between removal of the presentation and the judgment task was also very short, so no long-term memory system was needed.)

For the purposes of this article, what is especially interesting is that the control subjects, whose brains have the same functional EN sensory buffers as the patients, did not use the information from those buffers in their judgments but relied, instead, upon the less accurate images provided to them by their HC recall. This implies that the short-term sensory-buffer images were not available to the control subjects, and only the HC version of memory was available for recall. The AOCBHD patients, by contrast, had no HC and thus no HC recall. For those patients, the pre-HC EN buffer held the only image available. This distinction between separate EN and HC representations of experience[88] will inform our discussion about AOCBHD patients in section 5: *What Does this Say about H.M. (And Other Patients Like Him)?*

What boundary extension suggests is that the visual representation in the HC simulates beyond the actual data from the senses.[89] The HC only uses the incoming conceptual/sensory data as a starting place and generates as useful a scene as possible in order to create a memory that is full of context, although some of that context is imagined. This ‘filling-in’ function is probably largely fulfilled by pattern-completion processes of field CA3.[68,90]

As we explore the possibility that NSE may be caused by a brand new episodic memory, this ‘filling-in’ capability may illuminate questions of why we do not usually perceive our noses or glasses, although they are always within our field of view. Why does our peripheral vision appear to be in focus and in color when at the retinal level, all that area is out of focus and monochrome?[91] Why do we not notice our own blinks, our scotomas, our saccades, and most of the shake and jitter of vision while we move? It is possible that these questions may be answered (at least partially) by the ability of the HC to simulate beyond the input of the senses. Our vision may only bring in the scarce details we need to conceptually populate a virtual world that is largely assumed and filled-in. The memory episode is designed to be sharp, steady, fully in color, and full of context for later recall. It includes elements that may be useful in memory, like changing and dynamic inputs, but excludes those which remain unchanging, like the view of our noses.

NEUROTYPICAL SUBJECTIVE EXPERIENCE FROM A BRAND NEW EPISODIC MEMORY

In our theory, NSE occurs when a brand new hippocampal engram reactivates the structures that originally contributed to the formation of the new memory. Our first argument to support that is: as we have seen in section 2.2: *Pyramid of Reports: The (Simplified) Anatomy of a New Episodic Memory*, the HC is the only network in the brain where all the sensory information comes together to form a complete scene. Different networks and departments laterally communicate throughout their processing, but the data from all over the brain only comes together in the HC, in preparation for memory. If we are looking for an answer to the ‘binding problem’ of consciousness (i.e., why NSE seems unified when the brain departments that process sensation are widely distributed[92]), it makes sense to look at the apex of the perceptual pyramid, in the one place where all the reports are bound together into a scene.[49,50]

Secondly, we have in the HC all the necessary components for generating NSE. We have concepts in the PA, which unite meaning and multimodal sensation. We have a hub in the EC, which brings all of the data together, and a 3D layout in the grid cells of the EC in order to build the scene. We have Holodeck functions in the HC that allow DMN simulations, like imagination, dreaming, memory recall, and Theory of Mind. We have autoassociational and pattern completion capabilities in CA3 to recall memories, fill-in, and put the current scene in context of previous episodes. We have a spatial lattice, temporal ordering, and binding capabilities in CA1. We have theta organization of hippocampal output to give the newscast a time stamp, so that all reciprocal brain structures can agree on when is the ‘now’ of NSE. Finally, we have reciprocal ‘broadcast’ abilities in the subiculum and EC.

Thirdly, NSE reflects an allocentric view of the world, which is only added to perception within the egocentric/allocentric conversion at the retrosplenial cortex and PHC.[9] The egocentric view (represented in the posterior parietal lobe) relates all physical stimuli to the location of one’s eyes. Thus, moving one’s head or eyes should cause the stimuli to swim about wildly (as evidenced by the point of view of a video camera strapped to one’s head). In our perception, however, we experience ourselves as moving through a stable world; eye saccades, body movement, and head tilt are all factored out in order to perceive a stable environment. In our model, that experience is explained by the egocentric to allocentric translation that happens at the retrosplenial cortex and the PHC. As NSE is allocentric, it must occur downstream of those structures.

Fourthly, salience is defined in the same way for NSE and memory: that which is novel, dynamic, or defies expectations by some threshold amount.[93,94] Stimuli that are nondynamic and unsurprising (like the feeling of our clothes or the view of our noses) are left out of perception/memory.

Fifthly, we offer an argument from parsimony. As we know that the HC is an experience simulator, which constructs new memories and imaginary scenarios, it seems unlikely that the brain would have an entirely separate experience generator just for NSE (nor is there currently any evidence that a separate generator exists).

