The Continuity of Context: A Role for the Hippocampus

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Abstract:

Tracking moment-to-moment change in input, and detecting change sufficient to require altering behavior is crucial to survival. We discuss how the brain evaluates change over time, focusing on hippocampus and its role in tracking context. We leverage the anatomy and physiology of the hippocampal longitudinal axis, re-entrant loops, and amorphous networks, to account for stimulus equivalence and the updating of an organism's sense of its context. Place cells play a central role in tracking contextual continuities and discontinuities across multiple scales, a capacity beyond current models of pattern separation and completion. This perspective highlights the critical role of the hippocampus in both spatial cognition and episodic memory: tracking change and detecting boundaries separating one context, or episode, from another.

Introduction

The problem of how the brain can produce perceptual equivalences across an indefinite number of input combinations has perplexed scholars for decades (1-5). The **stimulus equivalence** problem led Lashley (2), and subsequently Hebb (3), to argue against linear Stimulus-Response formulations of brain and behavior. An example of equivalence at the perceptual level is the 'reafference' from action systems to the visual system that negates the shift in retinal location by 'predicting' where an object should fall on the retina given the organism's current movements (including eye, head and full body movements) (6-9). Retinal location invariance allows us to maintain accurate knowledge of the location of immobile objects in the external world as we move through space and time. The corollary discharge that enables retinal invariance highlights the notion that input patterns are only meaningful in relation to other inputs, both past and present.

The perceived stability of stationary objects as we move through the world is itself nested within a broader framework – a **context** or **situation**. Context refers to the state of the organism's environment at any given moment, as reflected in the total set of brain activities, which is a direct function of the brain state just before that moment (10). Local stimuli may change as an animal moves in the world, but the context remains the same unless some threshold of change has been exceeded or some boundary has been crossed (11). The brain registers these varying inputs, but until that threshold has been reached, or that boundary crossed, the default assumption appears to be the continuity of context or situation. Clearly, tracking such continuity requires maintaining a sense of sameness at one scale (the context, or situation) in the face of change at other scales (local features within that context). While thresholds and boundaries are poorly understood at present, there is increasing evidence that the hippocampus is influenced by spatial and temporal boundaries (12-14) (15). Critically, pattern separation and pattern completion models (16)

are not sufficient to solve the stimulus equivalence problem. Pattern separation/completion theory assumes that patterns of brain activity represent unique states and that the hippocampus generates sharp transitions in activity between two well-learned states as input gradually changes (17-19). This approach sees the hippocampus as making binary decisions, incapable of reconciling situations in which small changes must be tracked and incorporated within a continuous context (e.g. gradual changes in perceptual input while an environment is traversed). Even in a novel situation, the brain must relate similarities between different contexts to quickly adapt and generate appropriate behavior. Neither of these scenarios can be adequately solved with pattern completion/separation. In this paper, we propose a novel framework for how the problem of equivalence is solved at this crucial level of **contexts**.

The Physiology of Context Continuity

Considerable evidence links the hippocampus to the brain's representation of context, and we argue here that the hippocampus is central to an organism's ability to track the "sameness" of context (11,20). Hippocampal recordings from awake-behaving rats reveal a striking firing rate correlate of principal neurons to the animal's location in space (21), leading to the idea that the hippocampus is the core of a cognitive mapping system (22). Roughly 5% of neurons are active at any single location in space (23). As the rat moves, the population of active cells "rolls over", with some cells becoming silent and others active (24,25). With each theta cycle, the population of cells changes in relation to displacement in the environment, either real (26-28) or imagined (29). The change in the active population can be strongly driven by movement cues. Thus, little movement yields little change in cues and neural activity, while a lot of movement yields big change.¹

¹ Although we focus here on functions of the hippocampus related to movement, we do not mean to imply that this structure has no role in situations where movement is absent (eg., sleep, creativity, decision-making).

Moving through an environment, an animal “maps” the fixed relations among the stable entities in that space. While moving, the position of various things in the environment relative to the animal changes, even though their absolute position in space is unchanged. The sensitivity of the hippocampal network to motion allows it to predict the extent to which stable objects in the environment should appear to have been translocated as a result of the organism’s movement. This information helps to solve the problem of context equivalence by off-setting the sensory consequences of movement through the world, allowing the hippocampus to generate and maintain patterns of activity that answer the question: “*how equivalent is the current context/situation to the last?*” That is, *hippocampal neurons instantiate context equivalence*. In our view, they do this by tightly linking displacement to shifts in its pattern of activity, in direct proportion to the magnitude of sensory change driven via self-motion cues (**Fig. 1**). That is why place cells are necessarily linked to spatial location, and why they can be used to anticipate future sensory states².

² This capacity provides a basis for viewing place cells as successor representations (30), should one prefer this approach.

