

Some Thoughts on Place Cells and the Hippocampus

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ABSTRACT: This commentary addresses five issues related to the functional role of place cells and the hippocampus.

Issue	Conclusion
1. Is the cognitive map located in the hippocampus?	Not exclusively
2. Is the hippocampus required for path integration?	Not exclusively
3. Is the hippocampus involved in selecting the appropriate reference frame?	Not exclusively
4. Are all episodic memories encoded by the hippocampus?	No
5. Does the hippocampus use attractor networks?	Not exclusively

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Hippocampal neurons: What do they do? As this century draws to a close, one wonders whether we are any closer to answering this question now? Since the findings following H.M.'s surgery, each passing decade has ushered in new theories, from memory encoding in the 1950s (Scoville and Milner, 1957), through response inhibition in the 1960s (Kimble, 1968), forming associations during classical conditioning tasks in the 1970s (Berger and Thompson, 1978), comparator/buffer memory (Rawlins, 1985), working memory (Olton et al., 1979), and spatial cognitive mapping in the 1980s (O'Keefe and Nadel, 1978), to configural associations (Sutherland and Rudy, 1989) and forming relationships amongst different stimuli in the 1990s (Eichenbaum et al., 1992) (and my apologies to those theories that I have neglected to mention). From surveying the theories from previous decades, it is apparent that the hippocampus has something to do with the formation of memories, although not necessarily all memories or under all contexts.

The H.M. findings embarked the field on understanding the functional role of the hippocampus. This endeavor naturally led to recording from single hippocampal neurons in awake, freely moving animals with the hope that it would elucidate some of the mechanisms underlying learning and memory. Although the earliest studies were conducted by Olds in rats performing classical conditioning tasks (Olds and Hirano, 1969), it was the remarkable finding of place cells by O'Keefe and Dostrovsky (1971) that received the most attention. Ranck (1973) also noticed similar findings in his recordings during the same time period, but did not focus on this aspect of his results, mostly because he found many hippocampal neurons that responded to non-spatial aspects in the environment. Following the work of Olds, in the late 1970s Berger and Thompson (1978) continued to look for,

and eventually found, changes in hippocampal cell firing as a consequence of learning a classical conditioning task. The last two decades have seen similar conclusions drawn from other non-spatial tasks (Wiener et al., 1989; Hampson et al., 1993; Young et al., 1994).

Nonetheless, for anyone who has ever witnessed a rat running around in an open field, and observed that a particular hippocampal cell only fires in one location (a location that doesn't contain any motivational significance), the spatial correlate is amazingly striking. How does one account for this clear and convincing result? O'Keefe and Nadel (1978) postulated that hippocampal neurons were responsible for encoding a cognitive mapping system. Subsequent experiments and theoretical revisions have led to a reevaluation of this hypothesis, at least in regards to hippocampal function in humans (Nadel, 1991), and even O'Keefe and McNaughton appear to be reconsidering, judging by their recent remarks at the 1998 Society for Neuroscience symposium. So, we are back to the original question again: what do place cells and the hippocampus do? This commentary discusses five issues, each of which bears on the functional role of the hippocampus:

- Is the cognitive map located in the hippocampus?
- Is the hippocampus required for path integration?
- Is the hippocampus involved in selecting the appropriate reference frame?
- Are all episodic memories encoded by the hippocampus?
- Does the hippocampus use attractor networks?

Is the Cognitive Map Located in the Hippocampus?

Many findings in the rodent as a result of lesioning the hippocampus can be explained by the notion that a map-based representation of the environment (i.e., cognitive map) is stored on-line in the hippocampus. The finding that more than half the complex spike cells recorded in the hippocampus can be classified as place cells, and that their firing is most clearly explained in terms of the animal's location in the environment, also supports the notion that the hippocampus may act as a cognitive map. Although appealing, there are numerous examples that suggest that this cognitive map cannot be represented, or formed, solely in the hippocampus.