More evidence that NSE is a new memory broadcast is explored in the following sections.

Multiple Drafts: Memory Is Generated Predictively and Edited Retrospectively

One obvious exception to the idea that NSE is caused by episodic memory is that there seems to be a temporal mismatch between the two. We think of NSE as defining the 'now,' whereas new sensory data takes ~300 ms to reach the HC (as measured from the retina).[51] However, the sensory reports that are fed from the EN to the HC are predictive ones, designed to compensate for the time spent processing that information.[95]

There is also increasing evidence that the HC itself is able to form predictions for the scene as a whole.[93,96] Lisman and Redish[97] demonstrated that as rats learned sequences of behaviors, or pathways in an environment, their hippocampi were firing in expectation of their next behavior and/or of the location that they were headed toward. Chadwick et al.[98] found that neural patterns in the human EC, when that subject is about to turn in one direction or another, anticipate the neural patterns of actually facing that direction. Hippocampal field CA3, in particular, by comparing the current scene to previous memories, is able to use pattern completion to form predictions about what will happen next.[66]

This predictive power of the sensory cortices and HC allows the new memory episode to be formed almost contemporaneously with actual events, compensating when possible for the neural time lag of sensory processing. Only when the stimulus is unpredictable do we start to see a real-time lag between the EN and HC representations of that stimulus.

One example of that time lag may be Ben Libet's[99] experiment in which he stimulated a pre-op patient's exposed somatosensory cortex. To his surprise, it took a half-second for the patient to become aware of the stimulation. Libet interpreted this time lag as a necessary build-up of potential before consciousness could be achieved, but we think his results can be alternately explained: the stimulus just needed time to be integrated into a new memory.

The length of time it takes new stimulus to travel from the sense organs to the HC varies, but it is ~300 ms as measured from the retina.[51] When predictions in the HC are contradicted by unpredictable new stimuli (like Libet's electrical probe), the HC buffers the original prediction and retrospectively edits it, at ~450 ms after initial stimulus,[100] to include the new stimulus in its interpretation of events. The 500 ms time lag that Libet found for NSE of the neural stimulation may reflect the time it took for the stimulus to reach the HC, for the HC to revise the current predicted episode to include the new stimulus, and then for the revised memory to be broadcast to the rest of the brain.

Another compelling example of how the HC's predictive and retrospective functions may shape NSE are what Dan Dennett[101] called 'multiple drafts' phenomena. These include the Kolers and von Grünau[102] experiment in which an observer watched a stationary red pool of light be immediately replaced by a nearby, also unmoving, green pool of light. In the experiment, the red light was extinguished at the exact same time the green light turned on, so the brain's object-permanence heuristic interpreted the pools of light as being one phenomenon. Interestingly, the subjects reported perceiving the red light moving to the new location, becoming green as it moved, even though no actual movement happened. This perception seems impossible because the red light would already have extinguished before the brain could start sensing the green light, so any mental perception of the red light moving to the new location would have to be a retrospective mental edit, a looking backwards-in-time to change one's own perception.

We believe that this experiment only starts making sense if we see perception as being reflective of memory rather than of immediate sensation. The HC interprets most visual phenomena as being permanent objects, so the red light pool is predicted to remain. When it vanishes, the predictions are confounded, so the HC buffers the red-light episode and sends a mismatch signal to the EN. The EN provides the new information of the nearby green light pool, and the HC adds the appearance of motion to the buffered red light pool signal in order to maintain the assumption of object permanence. Multiple drafts phenomena show that the story of perception is 'what I remember' rather than 'what actually happened.'

WHAT DOES THIS SAY ABOUT H.M. (AND OTHER PATIENTS LIKE HIM)?

A male epileptic patient from Connecticut, commonly known as H.M., was the most famous patient with AOCBHD. Most of his HC was removed surgically to save him from the overwhelming epilepsy that was focused there.[14]

Patients like H.M. are unable to form detailed or coherent intrinsic simulations, like mental navigation, future projection, vivid imagination, and social rehearsal.[29] These patients are afflicted with anterograde amnesia, the inability to form new episodic memories, and retrograde amnesia, the inability to replay previous episodic memories.[103]

In the model we are proposing, such patients cannot have NSE, which may sound implausible. Specialists who work with AOCBHD patients describe the patients' responsiveness to the outside world, their personality, sense of (short-lived) continuity, an ability to respond to queries about one's inside state, and even some ability to learn procedural skills and semantic information. This is what we mean from the third-person view when we describe someone else as 'conscious,' and indeed, H.M. was that, when awake. These are all part of the usual working definition of consciousness, but none of them are part of how we are defining NSE.