Figure 1. Population vectors evolve based on changing input. Stimulus equivalence refers to the situation where different sensory inputs yield the same output. Here, we propose that the nervous system solves this problem by (i) expressing a pattern of activity influenced by the stimulus; and (ii) progressively transforming the pattern of activity in proportion to ongoing change in the stimulus. **(Top Row)** For instance, if the nervous system were to track the equivalence of motion direction, it would contain a population of neurons that progressively shifted as the angle changes. While this activity has been observed by Hubel and Wiesel (31), our approach provides the novel extension that V1 is not providing a “reduced representation” of a complex environment that is built back up as activity moves to downstream cortical areas. Rather, it is part of a larger dynamic, iterative process that allows changes to be tracked in real-time ensuring that an object is considered equivalent despite changes in motion direction. **(second row)** Equivalence illustrated with the morphing of an object. As done on computer monitor screen savers a decade ago, a single stimulus changes shape and color as it traverses the screen, although simultaneously retaining the capability to be described as the same object. **(Third Row)** The same sort of description can be applied to a rat traversing an L-shaped track. Each step yields changing environmental stimuli and at the same time provides a measure of the amount of change that should have occurred. **(Bottom Row)** A proposed stimulus/context equivalence solution: a population of neurons maintains and updates a pattern of activity as a function of the amount of change in external stimuli. As the pattern of activity for the red square slowly shifts in the first part of the morph, the remaining similarity supports continuity (it is the same object!) while accounting for change. Of course, the blue circle yields a completely different pattern of activity than the red square. In the same way, the end of the rat’s track has a different pattern than the start. How does the nervous system maintain equivalence across such large changes? By allowing the neural pattern to change in concert with the stimuli, it provides a scaffold that enables the nervous system’s maintenance of equivalence across large changes by, essentially, packaging small changes into larger containers. Below, we will discuss this in terms of the changing spatial scale of hippocampal place fields.

Both external sensory cues and internal states, including its own prior state, influence the hippocampus, as it monitors and maintains equivalence (or continuity) over contiguous inputs. Unless there is a significant change, generated either by external or internal sources, the system signals “sameness” – that is, contextual or cognitive equivalence. And the animal or human continues to act as though it is still in the same context/situation. Several problems need to be solved in order to accomplish context equivalence. First, some amount of change has to be tolerated, in the service of maintaining context stability. Second, rapid shifting from one context representation to another must be accomplished when change exceeds a threshold. In what follows, we suggest a solution to these problems that relies upon known anatomic and dynamic features of the hippocampus.

Maintaining Stability in the Face of Change

Consider a rat seeking rewards on a maze, whose sensory-motor experiences differ when it runs on the right or left side of the maze. In both cases the rat moves in pursuit of a reward associated with the global context. Even though sensory experience is different, the context and task situation remain the same. The rat makes the contextually appropriate turn at the central platform regardless of the sequence of local sensory and motor cues it experiences, indicating that behavior continues to be determined by the stable global context. We propose that the hippocampus, along with its nearest neighbor, the entorhinal cortex, has certain architectural features that provide a basis for solving the context equivalence problem. **Figure 2A** shows that the hippocampus can be “sliced” in two ways. Along its transverse axis lies the well-known tri-synaptic loop, while its longitudinal axis goes from the septal (dorsal or posterior) end to the temporal (ventral or anterior) end. An important feature of the cells along this longitudinal axis is that the size of the place fields systematically increases as one moves from dorsal to ventral in the rat hippocampus (32). Similarly, the grain of the grid cells that provide inputs to the hippocampus also increases as one moves from dorsal to ventral within the medial entorhinal cortex (33,34).

The hippocampus most-likely operates as a continuum, with activity propagating from the dorsal to ventral hippocampus in a peristalsis-like process (35-38). Along this longitudinal axis, hippocampal organization can be considered as a discrete set of amorphous pools connected in series (34). Modules project to other modules with larger place fields. Each module engages in a pattern formation process, being driven by current inputs, and previously trained states. Pattern formation succeeds and is maintained when there are only modest changes in the input, allowing patterns to evolve without losing connection to the particular features of the outside world. This is how “sameness” is achieved in the face of continuously changing input. Similarly, when environmental contexts are slowly morphed from one to another, hippocampal ensemble activity smoothly changes between these contexts (17). The change from the pattern observed at the start to the one seen at the end is not a competitive process (pattern separation or completion) but the pattern formation that emerges from recurrent hippocampal neural networks.