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Descriptions of H.M.'s spatial deficits are not that prevalent, but there is little indication in his case, or others like him, that bilateral hippocampal damage severely impairs spatial mapping or orientation skills. Although anecdotally, H.M. does have difficulty navigating in novel environments, he appears to maintain a good sense of space in familiar environments and does not get lost, suggesting that he does retain some kind of cognitive map.

In humans, topographical disorders may be classified into one of two categories: topographical agnosia and topographical amnesia. Topographical agnosia is usually distinguished from topographical amnesia on the basis of whether subjects understand or are familiar with the spatial relationships among a set of landmarks. The deficits in topographic agnosia are readily apparent when subjects are asked to sketch maps representing the spatial relationships of objects. Their sketches bear little resemblance to the actual spatial arrangement of the landmarks. The characteristics of topographical agnosia are similar to those one might expect in a subject lacking a cognitive map. This disorder is most commonly associated with damage to portions of the parietal lobe (De Renzi, 1982; Hublet and Demeurisse, 1992), although a recent study reported three cases with a similar clinical picture following damage to the posterior cingulate cortex (Takahashi et al., 1997), which is analogous to retrosplenial cortex in rats. In contrast, the primary deficit in topographical amnesia is a loss of familiarity with landmarks, although some understanding of the environment's spatial layout may be retained.

Functional imaging studies have also shown that brain areas other than the hippocampus are activated when the use of a cognitive map is required. These other areas include the parahippocampal gyrus, posterior cingulate and inferior parietal cortex, precuneus, and cerebellum (Aguirre et al., 1996; Maguire et al., 1998a). Although Maguire et al. (1997) reported selective activation of the right hippocampus when taxicab drivers recalled routes through London, the hippocampus was *not* activated on two different virtual reality navigational tasks (Aguirre et al., 1996; Maguire et al., 1998a). Maguire et al. attributed the differences to the more complex, real-world environments that contained multiple choices required in the task given to the taxi drivers. In contrast, the computer-simulated environments in the virtual reality tasks did not contain as many choice points and the decision-making processes were not as demanding when compared with the real-world task. However, the virtual reality tasks would have required an accurate cognitive map of the environment in order to be performed correctly. If the hippocampus is important for spatial mapping, why it wasn't activated under these conditions is not clear. Interestingly, another recent study by Maguire et al. (1998b) using a virtual reality task did show activation of the right hippocampus along with the inferior parietal cortex. In sum, it appears that some investigators observe hippocampal activation on some spatial tasks, but not on others, and further experiments are warranted to understand the precise spatial conditions that activate specific brain sites.

Returning to place cells, given that well over 50% of recorded complex spike cells in the rat hippocampus are classified as place cells, if place cells are involved in cognitive mapping, then one might expect to find similar types of cells in the hippocampus of

other species. Although Ono et al. (1991) have reported cells in primates that have characteristics resembling those of rodent place cells, cells with location-specific correlates have been much more difficult to observe in primates. For example, Robertson et al. (1998) were unable to find such cells in primates whose heads were fixed relative to a cart, but were otherwise able to move about the room freely by pushing the cart. Instead of location-specific firing, these investigators reported that a small percentage of hippocampal cells discharged with respect to the animal's spatial view, independent of location and whether the animal's view was obscured by a curtain or by darkness. Like place and head direction (HD) cells (Taube, 1998), spatial view cells discharge with respect to the animal's spatial relationship to the environment and, hence, are allocentric in nature. Although spatial view cells cannot be considered place cells, a network of these cells would be useful for determining where objects are in the environment allowing for construction of what might be considered an alternative type of cognitive map. Theoretically, if one's location and directional heading are known, one can determine their spatial view. Similarly, if one's spatial view and directional heading are known, then one's spatial location can be determined. Because HD cells have recently been identified in the primate (Robertson et al., 1999), it is possible that the primate's hippocampus may be participating in the computation of the animal's location, but that the hippocampus itself does not store the map.

On another level, spatial view cells encode where in space the animal is focusing its attention. One key issue that needs to be addressed, however, is whether all possible spatial views are represented by a network of spatial view cells or whether these cells only include spatial views for items that are present within the environment? Such knowledge would aid in understanding the significance of spatial view cells in terms of their underlying function. For example, if cells were present for all spatial views, then this finding would support the notion that the hippocampus is representing some type of map of the environment. Alternatively, if spatial view cells were only present for views that contained specific items along the walls, then this finding would indicate that perhaps the cells are encoding relevant aspects of the environment that are useful for orientation or, if the situation demanded, locating an item in the room.