We are neither saying that H.M. lacked subjectivity nor that he lacked experience. What he was missing was the specific phenomenon that the phrase 'Subjective Experience' refers to (among those of us with working hippocampi), which is cortical activation by a specific type of neural information. According to our theory, NSE is caused by internetwork information (the engram), which helps to expedite processing and which may be stored for future recall. It subjectively *represents* processes like responsiveness, personality, etc., but it should not be confused with them. All of the processes that are represented in the hippocampal simulation are only news reports of the actual processes in the EN and DMN, and patients like H.M. still have access to those original processes (see section 3.3: *Memory Generation as Simulation* on boundary extension).

Unlike the Cartesian model (Figure 2), we believe that NSE is not necessary to engage with the

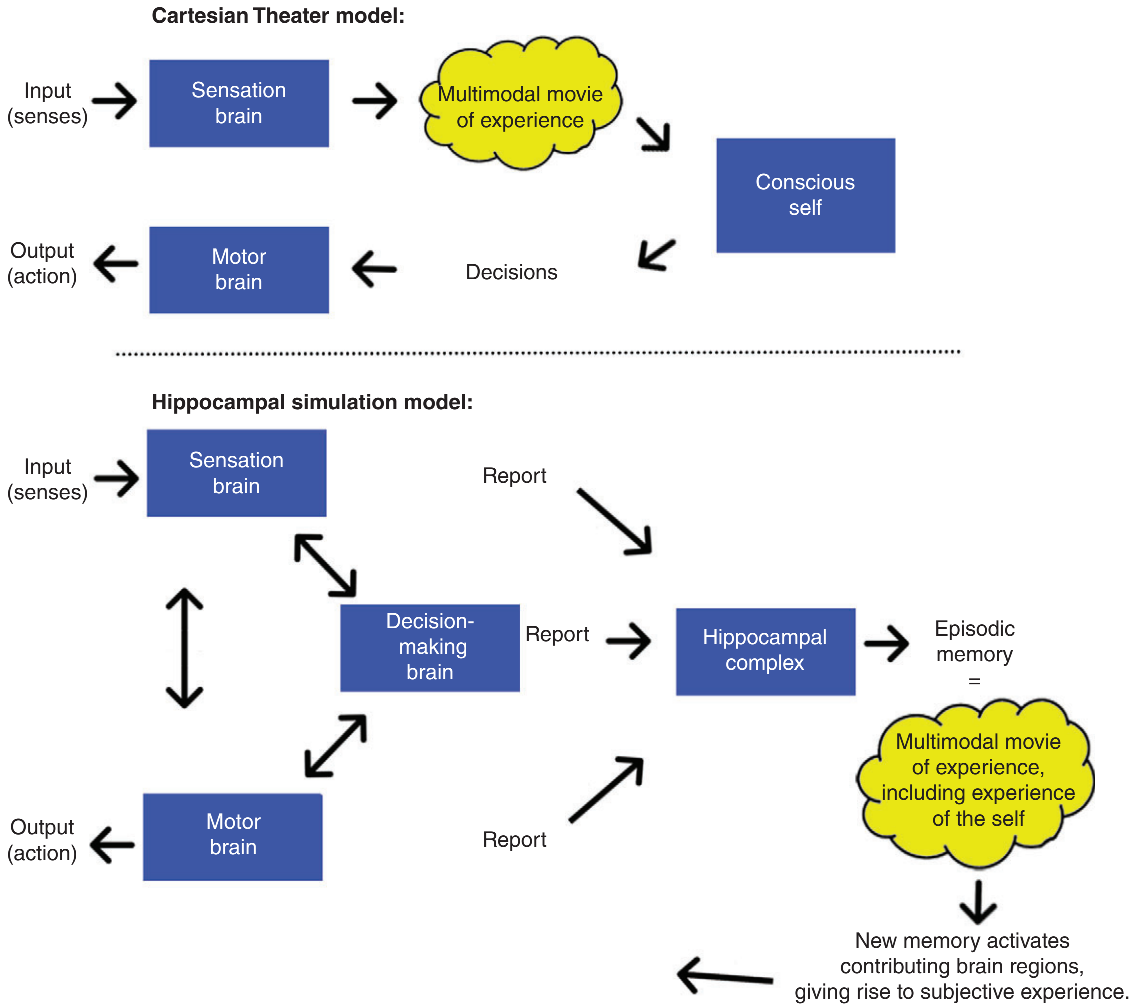

FIGURE 2 | In Daniel Dennett's Cartesian Theater thought experiment (1991), an inner 'I' or 'consciousness' is the witness of the multimodal movie of experience and uses that movie to decide and enact behavior. In contrast, the model we are proposing has no 'conscious self,' only the unified representation of pre-memory self-processes and body states. The multimodal movie of experience, including the representation of self, is generated in the HC for the sake of memory and for communicating one specific interpretation of reality with the rest of the brain.