In our view, the recurrent circuits of the hippocampus are capable of self-organization, such that they do not require *a priori* learning to form a spatiotemporal pattern. Afferent excitatory input to such networks triggers nonlinear interplay between the network’s neurons, resulting in emergent order and structured activity (39). This emergent pattern is robust, that is, recoverable in the face of mild perturbations, but also adaptable. If the pattern is changed slightly, some number of neurons cease to fire while others begin. Thus, organisms have the ability to detect both similarity and difference, and an appropriate way to deal with moment-to-moment change would be to generate a physiological “envelope” that maintains and adapts a pattern of activity in accordance with changes in input. This is best thought of as pattern formation, rather than pattern completion or separation.

How does the hippocampal system determine the switch from “modest” to “substantial” change, i.e., when one has transitioned to a new context

or situation? In our view, this capacity emerges from the varying thresholds for change detection available in a system with varying scales of representation. The most dorsal module, with the smallest place fields, recreates its trained pattern up to, say, a threshold of 5% change, beyond which it transitions to a different pattern to be transmitted to the next module. This next module, with larger fields, will 'smooth over' 50% (let's say) of any change it receives, so in effect receives an input signal that is only 2.5% changed. As a result, this level transmits a "same" context message to the next module – that is, it sustains its ongoing, trained, pattern. A 10% change in the first module would however yield a 5% change in the second, sufficient to shift its output. And so on. This convergence activity has been modeled in recurrent neural networks as “contraction” or the stabilization of the trajectory as activity moves through the brain (40). A system wired up this way would dampen relatively minor changes detected at a fine scale, in the service of preserving sameness at the situational or contextual scale (**Fig. 2**).

Fig. 2: Variable threshold detection along the hippocampal long axis. **(A)** The three-dimensional organization of the hippocampus. Theta activity propagates as a traveling wave along the longitudinal axis. **(B)** Consider a series of networks capable of both pattern completion or pattern separation (more appropriately, “pattern formation”; see text) **(C)** indicated by the sigmoidal response to changing input. The consequence of linking these networks in series is that each region becomes progressively less sensitive to the input (or distance traveled in terms of the hippocampus) indicated by the 5% change in the dorsal output serving as the input to the intermediate region (arrow), which only registers as a 2% change. This notion, which overlaps with the recently described convergence activity within recurrent neural networks (40), supposes that the activity in the ventral hippocampus is as much a consequence of intrahippocampal input, conveyed as a traveling wave of afferent activity, as it is a consequence of extrahippocampal input. **(D)** Operationalizing this model as a function of spatial movement, the change in the pattern of active neurons is less dramatic in more ventral regions (Compare colors to panel A). That is, based on panel B, place cell activity will change more slowly in the ventral region. **(E)** Considering hippocampal look ahead, or the sequence of cellular activity within each theta cycle (with the activity of an individual cell assigned a letter), we can actualize how this model might work. Between positions “1” and “2” in panel “A”, the input changes enough to alter the manner in which the network responds in the dorsal hippocampus. The intermediate hippocampus performs a sort of “low pass filter” on this change, converging to a mildly altered population. That is, some cells are still active, some cells have gone silent, and new ones are active. However, this partially changed population in the intermediate hippocampus is seen as being the “same” in the more ventral regions. Therefore, despite dorsal hippocampal population activity changing while moving between positions 1 and 2, ventral hippocampal population activity shows little change. Thus, the hippocampus is capable of tracking continuity across a continuum of scales. Panel A from Gloveli et al (41).

The extent of the change detected by the organism determines how far a “change” signal is propagated along the module stream characterizing the hippocampal long axis. Only substantial change, e.g., an actual context shift, will make it to, and out of, the modules at the ventral (anterior) end of the hippocampus. This proposal is consistent with the evidence linking ventral/anterior hippocampus to context representation³ (42) and recent resting-state functional connectivity studies (43) suggesting privileged communication channels between the anterior (ventral) hippocampus and those areas in cortex concerned with context, prominently including the ventromedial prefrontal cortex. In our view, this mechanism, based on known anatomy and physiology of the hippocampus, can account for how the brain represents contexts,

³ Some have argued that the ventral hippocampus plays a special role in anxiety and fear, given its connections with amygdala and prefrontal cortex. We argued in Poppenk et al. (42) that while the hippocampus does indeed influence such behaviors this can be seen as subsidiary to its core function of representing places and contexts.

maintains their continuity and signals their discontinuity. This formulation is similar to the notion of hierarchical prediction error (PE) signaling, at the core of current “free energy” approaches to brain function (44). Unlike much of the brain, the hippocampus receives dopamine-mediated PE signals from locus coeruleus (LC) (45,46), suggesting that it is affected as much by novelty per 4as by reward prediction error. Prediction errors generated by the hippocampus are propagated to the vmPFC. Elaborating on these aspects of the model is beyond the scope of this paper.