Another well-known aspect of place cells in the rat is their large degree of variability in firing within the place field. This finding was recently demonstrated using quantitative analyses by Fenton and Muller (1998). If place cells constituted a cognitive map, then one would expect to observe more consistency in their firing, similar to that found for HD cells when the rat points its head in the cell's preferred direction. The high degree of variable firing in place cells is *not* conducive for a highly accurate sense of spatial location, although one can circumvent this problem by postulating that a large network of interconnected place cells could achieve good spatial resolution.

Finally, it is worth considering some preliminary findings from our laboratory showing that inactivation of the vestibular system, via injections of tetrodotoxin (TTX) into the middle ear, disrupts location-specific discharge in hippocampal place cells (Stackman and Taube, 1996). Although these animals were not tested on a

navigational task, other behavioral studies in rodents with labyrinthectomies have shown impairments on spatial tasks (Miller et al., 1983). Is it possible that the altered place cell discharge of these vestibular-impaired animals is responsible for an inaccurate cognitive map? Although this notion is appealing, extrapolation to humans suggests otherwise, as it is well known that patients with vestibular dysfunction maintain a good sense of spatial orientation, as well as accurate wayfinding abilities. Although these patients have difficulty maintaining their sense of orientation in the dark, when they would be more dependent on vestibular cues (Heimbrand et al., 1991), there is little indication of poor navigational skills under light conditions. Thus, although vestibular dysfunction disrupts hippocampal place cell discharge in rats, and presumably spatial view cells in primates, humans with vestibular dysfunction apparently have intact cognitive maps, suggesting the presence of a cognitive map without a normal functioning hippocampus. Is this outcome true because the cognitive map resides elsewhere in the brain besides the hippocampus?

In sum, there is good evidence to indicate that at least some form of a cognitive map exists external to the hippocampus. Coupled with findings that place cells can discharge to non-spatial aspects of the environment, it is challenging to conceive how the sole function of hippocampal place cells is to serve as a cognitive map, or that the only spatial map of where the animal is in space is contained within the hippocampus. What then can place cells be doing? One possibility is that cognitive maps are distributed in multiple brain regions and hippocampal place cells reflect the spatial map represented in the hippocampus. This view, however, is difficult to reconcile with the frequently observed non-spatial firing characteristics of hippocampal place cells. Alternatively, place cells could be signaling various aspects of the animal's relationship to its environment, including both spatial and non-spatial features. This notion seems to be emerging as the consensus view (e.g., see Eichenbaum et al., 1992), and I favor the idea that "the cognitive map" is probably contained within the parietal cortex (or possibly the parahippocampal cortex) where damage is more likely to result in spatial disorders. Although global in nature and difficult to refute, a role for the hippocampus in encoding complex associations is more consistent with the existent data.

Is the Hippocampus Required for Path Integration?

Somewhat different from the view of a cognitive map are recent ideas that the hippocampus is involved in path integration (McNaughton et al., 1996). Path integration is defined as the process whereby an animal's orientation and location are updated continuously based on how fast, how long, and in what direction it is moving through the environment. In strong support of this notion are behavioral data showing that rats with either fimbria-fornix lesions (Whishaw and Maaswinkel, 1998) or neurotoxic lesions of the hippocampus (Maaswinkel et al., 1999) were impaired in a task requiring path integration. In addition, recent experiments from our laboratory have demonstrated that the HD

cells recorded from rats with hippocampal lesions exhibited large shifts when the rats locomoted to a novel environment (Golob and Taube, 1999). For HD cells to maintain a constant preferred direction when locomoting into a novel environment, path integration is most likely required. Careful examination of the brains from these rats, however, showed that they had significant damage to portions of the neocortex overlying the hippocampus. In addition, we found that HD cells exhibited large shifts in their preferred directions in a group of rats that had sustained damage only to the overlying neocortex, suggesting that the overlying cortex may also be involved in path integration processes. Interestingly, the cortical areas that sustained damage included areas of the parietal cortex that other investigators have shown to be critical for successful completion of allocentric spatial tasks (Kesner et al., 1992; Save and Moghaddam, 1996). Consistent with the notion that other non-hippocampal structures are important for the path integration computation is a recent study showing that rats with hippocampal lesions can successfully perform a tunnel-digging task on the basis of path integrating (Alyan and McNaughton, 1999).