outside world. All immediate interaction with the world is handled by pre-memory EN departments. We could not survive otherwise because the ~500 ms it takes to revise a new memory to account for unpredictable activity would leave us a half-second behind reality. We could never drive, for example, if we were always a half-second behind changing conditions.[22]

'Driving Mind' as Insight into H.M.'s Processes

The ability of the EN to act independent of the HC representation is probably not uncommon, but we tend to notice it only in extreme cases, like 'driving mind.' Most of us who drive have probably experienced the phenomenon of driving someplace (usually on a familiar route) and then upon arrival, realizing that we have no memory, whatsoever, of the drive. In fact, it seems as if I was not involved in the drive at all.[104]

The explanation that is usually given for 'driving mind' is that the driving is done 'automatically,' but we see that as a highly problematic, dualistic explanation. The body and brain are checking the mirrors, braking and accelerating, changing lanes. All the functions of sensation, evaluation, decision, and action are clearly being employed in the drive or the car would crash. The driving functions are performed by the same EN departments as usual, so the behavior is only 'automatic' if it is missing oversight from sort of 'I,' some 'self' that is distinct from the brain. This would imply that the brain is somehow an unconscious vehicle, driven by a nonbrain conscious self, which puts us in dualism (i.e., Descartes' notion that 'mind' is a nonmaterial intelligent essence), and back into the Cartesian Theater.

But what is startling about 'driving mind' is precisely the lack of memory of the drive. So we think it much more likely that the exact same brain departments as usual are conducting the drive; however, there is just no memory formed of it.

That lack of memory can be explained by the fact that the HC serves very different purposes for the EN versus the DMN. As we have seen in section 3: *The Hippocampal Complex as Experience Simulator*, the DMN uses the 'Holodeck' features of the HC as a virtual workspace in which to manipulate representations. The DMN runs predictive simulations, imagining a conversation or exploring scenarios before trying them on the world. It examines, and tries to make sense of, previous memories. It is even tasked with daydreaming/fantasy, in which we get to simulate our wish fulfillment.

In the case of 'driving mind,' we see it likely that the EN is performing all the driving tasks, as it always does. However, the reports from the sensory and motor cortices do not make it into memory because the HC is already fully occupied with a DMN simulation, like daydream, memory recall, or social rehearsal. Because episodic memory only contains what was processed in the HC, the DMN simulation is all that is remembered, leaving the brain with no memory of the drive, and because NSE is due to the broadcast of episodic memory, I had no NSE of the drive, although my EN was fully engaged during it.

In the case of driving mind, my 'inner H.M.' is doing the driving, and the resultant NSE is only of the DMN/hippocampal simulation.

Was H.M. a Zombie?

Philosophers have invented a rhetorical being, which they call a zombie, that behaves and self-reports exactly like a conscious human but who somehow lacks any kind of inner awareness or experience.[105] As we are proposing that AOCBHD patients lack the phenomenon that those of us with working hippocampi know as Subjective Experience, it may sound like we are claiming that H.M. and similar patients fit that zombie category.

However, as we have seen in 3.3: section *Memory Generation as Simulation* on boundary extension, AOCBHD patients are aware of the photo they see and can report based on that awareness.[89] The neural information that they report, however, is from an EN pre-memory buffer that those of us with working hippocampi have no direct access to. Despite the fact that we have the same functional pre-memory buffers as AOCBHD patients, those of us with working hippocampi (according to our theory) only experience the HC output, and that output obscures the pre-memory awareness. In section 7.3: *The Causal Power of NSE*, we more fully explore the possible reasons why pre-memory processes are left out of awareness.

Based on his work with another AOCBHD patient D., Antonio Damasio[15] wrote that the patient D. does not have 'an elaborate sense of self … at a point in individual historical time, richly aware of the lived past and of the anticipated future' (p. 16). Endel Tulving[106] essentially wrote the same about AOCBHD patient N.N. What is missing in patients D. and N.N. is the context and expanded sense of self that is provided by memory. They are NOT zombies, because they have inner lives, albeit transient ones. We hypothesize that their EN experience is probably substantially different than the NSE of those of us with working HCs.