In the mechanism we sketched out above, sharp transitions can occur anywhere along the longitudinal axis of the hippocampus (see Fig. 2B-E), but only transitions at the most anterior end are registered psychologically as a change in context. The circuit involving the anterior hippocampus and the vmPFC concerns contexts because the anterior end of the hippocampus has large “fields”, and the ventromedial part of the PFC to which it projects, is itself concerned with contexts and situational frameworks. Activity in this circuit indicating that there has been a context shift, has substantial consequences for the organism.⁴ Change signals from more dorsal aspects of the hippocampus project to target structures that are not

⁴ The recently described syndrome of developmental topographical disorientation (47), which involves an inability to sense where one is in the world, reflects diminished connectivity between the pre-frontal cortex and the hippocampus, although the region within hippocampus was not sufficiently specified to tie this effect to the anterior end (48). More specific data comes from a just-published study (49) investigating the acquisition and retrieval of trace-fear conditioning in the rat, explored the role of inputs from ventral hippocampus to prelimbic areas in the rat. The authors concluded that “the VH continuously updates the PL with the current contextual state of the animal, which, when disrupted during memory acquisition, is detrimental to the subsequent rapid retrieval of aversive contextual associations. Though more research is clearly needed, these new data provide support for our proposal. Also, see Nadel & Sederberg (50) for a related discussion of how the brain registers and deals with contexts and context shifts in the domain of memory.

concerned with contexts, hence should not affect the organism's understanding of its situational and spatial context.

Changing State Space

Our focus to this point has been on what it takes to stay in the same state space when confronted with variation. Equally important, however, is the ability to rapidly recognize when these variations exceed some threshold and one is confronted with something different. A system structured to track variation, and to adjust to minor perturbations, seems well-placed to determine the presence of major perturbations. The mechanism specified above reacts to such a determination by generating a different pattern of activity in the network, in what is commonly referred to as “remapping”. In our view, understanding how one part of the brain, the hippocampus, both forms and evolves patterned signals relevant to its role in cognition demands a dynamic approach to the nature of neural connectivity. Such a perspective focuses on the fact that activity in the nervous system involves highly recurrent patterns projecting iteratively back onto themselves in a manner that is swayed by ongoing experience.

Amorphous, highly recurrent networks can implement pathways that optimize for robust, yet adaptable dynamics (51-53). Robust coding implies that modest change in the pattern of input has little to no effect on the output of a network. Adaptable coding suggests that a network has a high degree of pliability in terms of structure and function. For instance, a network could be trained to develop a specific pattern of activity by modulating specific synaptic weights. While this network can be precisely tuned, it is not necessarily fault tolerant (not robust). Any failure in the input would inevitably alter the output. Furthermore, the ability to tune the output to a specific pattern is relegated to changing synaptic weights, making one-trial learning problematic.

How can the brain achieve both adaptation and robust dynamics when, at first glance, favoring one may come at the detriment of the other (as pattern completion/separation would suggest)? Interestingly, the answer may reside in having convergence and divergence within the same network⁵. Specifically, allowing multiple neurons to project into a network with amorphous connectivity favors robust operations that remain capable of adaptation (57). Densely connected amorphous networks provide **degenerate** connections by which the brain forms and transmits analog patterns through large recurrent loops. Degenerate connectivity allows different components to perform either similar or distinct functions depending on conditions.

Interactions between inhibitory and excitatory neurons in these amorphously connected pools of neurons are critical for complex pattern formation. As seen in Figure 3A, a network solely comprised of recurrently connected excitatory cells is liable to kindle excitation to epileptic levels⁶. A predominantly inhibitory network, on the other hand, will rapidly quench activity. The ratio between these two populations of neurons is what gives rise to more complex dynamics⁷. These networks go beyond “digital-like” pattern separation vs. pattern completion mechanisms (60), to instead express an analog quality in which the firing properties of any individual neuron has minimal consequences for the pattern of the whole. As long as the output is “close enough”, local mismatches are tolerated. However, as described below, the network is capable of converging onto other patterns. The nonlinear nature of

⁵ Our answer is that stimulus equivalence, or cognitive contiguity, is solved through having convergence and divergence within the same recurrent neural network (see text and figure 4). During revisions we became aware of a model by Kozachkov et al. (40) that complements the idea presented here. Kozachkov and Miller suggest that when the internal weights of a recurrent neural network are either held fixed or slowly varied (ensuring contraction within the network) while the feed-forward weights between networks are free to adapt with the “ever-changing world”, the system will indeed have both robust and adaptable dynamics. They suggested to us (personal communication) that a collection of independently contracting networks combined in series, as we propose herein, will provide contraction automatically.

⁶ Hebb’s first version of cell assemblies consisted only of excitatory elements, and suffered from exactly this problem when early efforts were made to simulate it with the primitive computational resources available at the time (58). Milner (59) subsequently made the argument, and convinced Hebb, that inhibition was critical to making things work.