These findings have led to the hypothesis of a neocortical locus for path integration processes (Recce and Harris, 1996; Save et al., 1998). Path integration most likely involves several processes, including (1) the establishment of an initial reference point, (2) monitoring the appropriate motion cues, (3) computation of the animal's new position based on its initial position and subsequent movements, and (4) a mnemonic component that stores "on-line" the distance and direction of the initial reference point relative to the animal's current position. A disruption in any one of these processes would interfere with accurate path integration. There is no evidence or a priori reason to suggest that the path integration processes are executed in a single brain area. Therefore, one might expect that damage to one of several brain areas will affect path integration abilities. Moreover, because each of these processes requires different computational demands, it is more plausible that multiple brain regions, and not solely the hippocampus, will prove to be participating in path integration.

Is the Hippocampus Involved in Selecting the Appropriate Reference Frame?

One important aspect of spatial orientation is the selection of an appropriate reference frame. Place cell discharge occurs with respect to salient landmarks within the environment. Rotation of the landmarks usually leads to an equal rotation in a cell's place field, indicating that landmarks exert control over the place field's location. The landmarks within the surroundings define the environmental context. Thus, when the environmental context changes, place cells will also change where they fire. For example, Kubie and Ranck (1983) showed that a place cell could fire at different locations in the same room depending upon the apparatus used, even though all the apparatus were located in a similar position within the room. Gothard et al. (1996) showed that distinct groups of hippocampal cells encoded different representations with respect to various aspects of the environment. Some cells were classic place cells and discharged with respect to

the external surroundings. Other cells discharged in relation to a moveable goal area that contained a reward, while other cells fired with respect to the rat's home (start/end) point.

One issue that needs consideration, however, is that a subject usually maintains multiple and different reference frames on-line simultaneously. For example, one may know how they are oriented within a particular room of a house, but at the same time that person probably also maintains an awareness of where they are with respect to the entire house. Similarly, the person is also aware of where they are with respect to the town, state, country, and probably the continent. Thus, the person has a sense of where they are with respect to several different environments all at the same time. Therefore, to argue that the hippocampus is involved in selecting the appropriate reference frame doesn't seem to capture the fact that an individual maintains several reference frames on-line simultaneously. Where and how these multiple representations are processed in the brain is unclear, but it probably involves structures external to the hippocampus, since human subjects with hippocampal damage continue to maintain their sense of orientation across many reference frames simultaneously.

Are All Episodic Memories Encoded by the Hippocampus?

The traditional view of hippocampal function posits that the hippocampus is important for encoding episodic (declarative) memory (e.g. Cohen and Eichenbaum, 1996). According to this view, both humans and animals with hippocampal lesions are impaired at performing tasks that require them to recall information concerning the learned relationships amongst items across time and space. Fear-conditioning experiments in animals have shown that hippocampal lesions abolish fear to the contextual aspects of the environment without interfering with fear displayed to a single sensory cue (a tone) (Kim and Fanselow, 1992). These results demonstrate that the hippocampus is important in encoding the contextual aspects of a task. One of the primary components of context is the spatial features of the environment, for example, a room's spatial configuration, where salient stimuli are located, or how an animal is oriented with respect to that environment. This type of material can be considered spatial episodic information because it involves the formation of associations among various items in the environment. Such associations not only define the shape of an environment, but also enable one to determine their orientation with respect to those stimuli. Additionally, most episodic memories contain a positional and/or locational element to them, such as where I was and how I was oriented when a particular incident occurred, or that my keys were located next to the umbrella.