This is where we think H.M. lived: he sensed and interacted with the outside world, could rely upon his short-term visual and auditory buffers, and could report body states and a few details about his self-identity. What he could not do was benefit from the HC's newscast. He could not use the gestalt from a moment ago to expedite his processing. He could not place himself within a broader sense of what came before and what is likely to happen next.[106]

Unfortunately, it is impossible to guess, from our perspective, precisely what H.M.'s, N.N.'s, or D.'s non-memory experience is like, as our own normal pre-memory experience is not available to our subjective view. It is like asking ourselves to describe the unremembered act of driving during 'driving mind'; there is nothing to remember and thus no way to report. Nor can we expect patients with AOCBHD to reliably know how their perceptions have changed post-morbidity because, missing their HC, they can no longer evoke the vivid memories of previous experience to compare to their current way of seeing the world.

Some evidence from the literature does exist, however, and suggests that perception does change for such patients. Graham et al.[49] quoted one patient with limited hippocampal damage, who could still remember fairly well, but whose perception lacked qualities that the HC usually provides. She could form and remember snapshot images of her environment but still had a very difficult time navigating through the world because "whichever angle I look, everything looks the same" (p. 832). The patient continued: "I would prefer not to call my experiences 'memory problems,' they are not. This is a total misrepresentation of the damage I have. What I experience are 'orientational problems.'" Her perception of the world is missing some of the context of the allocentric environmental information from the PHC and hippocampus, elements that those of us with fully working hippocampi take for granted.[107] NSE reflects a simplified, but much more contextualized, representation of events than the pre-memory reports in the EN.

THE PERCEIVED SELF

There are several overlapping definitions of 'self.' From the third-person perspective, the self is the organism, the body. The self we are concerned with is the first-person view of self, the 'I' as experienced from within. We will call it the 'perceived self' because it is our own process, reflected back to us as part of the function of our brain. It is part of how our organism keeps track of itself.

It is relatively easy to make the leap that the experienced outside world is a simulated gestalt of brain representations, as the actual world is never directly accessible to our brain. However, coming to the same conclusion about the perceived self is much more difficult because that questions the reality of the only 'me' I have ever known.

As Thomas Metzinger pointed out in "Being No One,"[108] the perceived self does not have to be a command-and-control process or entity in order to feel like one. After all, the feeling of being a self, having perceptions, and making decisions all happen in dreams as well, where it does not reflect actual sensations or behavior. That feeling, while awake, may be just a post-hoc representation of processes that happened prior to NSE (as in the bottom half of Figure 2). The perceived agentive-self-making-decisions may reflect just another pyramid of reports, this time originating from within the prefrontal, executive areas of the EN and DMN rather than from the sense organs. Decision-making, motor, emotional, and cognitive departments send their reports to the HC for simulation into memory/NSE, just as the sensation departments do.

In this simulation of experience, 'I' do not have 'access' to my perceptions. Rather 'I' and my perceptions are simulated together as part of the gestalt of memory. The gestalt movie story of experience includes a simulated self in the center of a simulated world.

The remembered 'I' is a model built upon a semipermanent armature of habitual self-concept and body image.[109] This model is fleshed out with the newly formed body sensation, cognition, and 'fringe'[16] reports from the various inward-oriented departments of the brain, and it is that self-construct that is remembered as part of the event. The self-memory gives the event memory context for recall so that the organism can later remember what its various departments were doing, what they thought, and how they felt about the event.[59] We think that this is likely the reason why experience is subjective, because the self-perspective is needed as context for memory.

The Mind as Representation

We experience ourselves as bodies, with motor, somatosensory, and emotional perturbations, and we experience ourselves as minds, with thoughts, images, fantasies, and intentions.

A good deal of what we think of as 'mind' belongs to the realm of intrinsic simulations, guided by the DMN, using the HC holodeck as a virtual workspace. As stated in section 3: *The Hippocampal Complex as Experience Simulator*, these simulations include previsualizations, daydreams, memory recall, and Theory of Mind scenarios.[29,60] Concepts are the currency of these simulations. Concepts are represented and manipulated in the virtual workspace, often in order to simulate possible actions and their outcomes.[80]

Image thought is the currency of spatial planning, e.g., figuring out how to pack bags in the trunk of one's car, or a chess player moving virtual pieces around the board in her mind before actually making a physical move. In both examples, the image simulation may be overlaid directly upon the current moment scene and virtually manipulated. AOCBHD patients lack the ability to create vivid mental images in their minds' eyes,[76] showing that the hippocampus is needed for imagery simulation.