⁷ This fact may help us understand the aberrant excitatory/inhibitory (E/I) balance seen in various developmental disorders, such as Down syndrome.

excitatory-inhibitory interactions (39; **Fig. 3B**) makes it difficult to predict how much the input must vary to initiate substantial change in the network's pattern.

Figure 3. As described in *Rhythms of the Brain* (39), (a) a network of “excitation only” neurons will spiral out of control whereas (b) driving a network of inhibitory neurons will generate a transient pattern. However, the combination of these two populations of cells offers the ability to achieve complex spatiotemporal patterns, transient events and/or oscillations. This figure was used by Berg and colleagues (48) to describe spinal motor circuits, but the amorphous connectivity of the nervous system lends it application to other systems such as the hippocampus. In the absence of a hard-wired pattern from neuron to neuron, cells can connect to each other in an “approximate” and amorphous manner. The dynamics of the amorphous connectivity network provides the first aspect of the solution to stimulus equivalence: to develop a spatiotemporal pattern of activity that can be roughly recreated (that is, the pattern is recoverable although with some noise) given a stable pattern of input. Should the input change, so does the amorphous network. The dynamics of how the amorphous network changes in relation to input is most-likely non-linear (see Figure 3 above). Figure adapted from 61).

Hebb’s seminal cell assembly notion was inspired by what appeared to be recurrent neural networks captured by Lorente de No in his anatomical drawings of the hippocampal CA3 region (62-64). In these networks, Hebb imagined,

“...excitation might theoretically continue for an indefinite period, ‘chasing its tail’, and not leave the circuit until some other excitation came along with which it might combine to produce a motor effect that neither could produce alone” (65, p. 56).

This notion is suggestive of “recurrent neural network” models, incorporating the insight that activity is neither upstream nor downstream in brain circuits. Rather, the network’s global activity matters, with afferent input superimposed so that prior activity history is

consequential to its dynamics. Such recurrent neural networks have been described as being able to support “*rich intrinsic activity patterns, reminiscent of ongoing activity observed in the brain*” (66)

We seek to mesh the ideas of Hebb and Lashley with contemporary research into ‘reservoir computing’ (67) models, e.g., liquid-state machines (68) and echo-state networks (69), in describing how hippocampal networks function. Consider the ‘chaotic neural networks’ of Sussillo & Abbott (70; **Fig. 4**) in which a recurrent network generates spatiotemporal patterns of neural activity that could support either walking or running motions depending on the input. This example shows that these networks can spontaneously generate complex dynamic activity patterns that are also recoverable. Further, tolerance is built into these network dynamics, such that inputs that are “close enough” count, as the ability to approximately recreate a spatiotemporal pattern of activity is an emergent property of the excitatory and inhibitory connections within the network.

Figure 4. Amorphous networks have the ability to recover dynamic patterns based on the input. (A) Constant neural input (e.g., either “running” or “walking”) provides the activity into either linked amorphous networks (with modifiable connections between them; top panel) or a single amorphous network with modifiable connections between neurons (red connections denote modifiability; bottom panel). After training, the dynamic activity of recurrent neural networks can be relayed to motor units, with motor patterns that match human motion capture data (arrows from A to B), to supporting complex actions such as running (B) or walking (D). Importantly, the network can respond with a time-evolving pattern as shown. (C) Activity of 10 neurons during walking motion shows the transition or activity within the network in relation to walking. Akin to the sequences of cell firing within a cycle of theta, the input into this network kicks off a pattern of activity. While some neurons appear to correlate to behavior, others do not. The network is simply evolving a pattern of activity in response to an input. Figure from Sussillo and Abbott (70)

As already indicated, the temptation to consider this merely a “pattern completion” network should be resisted: when the active inputs into such a network are redistributed, an entirely different yet equally stable pattern can emerge. To reiterate, the term pattern formation more accurately describes what these networks do. Sussillo and Abbott (70) had the insight that these randomly connected networks will not exhibit any obvious relationship between the function they are currently performing (e.g., running versus walking) and their fixed anatomical connectivity alone is insufficient to precisely specify function (71).

Amorphous neural ensembles of this type in the hippocampus could accomplish the goals of tracking context continuity and discontinuity in the following way:

1. Given a set of inputs, an amorphous network would converge on a stable activity pattern. This accounts for the rapid formation of place fields in a novel environment.
2. Such an ensemble would gradually change its pattern in a conserved manner, generating predictable sequences linked to the organism’s interaction with the environment. Sequences are inherent to amorphous, recurrent networks, which have asymmetric connectivity that render the appearance of repeatable sequences, such as phase precession, replay and preplay (e.g., 72) inevitable.
3. As seen in figures 2 & 3, afferent input initiates spatio-temporal patterns of activity in the hippocampus, redistributing activity from one

moment to the next. The strength of afferent input determines how many neurons are active within a particular sequence while the initial starting spatio-temporal pattern is determined by the pattern of afferent input interacting with the present state of the network (which in itself is a function of the prior activity history). Firing rates and look-ahead would increase with velocity⁸.