Given these considerations, one would expect that animals without a hippocampus would have difficulty recalling their spatial experiences in an environment if their only experiences in that environment occurred subsequent to the brain damage. For this reason, we were surprised to find that the preferred directions of HD cells recorded from hippocampal-lesioned animals were stable across days in a novel environment (Golob and Taube,

1997), spanning a length of time that usually results in memory impairments in animals with hippocampal lesions. This stability reflects the encoding and retrieval of new spatial information about the environment by these cells, and suggests that selective episodic information concerning spatial aspects of the environment can be stored and maintained over time without a hippocampus.

To further determine whether the hippocampus is required for the storage of episodic spatial information, we assessed the ability of a novel cue to gain stimulus control over the HD cell's preferred direction (Golob and Taube, 1999). Animals with hippocampal lesions were trained to forage for food pellets in an apparatus without a prominent polarizing cue. When an HD cell was identified, a salient novel cue was introduced into the apparatus for 8 min, after which the animal was removed and returned to its home cage. Following a 4-h delay, the cue was rotated by 90° and the HD cell was monitored again. We found that the preferred direction of most cells shifted by an amount that corresponded with the cue's angular rotation, and that all cells shifted their preferred direction after a second set of test sessions. These results show that the hippocampus is *not* required for the establishment of stimulus control by a novel cue. These findings also demonstrate that the shift in preferred direction observed when the hippocampal-lesioned animals locomote into a novel environment (see above) cannot be attributed to a general impairment in establishing stimulus control by the cues contained within the novel environment.

Taken together, our results suggest that extra-hippocampal structures are capable of creating and maintaining a novel representation of the animal's spatial context. This representation has features in common with mnemonic processes involving episodic memory, which are usually thought to require an intact hippocampus.

Does the Hippocampus Use Attractor Networks?

Recent models on the neural mechanisms underlying the generation of location-specific firing have postulated that place cells are arranged in a stable attractor network (e.g., Samsonovich and McNaughton, 1997). This network contains a two-dimensional "ring" of place cells that are interconnected with both excitatory and inhibitory connections. Cells with overlapping place fields are linked with excitatory connections to one another, whereas cells with place fields far apart inhibit one another. This type of attractor network will self-generate a "hill" of excitation that corresponds to one location. This hill can then be moved around to different locations depending on external influences, such as inputs from the vestibular or visual landmark systems.

A prediction from attractor models is that the hill of activity is generated naturally from the connections within the ring-network and in the absence of external input. External inputs are only used to modulate or update the place cell signal by moving the hill of activity around. Consequently, one might predict that the disruption of activity afferent to the hippocampus should have little impact on the location-specific firing of place cells, but might disrupt the ability to move the activity hill around. However, our

recent findings have not been consistent with this prediction (Stackman and Taube, 1996). Temporary disruption of vestibular inputs to the brain, through injections of TTX into the labyrinth, led to the abolishment of location-specific firing of hippocampal place cells. Thus, despite the fact that these vestibular effects are several synapses removed from the hippocampus, these temporary vestibular lesions have a major impact on place cell firing such that the activity hill is abolished. Vestibular lesions had similar effects on HD cells (Stackman and Taube, 1997). These results pose a problem for explaining how location-specific firing arises from a network of neurons arranged in an attractor ring. Finally, the effect of vestibular disruption on place cell discharge is unlikely to be attributed to altered firing of HD cells, because lesions of the HD system, at least at the level of the anterior dorsal thalamus or postsubiculum, do *not* abolish location-specific discharge in hippocampal place cells (Dudchenko et al., 1995; Archey et al., 1997).

SUMMARY

Hippocampal research has come a long way in this last half century. We certainly know more than we did 50 years ago, but a precise understanding on the functional role of place cells and the hippocampus remains elusive. It will be interesting to see what new theories emerge as we embark on the new millennium.