Language thought is a curious phenomenon of the mind in that it does not reflect the brain's normal interdepartmental communication, which is all electrical/chemical. In fact, it is much less precise and much slower than the communicative processes that underlie it. We see it likely that language thought serves the same function as image thought: representations that can be buffered and manipulated within memory, primarily for the sake of problem solving.

Certainly, language thought is part of what allows us to simulate other minds; we can imagine potential conversations and test how various statements might be heard by another. Language thought may also serve as a mnemonic, adding narration[110] to an episodic memory as it is encoded, to help make sense of it later. Language thought also allows us to buffer ideas within memory and to increase the complexity of processing, like weighing pros versus cons of a decision, or making logical inferences. This is what we know as 'conscious deliberation,' but we believe it is only 'conscious' because the process is part of the HC simulation, not because a thing or process called consciousness is doing the deliberating.

Multiple pieces of evidence suggest that language thought may be buffered and manipulated within the HC. (1) AOCBHD patients show great impairment for remembering word lists. (2) Watanabe et al.[111] found that multivoxel patterns in the HC could predict whether visually presented pseudowords would be remembered. (3) AOCBHD patients H.M. and E.P. were significantly impaired in their ability to detect and explain ambiguity in sentences.[112] (4) MacKay et al.[113] asked patient H.M. to include two to three target words in a grammatically correct and comprehensible sentence, describing a presented picture. Although he displayed normal skill in verbally describing familiar situations with obvious target words, he displayed gross deficits in using nonobvious target words to describe unfamiliar situations, especially upon the first iteration. This suggests that (although his language centers were fully intact) he lacked some ability to internally buffer and manipulate his words before speaking them out aloud.

The Body as Representation

Normal DMN/HC simulations can include deeply immersive multimodal imaginings, like previsualizing running a race. In this example, the sight, sound, and maybe even smell of the racetrack are simulated in order to prime the brain and body for the race. Most central to the race simulation, of course, is the concept of one's body, the feel of running the race. This concept may be entirely divorced from the actions of the physical body, which may be unmoving during the previsualization.

The fact that we can imagine or dream our body shows that it can exist in simulations as a concept, which can act independent of the actual body. Recent amputees, for example, tend to dream of themselves with fully intact bodies. The older the patient at amputation, the longer their dream body resists updating, with some patients exclusively dreaming themselves with intact bodies more than 12 years after the amputation. This suggests that the HC's body representation is much more habit-bound than the EN somatosensory representation, which adjusts much more quickly.[114]

Dreams and mental rehearsal suggest that an HC body image exists, but what evidence do we have that the HC body image (albeit informed by the pyramid of reports from various body-state structures) is the body that we perceive? We believe that strong evidence exists in everyday NSE, although this evidence seems so obviously normal that it is rarely commented upon.

The brain receives an enormous amount of information about the body, which allows for coordination, balance, hormone regulation, etc., but very little of that information is included in the perception of the body. Most body data that makes it to awareness are alarm signals, like pain, hunger, cold, nausea, and tension, as well as pleasure and mismatches between predicted and actual effort in any task. Michael Graziano[3] pointed out that the body, as experienced in awareness, seems to be 'magical,' as little of the muscular and visceral feedback ever makes it to perception.

We think it likely that this is a function of the needs of memory. Details become salient for memory if they are novel, dynamic, or defy predictions by some threshold amount.[93,94] In vision and hearing, the stimulus is usually quite dynamic and so is continually updated. The body, however, is always present and very well understood by the brain, so very little of its data need be represented for memory (as is true of our experience of the feeling of clothing, which quickly fades after we put them on). Therefore, NSE only includes a limited input of reports about the body, the reports that might be useful in memory, and the rest of the brain's enormous amount of information about the body is left out.

A.D. 'Bud' Craig[115] argues that the anterior insula holds a model of the feeling body. The posterior insula receives inputs from all the major body-state departments, including pain, pleasure, proprioception, motor, and taste. Those inputs are processed in the insula from posterior to anterior, so that "activation in the anterior insula is uniquely associated with subjective feelings of all kinds" (p. 74). Craig[116] also writes: "This same site is activated in virtually every imaging study of human emotions, and so it seems to provide an image of the physical self as a feeling (sentient) entity, which is characteristic of human consciousness" (p. 503). The anterior insula feeds to the PA and EC, among other places,[117] perhaps contributing a body model to memory.

If indeed, the body is represented in NSE by an HC body image (as prepared by the insula), then this may lead to explanations for some pathologies of bodily subjectivity. Anosognosia, phantom limb, and anarchic hand syndrome, among others, are all pathologies that reflect a mismatch between the perceived body and the actual one.[118] Mounting a full argument for each pathology is beyond the scope of this article, but we can speculate, in each case, how breakdowns in communication between the EN and HC could lead to a perceived bodily self that is somewhat imagined or 'filled-in.'