4. Should afferent input change enough, a different stable pattern, also capable of generating reliable sequences, would emerge. Remapping is a change in the pattern of the active population that occurs as a function of pattern formation, or how a different pattern results in a different spatio-temporal pattern of input.

That is, the network ensemble has the property of multi-stability, allowing for multiple states with substantially different outcomes⁹. When the system determines that the organism is no longer in context X, given the extent of unexpected stimulation, it shifts into a brain state appropriate for the context it is now in – or its best guess at what that might be. This need for a specified context puts a premium on a multi-stable network. It is worth noting that, while correlates between individual neuron activity and behavior may exist, they can be spurious by-products of the larger network dynamics functioning to maintain context equivalence. While it is tempting to link hippocampal place cell patterns to specific behavioral correlates, this approach loses sight of the operation of the network as a whole.

Predictions

⁸ If input comes into the network at theta frequency, a sequence or “look-ahead” is the consequence. This model has implications for theta phase precession (72) that will not be covered here.

⁹ Work by Jezek et al (73), in which rats were subjected to instantaneous context shifts, uncovered fascinating dynamics in the underlying hippocampal code -- the network flickered back and forth between the two very different states representing the two contexts, until it settled into the one the animal was in at the moment. Having no idea what context one is in is typically profoundly disturbing, highly stressful and actively avoided. It is a fascinating fact that rats with hippocampal lesions act as though they are unaware of “context”, showing little to no fear of open spaces.

Our proposal specifies the roles played by different segments of the hippocampus, as they enable the internal modeling of experienced events and environments, both novel and largely familiar. Limiting the function of either the dorsal or ventral hippocampus in rodents should yield rather different effects, something known for 50 years (74). Early speculation focused on the role of the dorsal hippocampus in spatial tasks, and a putative role of the ventral hippocampus in regulating anxiety (75). More recent views emphasize the multi-scale nature of hippocampal organization (eg., 41), as does the present proposal. We and many others would expect damage to the dorsal hippocampus to impair precise behavior in space, while damage to the ventral hippocampus should primarily affect the animal's ability to utilize contexts adaptively. Recent studies support these predictions (49, 76, 77).

Similarly, in humans, the posterior hippocampus should be especially important in the retention of detailed information about past events and environments, while the anterior hippocampus should reflect the engagement of more coarse-grained representations. A novel prediction about boundary detection tests the model's assertion that a contextual boundary is signaled from the anterior (ventral) hippocampus only when mismatches along the length of the axis are extensive enough to reach the anterior end. Novelty, that might or might not be signaling a new context, will yield large increases in BOLD activity in posterior hippocampus, quite possibly larger than those seen in anterior hippocampus, but only in anterior hippocampus will the extent of activation be related to the perception of a boundary. As well, damage to the anterior hippocampus would have a greater impact than damage to the posterior hippocampus on the perception of a boundary. There is evidence consistent with these predictions (78-81) but critical studies remain to be done.

Place cells track equivalence in the midst of change, hence are key elements in the continuity of contexts. Remapping when exposed to distinct environments reflects the response of a recurrent neural

network to input from two “unique, non-continuous contexts” . If the animal ambulates between these, they can be knitted together, providing a mechanism by which one context is related to another.

As already noted, the brain is capable of driving itself during sleep, evolving a pattern based on internal states. Our place cell description can be extended to the process of imagining the future, in which the brain moves from a familiar “context” to a “novel” one based on internal dynamics. Thus our model is consistent with the burgeoning evidence of a role played by the hippocampus in imagining future states (82).

We believe that our proposal, based on known anatomy and physiology of the hippocampus, can account for how the brain represents contexts, and monitors their continuity or discontinuity. Within this perspective there is no “solid index” or engram stored in synapses or a definable population of neurons, but rather a “liquid” congruence capable of maintaining continuity in an approximate, but updatable format. As long as the densely recurrent networks of the hippocampus respond in the way described by Sussillo and Abbott (70), the exact neurons within the hippocampus that are active is of little consequence. The iterative ‘dialogue’ between hippocampus and neocortex, each step informing the next, either brings these two into ever-closer registration, to reduce prediction error; or drives them completely apart, forcing the system to utilize separate representations (see Figure 2 of Hwaun and Colgin, 83). Lashley, it should be noted, avoided ideas that placed emphasis on single cells or synapses. Rather, he saw the recurrent flow of activity as akin to waves and would most likely have taken a more dynamical perspective. Similar to Rayleigh–Bénard convection, Lashley's approach suggests “pattern formation”, by which activity takes similar paths through recurrent networks, but in a manner significantly more malleable than index theories would predict (84,85). Recall that Lashley viewed the nervous system and its activity in terms of “statistical accuracy” (86).

