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Review

Rodent spatial navigation: at the crossroads of cognition and movement

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Abstract

Tasks that measure spatial learning and navigation have become central to contemporary research programs concerned with identifying the neurobiological bases of learning and memory. Although the past three decades have seen an explosion of research reports on rodent navigation, only a small proportion of this research has been directly aimed at identifying the constituent psychological and behavioral processes involved in navigation. Such efforts are critical for establishing a complete neuroscientific explanation of spatial behavior and navigation, however, the majority of these research efforts have focused on identifying a single behavioral dissociation (e.g. place learning vs cued navigation). Experimental comparisons limited to only two possible alternatives can lead to erroneous or otherwise incomplete conclusions regarding how animals navigate. Because multiple sources of information may come to bear on an animal's behavior in spatial tasks, consideration of these sources and their interaction may avoid certain pitfalls inherent in the single dissociation approach. We offer a descriptive model of rodent navigation which includes three important dimensions: *reference frame, information*, and *movement control*. A variety of extant behavioral and neurophysiological data that support the basic utility of this conceptual framework are discussed.

Keywords: Place learning; Morris water task; Hippocampus; Dead reckoning; Path integration; Place cell

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1. Introduction

During the years just before and after 1980 there was a renaissance in research on spatial navigation involving rodents. A small number of laboratories began to analyze behaviour in some interesting spatial tasks in relation to forebrain neural circuits. There was a fortuitous confluence of streams of work on single unit recording in freely moving rats, selective brain lesions, and synaptic plasticity, all of which were accompanied by more conceptually interesting theorizing than in previous decades. The most significant impact of this resurgence was to create a quantum jump in understanding the functions of hippocampus and related forebrain structures. Most of the seminal work relating hippocampus to spatial learning and memory was carried out in a very small number of laboratories, perhaps ten. Given the small number of researchers who were at the center of this confluence, the impact of this work on subsequent research is all the more surprising. We present just one aspect of this research literature which is a crude measure of impact: number of papers that have included measurement of spatial learning using rodents as a central method. Fig. 1 shows the number of papers published during each 5-year interval from 1975–2004. For the first 15 years there were fewer than 10 papers per year. By the mid-1990s there were hundreds each year. These data highlight the tremendous positive impact of the earlier work, as well as point to an obvious pitfall. The seminal work was carried out by investigators with relevant training who were interested in clarifying basic learning and cognitive processes. They took advantage of a unique window opened on neurobiology by the successful experimental analyses of the relationship between hippocampus and spatial learning and memory. Newer spatial behavioural tasks were used in such a way as to test hypotheses about the basic cognitive or associative processes underlying spatial memory. The successes spawned an industry that uses behaviour in a small number of spatial memory tasks as an assay. It is worth pausing to consider if investigators proceed without regard to the constituent processes that likely contribute to their behavioural outcome measures. By way of illustration, we have pondered the following paradox derived from two papers presented at scientific meetings by very widely respected neuroscientists. One investigator concluded that disrupting hippocampus did not affect spatial learning because over the course of the training trials in the Morris water task the rats displayed no evidence of learning, so no conclusion could be made about the learning process. Another investigator concluded that since heroic training measures could ultimately improve some aspects of the spatial memory performance of hippocampal animals in the Morris water task, then the hippocampus is not really involved is spatial learning at all. In this paper we will not pretend to resolve this fascinating debate, but we will discuss some of the constituent processes and issues in measuring spatial navigation and spatial memory.