Phantom limb, for example, may be due to an HC body model that has not adapted to match the severe changes of the actual body. The amputated limb is predicted to be there by the HC and so feels present, although it is not.

Anarchic hand syndrome may reflect the breakdown between a premotor area and the HC. When the premotor area decides to move the limb but is not able to report that decision to the HC, the NSE that arises is that the movement was done, but not by me. In this example, the perception of self-agency is due to a 'fringe' (i.e., contextual) datum, originating from the premotor area, that would normally flavor the perception of self-movement for the sake of clarifying who did what in the story of memory (see section 7.1: *Rethinking Consciousness* on Libet's famous 'will' experiment).

With anosognosia for hemiplegia, a patient with motor cortex damage is paralyzed on one half of her body but is mysteriously unaware of her condition.[119] If the patient's doctor asks her to move her paralyzed arm and she wills it, the patient's premotor area activates in a way that would have, premorbidity, led to movement but does not because of damage to the downstream motor area. However, the premotor area also reports directly to the HC, which predicts the movement, updating the body model. If the damaged motor area is no longer able to communicate to the HC, then it will not supply the error correction to the HC that the movement did not happen. Without that error correction, the HC prediction is unchallenged, and thus, the prediction becomes part of NSE. The patient experiences movement, although no movement was made.[120]

FURTHER THEORETICAL CONSIDERATIONS

Rethinking Consciousness

The Cartesian notion of consciousness is like that presented in the top half of Figure 2, an internal aware self or essence that 'watches' the movie of subjective experience and then uses its will to command the body into action. As stated in section 6: *The Perceived Self*, the fact that the *perceived self* seems like the chooser and actor does not necessarily mean it is so. This perception may just be due to a representation of other processes that came before it.[108]

This fits with Benjamin Libet's famous 'will' experiment,[121] in which the subjects were asked to perform a mundane physical action, like flexing their wrists, whenever they felt like it. The only thing they had to do was pay attention to their own subjective experience of 'will' (i.e., the impulse to do the task now) and report, within milliseconds (based upon a very accurate clock) when they perceived the will arise. What Libet found was that the perceived sense of will could be predicted by premotor activation that preceded it by ~300 ms. What the experiment suggests is that my perception of my own will is just an after-the-fact representation of what part of my brain was already doing. My perception of my own will may be due to another pyramid of reports making its way into the memory simulation.

If ‘I,’ ‘my will,’ and ‘my experience’ are constructs for memory, then this turns on its head the very concepts of ‘unconscious’ and ‘automatic.’ I am not the actor; rather, I am the memory of actions initiated elsewhere in the brain. I am not the pilot of an ‘unconscious’ brain; rather, I am just part of the news report about what the unconscious processes did.

In our theory, ‘conscious’ just means: that which is part of the episodic memory newscast, and ‘unconscious’ just means: that which is not (hereafter, we will use the word ‘pre-memory’ instead of ‘unconscious’ to avoid confusion). All the processes of the brain, including memory formation itself, are pre-memory (i.e., they contribute to the creation of memory but are not themselves part of it).

What we experience as ‘conscious processes’ are not processes at all. They are merely memory representations of pre-memory processes. They are information. Just like dream representations of me-performing-processes seem real, so too do NSE/memory representations of me-performing-processes. Consciousness, as we normally experience it, we believe to be an illusion.

Of course, if there is an illusion, there must be some entity or entities that are deluded by that illusion. Because the output from the HC is fed back to the EN to help expedite predictive processing,[9] and to the DMN to help scene analysis,[61] those feeds essentially tell the rest of the brain ‘this is what happened.’ In essence, the rest of the brain is fooled by that new memory into believing that the memory is the actual experience of the self-in-the-world.

By feeding back to itself its own pared-down representation of what just happened, the EN has a constant loop of (1) sense reports eliciting concepts, which (2) feed the formation of a new memory, which (3) feeds back to the originating sensory cortices to expedite their tasks. The DMN has its own loop with the HC: (1) receiving the episodic engram for scene analysis and then (2) adding the constructs of imagination into the HC simulation. By means of these loops, memory dictates to the rest of the brain a somewhat inaccurate but coherent-seeming and generally adaptive story of self and reality.