To summarize: the hippocampus accomplishes context continuity through mechanisms leveraging the changing scale of spatial representation along the longitudinal axis of the hippocampus. It accomplishes context discontinuity by utilizing amorphous networks that keep pattern formation within bounds whilst managing a certain level of fault tolerance, but that also have the capacity to rapidly shift to a different pattern of activity when sufficient prediction error indicates a new context.

Conclusion: Whither Memory?

What are the implications of our position for the role of the hippocampus in memory? First, our approach sees the physiological basis of episodic memories as fluctuating from moment to moment, even as the ‘content’ of any given memory may be held constant. Second, our view stresses ongoing linkages between hippocampus and cortex as a main contributor to the evolving hippocampal state. This implies that as long as a memory for a given episode persists, both hippocampus and cortex will necessarily be engaged, and this in turn has implications for current debates about the role of the hippocampus in remote episodic memory (87-89).

Barry & Maguire (87) argued that the physiological flux observed in hippocampus rendered it unsuitable as a site of long-term memories. While they were correct in pointing out the challenge created by an unstable substrate, there seems little reason to think things are much better in the neocortical sites involved in long-term memory. Instead, we need to understand exactly how dynamic “representations” can undergird a stable mental life. The approach adopted here is an attempt to provide such an account, and it depends upon continued engagement of both hippocampal and associated neocortical sites throughout the life of a “memory”.

In this paper, we offer not a fine-tuned theory of how the hippocampus

accomplishes its role in context or episodic memory, but rather a conceptual framework that leverages dynamics, re-entrant loops and amorphous networks. This framework accepts Hebb's admonition about assigning functions to isolated brain structures: "There is a trap.....the student must be warned about. No psychological function can exist within a segment of cortex by itself." (65, p. 83). The brain's representation of context resides neither in the hippocampus, nor the entorhinal cortex, nor in isolation in any of other structures in the loop.

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Box 1 Linear cognition: Does sensation → perception → memory?

Cognitive models emerging from the 1940s and 1950s adopted an information processing approach in which information is relayed bottom-up, from the environment, through the periphery of the nervous system, and then to the deeper structures of the brain, including the hippocampus and neocortex. This feed-forward view was captured, and reinforced (perhaps unintentionally), in the iconic wiring diagram of the visual system published by Felleman and Van Essen (90). Behavioral evidence emerging in the 1990s showed that feedback influences even the earliest stages of perception, including figure-ground segregation (91). Such data made it increasingly difficult to sustain a feedforward, linear, view of cognition.

The limits of a linear cognitive framework have been widely discussed (92-94). Edelman rejected it for requiring too much “agency”. He argued that the point-to-point connectivity of the nervous system is never precise enough for any specific anatomical connection to have inherent meaning. Freeman also dismissed the approach for being too rigid. Patterns, he argued, are amorphous, and the classic perception → encoding → consolidation → memory scheme cannot work with neural representations that are effectively moving targets (95). Buzsaki noted that interneurons add nonlinearity to how activity is distributed within a small circuit, and also described the nested, circular loop architecture prominent in the brain.

In point of fact, connectivity between the primary visual cortex and hippocampus is as circular and reentrant as it is hierarchical, and the contemporary neuroanatomical literature documents feed-forward and feed-back connections between pairs of neurons, small clusters, and larger reentrant networks, including the hippocampus and scaling up to include cortical-cerebellar loops (96-102). The largest loop of all incorporates both the organism and the environment.

Re-entrant circuitry gibes well with Hebb’s perspective that activity

circulates through loops in the brain all the time. Incoming information, from any source, is necessarily superimposed on, and interacts with, ongoing activity in a way that can change the brain's trajectory:

"...excitation might theoretically continue for an indefinite period, 'chasing its tail,' and not leave the circuit until some other excitation came along with which it might combine to produce a motor effect that neither could produce alone" (65, p. 56).

The presence of neural loops allows the system to largely drive itself, thereby maintaining robust circulation of information. This provides a means by which the brain's models of the world (its "priors" in Bayesian terms) are refined and "filled in" by activity at one time-step informing the next. The loop structure of the brain shows that any simple linear understanding of its function must be incorrect. Our approach envisions brain activities that are continuously 'chasing their own tails', which renders any simple separation between such things as perception and memory implausible. Although such distinctions continue to populate the textbooks, it has been obvious for some time that there is at least as much feed-back in the brain as there is feed-forward. The loops of various sizes that we assume in our model build in both, and allow for modeling space and time at multiple scales. The amorphous networks that we discuss accomplish the key function of maintaining constancy (of context, of cognitive state) across inconstant input. Exactly how this way of thinking about the brain will map most appropriately onto psychological terms such as perception and memory remains to be seen. But one thing is certain, traditional models that see these as wholly distinct activities no longer make sense.