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REFERENCES

- Aguirre GK, Detre JA, Alsup DC, D'Esposito M. 1996. The parahippocampus subserves topographical learning in man. *Cereb Cortex* 6:823-829.
- Alyan SH, McNaughton BL. 1999. Hippocampotomized rats are capable of homing by path integration. *Behav Neurosci* 113:19-31.
- Archey WB, Stackman RW, Goodridge JP, Dudchenko PA, Taube JS. 1997. Place cells show directionality in an open field following lesions of the head direction cell system. *Soc Neurosci Abstr* 23:504.
- Berger TW, Thompson RF. 1978. Neuronal plasticity in the limbic system during classical conditioning of the rabbit nictitating membrane response. *Brain Res* 145:323-346.
- Cohen NJ, Eichenbaum H. 1996. *Memory, amnesia, and the hippocampal system*. Cambridge, MA: MIT Press.
- De Renzi E. 1982. *Disorders of Space Exploration and Cognition*. New York: John Wiley & Sons.
- Dudchenko P, Goodridge JP, Taube JS. 1995. The effects of lesions of the postsubiculum on hippocampal place cell activity. *Soc Neurosci Abstr* 21:945.
- Eichenbaum H, Otto T, Cohen NJ. 1992. The hippocampus: What does it do? *Behav Neural Biol* 57:2-36.
- Fenton AA, Muller RU. 1998. Place cell discharge is extremely variable during individual passes of the rat through the firing field. *Proc Natl Acad Sci USA* 95:3182-3187.
- Golob EJ, Taube JS. 1997. Head direction cells and episodic spatial information in rats without a hippocampus. *Proc Natl Acad Sci USA* 94:7645-7650.
- Golob EJ, Taube JS. 1999. Head direction cells in rats with hippocampal or overlying neocortical lesions: Evidence for impaired angular path integration. *J Neurosci*. In press.
- Gothard KM, Skaggs WE, Moore KM, McNaughton BL. 1996. Binding of hippocampal CA1 neural activity to multiple reference frames in a landmark-based navigation task. *J Neurosci* 16:823-835.
- Hampson RE, Heyser CJ, Deadwyler SA. 1993. Hippocampal cell firing correlates of delayed-match-to-sample performance in the rat. *Behav Neurosci* 107:715-739.
- Heimbrand S, Muller M, Schweigart G, Mergner T. 1991. Perception of horizontal head and trunk rotation in patients with loss of vestibular functions. *J Vestib Res* 1:291-298.
- Hublet C, Demeurisse G. 1992. Pure topographical disorientation due to a deep-seated lesion with cortical remote effects. *Cortex* 28:123-128.
- Kesner RP, Farnsworth G, Kametani H. 1992. Role of parietal cortex and hippocampus in representing spatial information. *Cereb Cortex* 1:367-373.
- Kim JJ, Fanselow MS. 1992. Modality-specific retrograde amnesia of fear. *Science* 256:675-677.
- Kimble DP. 1968. Hippocampus and internal inhibition. *Psychol Bull* 70:285-295.
- Kubie JL, Ranck JB Jr. 1983. Sensory-behavioral correlates in individual hippocampus neurons in three situations: Space and context. In: Seifert W, editor. *Neurobiology of the Hippocampus*. New York: Academic Press, 433-447.
- Maaswinkel J, Jarrard LE, Whishaw IQ. 1999. Selective ibotenic acid lesions of the hippocampus impair dead reckoning in rats. *Hippocampus*. In press.
- Maguire EA, Frackowiak RSJ, Frith CD. 1997. Recalling routes around London: Activation of the right hippocampus in taxi drives. *J Neurosci* 17:7103-7110.
- Maguire EA, Frith CD, Burgess N, Donnett JG, O'Keefe J. 1998a. Knowing where things are parahippocampal involvement in encoding object locations in virtual large-scale space. *J Cogn Neurosci* 10: 61-76.
- Maguire EA, Burgess N, Donnett JG, Frackowiak RS, Frith CD, O'Keefe J. 1998b. Knowing where and getting there: A human navigation network. *Science* 280:921-924.
- Miller, S., Potegal, M., Abraham, L. 1983. Vestibular involvement in a passive transport and return task. *Physiol Psych* 11:1-10.
- McNaughton BL, Barnes CA, Gerrard JL, Gothard K, Jung MW, Knierim JJ, Kudrimoti H, Qin Y, Skaggs WE, Suster M, Weaver KL. 1996. Deciphering the hippocampal polyglot: the hippocampus as a path integration system. *J Exp Biol* 199:173-185.
- Nadel L. 1991. The hippocampus and space revisited. *Hippocampus* 1:221-229.
- O'Keefe J, Dostrovsky J. 1971. The hippocampus as a spatial map. Preliminary evidence from unit activity in the freely-moving rat. *Brain Res* 34:171-175.
- O'Keefe J, Nadel L. 1978. *The hippocampus as a cognitive map*. Oxford, UK: Clarendon Press.
- Olds J, Hirano T. 1969. Conditioned responses of hippocampal and other neurons. *Electroencephalogr Clin Neurophysiol* 2:159-166.
- Olton DS, Becker JT, Handelmann GE. 1979. Hippocampus, space, and memory. *Behav Brain Sci* 2:313-365.
- Ono T, Nakamura K, Tamura R, Fukuda M. 1991. Place recognition responses of neurons in monkey hippocampus. *Neurosci Lett* 121:194-198.