There is also an odd and subtle trick of memory that can help us understand why NSE feels like the actual interplay of self and the world. H.M. and similar AOCBHD patients reveal to us that nothing enters episodic memory except through the HC.[122] Therefore, all retrievable episodic memories were previously simulated in the HC. Therefore, the only experiences we can compare the present moment to, are the experiences represented by previous HC simulations. NSE feels ‘real’ because all past ‘reality’ is known via previous NSE, i.e., memories.

Why so Much of Mental Processing is Left Out of Awareness

The exclusion of an enormous majority of pre-memory processes from NSE raises the question of why the brain would choose to leave so much information out of memory. We see it likely that a memory which is pared down in terms of inner processing is more ‘phenomenally transparent’[108] to experiences of the outside world. For example, the EN entertains many simultaneous parallel interpretations of incoming stimuli,[123] but to include each of them in the memory would make that memory confusing, cluttered, and inefficient. An effective memory episode is likely one that is unified, easily recalled, and which contains a simple comprehensible story or lesson that will efficiently drive future behavior.[37]

We see data management as another likely reason for excluding brain processes from the formation of memory.[11] The brain seems to include in memory only the data that would likely be useful later (defined as novel data, data of change, or data that differs from expectations by some threshold amount).[93,94] If the stimulus is consistently there (like a persistent smell, air-conditioning hum, the feel of one’s clothes, or the view of one’s own nose), then there is little reason to represent it for memory, and we only notice it if it changes. This would also mean discarding most data of the stereotypical brain processes that lead up to cognition, emotion, decision, and action, so that data is not included in the immediate memory simulation and cannot be recalled later.

The Causal Power of NSE

As mentioned in section 5: *What Does this Say about H.M. (And Other Patients Like Him)?* and Figure 2, we assert that the EN decides immediate behavior according to its own representations rather than directly according to the HC representations. However, in intact brains, the EN representations themselves are partially shaped by the HC newscast as part of top–down predictive priming. As memory defines subjective reality, and subjective reality shapes behavior,[61] we find that the simulation has profound causal power on ongoing behavior.

Also, whenever the DMN reflects (e.g., ‘how did I do?’) or introspects (e.g., ‘how do I really feel?’) or tries to simulate someone else (e.g., ‘how will he respond to these words?’) or consults its immediate memory (e.g., ‘what was that look on her face?’) or plans its own next best action, it consults the HC output and uses that apparent 'reality' to determine its emotional and behavioral response.[61]

There is also power in the way that today's memory shapes tomorrow's experience. In the anatomy section 2.2: *Pyramid of Reports: The (Simplified) Anatomy of a New Episodic Memory*, we described how the feed of experiential data flows from the EC into the hippocampus through two pathways, one of which creates the newscast in field CA1 and the other which invokes related memories from field CA3 to inform and revise the ongoing NSE. These memories from past simulations help define contextual reality for the new simulation. For example, if I am in a fight with my wife, the memories that will be invoked will likely be other such fights (i.e., state-dependent memories[124]), and those memories will help define how I simulate my wife and myself in the immediate NSE.

As ongoing reality is defined by the HC simulation, and the current simulation is informed by previous memories,[5] which are themselves shaped by earlier memories, what emerges are 'habits of simulation,' persistent ways of constructing the world[40] and the self.[11]

CONCLUSION

The neurotypical subjective experience (NSE) of being a conscious, agentive self, interacting with the real world, feels so obviously true that few ever consider that our internal experience cannot possibly be accurate. The simple fact of a brain is that it cannot experience the real body or the real world directly but rather can only interpret its sense data into a simulation of the body-in-the-world.[2]

NSE of the mind is also very inaccurate to the processes of the brain, most of which are never available in our awareness. We seem to think, move, and speak by magic[3] as most of the processes that underlie these actions are subjectively utterly unavailable.

In order to explain NSE, we need to find a brain mechanism that simulates the self-in-the-world and which has good reason to exclude from experience most of the activity of the body and brain. We need a mechanism that unites sophisticated conclusions from various brain departments and binds those conclusions into a 3D allocentric spatiotemporal multimodal virtual-reality movie-like event. We need a mechanism that unites representations of the outside world with representations of the body, with representation of mental activity like thoughts, imagination, and memory recall. We need a mechanism that has the ability and connections to activate structures all around the brain and which explains certain time lags in processing.

We find just such a mechanism in the HC for the generation of episodic memory. Many intractable problems of subjectivity, we believe, become comprehensible in this model. No special processes or powers need be proposed, no quantum collapse or dualist interaction; we just need to rethink what NSE actually is. We believe it is a post-hoc representation of self-in-the-world, built from the various interpretive brain processes that came before it, for broadcast around the brain and for possible future recall. NSE is the process of a brand new episodic memory, output from the HC, being shared with the rest of the brain.

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