Box 2. Does the Brain Represent Anything?

In our view, the nervous system does not computationally "encode" or "decode" such things as visual inputs. *Rather, it is in the business of transforming patterns of input and propagating patterns of activity.* Unique spatiotemporal patterns of activity within each region are

impressed upon the next region and this continues to higher-order visual areas, those considered to be part of the “what and where/how” pathways (103).

If the brain is simply relaying patterns from one region to the next, then in what sense can it be said to represent a percept, a memory, a thought, or an emotion, or anything at all? The notion of representation, when applied to the nervous system, raises complex epistemological issues, among other things (see 104, for some early discussion of these issues; and 94, for recent thoughts that share some similarities to the present position). Many current treatments of memory assume that there is a specific population of cells in the brain associated with an experience in a static manner akin to a hard disk writing down the video and audio related to a movie. Input, encoding, compression and later recall and replay are all presumed to engage this population (or a sufficient subset of it). The meaning of this activity, the content that it somehow represents, is said to reflect the particular neurons that are engaged by an experience.

This conceptualization of content and meaning can be misleading. The circuits generating a patellar tendon reflex are not a “representation” as such. There is no “encoding” of a hammer or even pressure. At best, we can say that from the perspective of the nervous system, there is a transmission of activity in service of executing an outcome. Should the stimulus not be large enough, propagation fails, and no outcome results. We may ascribe some content or meaning to all this, but we need not, given that we are talking about a reflex arc.¹⁰

Things get more complicated when we move beyond the simple reflex arc to the visual system, or indeed any sensory system. Meaning generally has to be acquired in sensory systems. Initially, there is little content to the patterns of activity that flow within and between V1 and

¹⁰ What could a reflex arc mean? Most concretely, it means that given a certain input the system must rapidly generate a specific output. No exceptions. This “meaning” is prewired in the reflex arc, the result of eons of evolution.

V2. Activity is abundant, but what it relates to in the environment is unclear. While sensory information is transduced and activity propagated, what this means to the organism remains to be determined. It is only through “training” (development and interaction with the environment) that patterns of cortical activity gain what psychologists refer to as semantic content, what we are here calling meaning.¹¹

Certain conclusions follow from this. First, while we cannot say that the nervous system has explicit “representations”, we can contend that its activities convey meaning to the organism. Second, such meaning derives not from the activities of a single brain region, but rather from re-entrant interactions between brain regions, as we implied earlier. Third, given the centrality of recurrence and feedback, sensation, perception and action must simultaneously co-exist. There is no simple “representation”, but rather a co-registration of patterns between brain areas and ultimately the environment, which anchors particular neural patterns to experience. And this in turn imbues these patterns with whatever content, and meaning, they come to embody.

It now seems clear that any “representation” of the facets and features of a particular memory, say for what one did yesterday, is distributed widely across different brain systems. As Lashley intuited, there is no single place in the brain where a memory exists (105).

At the same time, the organism acquires information about what it has experienced, and this information provides the basis for predictive models, which enable the organism to behave adaptively in the future. In order to do this the brain creates models to guide every

¹¹ Matters are more complex when discussing the hippocampal formation. There are good reasons to believe that some hard-wiring of circuits in these structures “embeds” knowledge about the environment – such things as space and time might be pre-wired into core circuits. Critical elements in these systems, such as place and grid cells, appear to emerge without specific “training” experiences. However, what these pre-wired elements “represent” are the spatiotemporal frameworks within which experience then sculpts specific outcomes. It is these latter experiences and outcomes that imbue cortical sites with meaning, which is then conveyed to the hippocampal sites binding cortical patterns in space and time.

aspect of behavior, including determining where it is in the world, where critical resources are located, and how to behave so as to obtain resources as needed. To accomplish this, these models must, at some level of description, “represent” the environment the organism exists in from moment to moment, as well as aspects of environments experienced in the past.

As we have seen, the hippocampus, in the dynamical way we described, can ‘represent’ the context in which an organism finds itself. It can do this even while many of the underlying elements that serve as the basis for such representations shift from one time-step to another. Considerable flux in the underlying substrate in hippocampus does not prevent it from forming stable models of places and contexts that allow the organism to both navigate effectively and to behave in a contextually-appropriate way (106, 107). Our approach incorporates these moment-to-moment shifts.

Looked at in this way, representations/models are at the heart of our approach. The hippocampal system models the context in which the organism exists. But it does this in a way that involves dynamic rather than static ‘representations’. This fits perfectly with what we take to be its core function: tracking the continuity of context, and in so doing the dynamical continuity of cognition.