- Ranck JB Jr. 1973. Studies on single neurons in dorsal hippocampal formation and septum in unrestrained rats. I. Behavioral correlates and firing repertoires. *Exp Neurol* 41:461–535.
- Rawlins JNR. 1985. Associations across time: The hippocampus as a temporary memory store. *Behav Brain Sci* 8:479–496.
- Recce M, Harris KD. 1996. Memory for places: A navigational model in support of Marr's theory of hippocampal function. *Hippocampus* 6:735–748.
- Robertson RG, Rolls ET, Georges-François P. 1998. Spatial view cells in the primate hippocampus: Effects of removal of view details. *J Neurophysiol* 79:1145–1156.
- Robertson RG, Rolls ET, Georges-François P. 1999. Head direction cells in the primate presubiculum. *Hippocampus* 9:206–219.
- Samsonovich A, McNaughton BL. 1997. Path integration and cognitive mapping in a continuous attractor neural network model. *J Neurosci* 17:5900–5920.
- Save E, Moghaddam M. 1996. Effects of lesions of the associative parietal cortex on the acquisition and use of spatial memory in egocentric and allocentric navigation tasks in the rat. *Behav Neurosci* 110:74–85.
- Save E, Poucet B, Foreman N, Thinus-Blanc C. 1998. The contribution of the associative parietal cortex and hippocampus to spatial processing in rodents. *Psychobiology* 26:153–161.
- Scoville WB, Milner B. 1957. Loss of recent memory after bilateral hippocampal lesions. *J Neurol Psychiatry* 20:11–21.
- Stackman RW, Taube JS. 1996. Temporary inactivation of the vestibular system disrupts hippocampal place cell activity. *Soc Neurosci Abstr* 22:1873.
- Stackman RW, Taube JS. 1997. Firing properties of head direction cells in rat anterior thalamic neurons: dependence upon vestibular input. *J Neurosci* 17: 4349–4358.
- Sutherland RJ, Rudy JW. 1989. Configural association theory: the role of the hippocampal formation in learning, memory, and amnesia. *Psychobiology* 17:129–144.
- Takahashi N, Kawamura M, Shiota J, Kasahata N, Hirayama K. 1997. Pure topographic disorientation due to right retrosplenial lesion. *Neurology* 49:464–469.
- Taube JS. 1998. Head direction cells and the neurophysiological basis for a sense of direction. *Prog Neurobiol* 55:225–256.
- Whishaw IQ, Maaswinkel H. 1998. Rats with fimbria-fornix lesions are impaired in path integration: a role for the hippocampus in "sense of direction." *J Neurosci* 18:3050–3058.
- Wiener SI, Paul CA, Eichenbaum H. 1989. Spatial and behavioral correlates of hippocampal neuronal activity. *J Neurosci* 9:2737–2763.
- Young BJ, Fox GD, Eichenbaum H. 1994. Correlates of hippocampal complex-spike cell activity in rats performing a nonspatial radial maze task. *J Neurosci* 14:6553–6563.