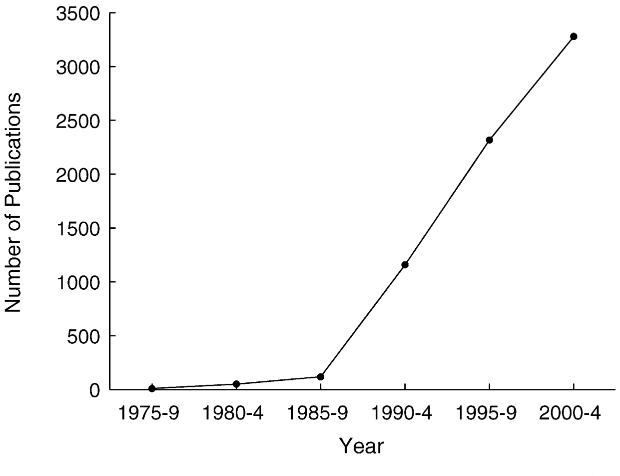

Fig. 1. Number of papers published for six 5-year periods between 1975 and 2004 for the keywords ‘rodent’ and ‘navigation’.

2. False dichotomies

The single dissociation reflects perhaps the simplest strategy in attempting to measure if a treatment (e.g. lesion, drug, genetic manipulation) selectively affects one constituent process in spatial learning/navigation. An early, useful dissociation using the Morris water task was the comparison of effects on navigating to a visual landmark marking a goal vs navigating to a hidden goal in a fixed spatial location. Performance in these two versions is thought to reflect the same motivational, motor, and sensory processes, but differ in the nature of the associative or memory processes, and certainly with respect to the identity of essential neural circuitry. Morris et al. [1], showed that damage to hippocampal circuitry can affect navigation to hidden fixed goals but not to landmarks. This dissociation emerged as an important point of departure for many subsequent experiments on neuropharmacology of memory, the relationship between synaptic plasticity and learning, and functional neuroanatomy of the hippocampal memory system, as well as providing a decisive result scoring heavily against the then dominant ‘working memory’ theory of hippocampal function.

It is important to recognize some of the limits on the application of the single dissociation. There is a clear temptation to map hidden vs cued platform versions of spatial learning tasks onto several conceptually related dichotomies. Given the connection between effects of damage to hippocampus and hidden goal learning there has been a tendency to extend the connection to components of the human memory system taxonomy that have been linked to the hippocampus through clinical work. For example, hidden vs cued goal learning could map onto episodic vs semantic or explicit vs implicit or more commonly declarative vs procedural (nondeclarative). The application of these dichotomies to human memory research depends upon an extensive supporting set of results, methods, and memory task analyses that does not exist for the rat. Imagine the lucky circumstance if it turns out, if the relevant analyses are carried out successfully in the rat, that when the goal platform rises up just above the water surface, there is a transition in memory system activation from episodic to semantic or explicit to implicit or declarative to procedural. It is just such an unlikely event that must be true if this oft-used dichotomy is now being applied appropriately. It might be true, but consider the following analogous situation. In untreated people without a functioning pancreas there is often retinal degeneration. So, parallel testing of vision vs olfaction yields a selective effect of pancreas loss on vision. The pancreatic exocrine tissue is linked functionally to digesting carbohydrates, proteins, and fats. Thus, we can measure digestion of nutrients by comparing visual vs olfactory acuity.

The most common and most subtle of the false dichotomies is that the hidden goal tasks depend upon hippocampus and the cued versions do not. The single dissociation described above implies that in the absence of a functioning hippocampus, the rest of the brain can readily solve cued navigation, but not hidden navigation problems. It does not imply that the hippocampal circuitry is selectively engaged during hidden goal learning and not engaged in cued navigation problems. In fact it is known through several demonstrations that the hippocampus is engaged during cued navigation, including demonstrations using single unit recording in behaving rats and through lesion experiments that demonstrate a critical hippocampal contribution to learning that is incidental to the cued navigation learning. Furthermore, just because the rest of the brain can solve cued navigation problems if the hippocampus is not functioning we should not necessarily conclude that those areas participate in the same way when the hippocampus is functional. By analogy if I am deprived of vision I could probably identify my house using odour, but that does not mean that with intact vision I will also use olfaction. In fact, we have shown that if rats are trained to navigate to one of two visibly distinct platforms in the Morris water task there can be severe retrograde amnesia after hippocampal damage, as severe as for hidden platform navigation [2] (see also Ref. [3]). Relearning of the visible platform navigation proceeds quickly but hidden platform navigation is not relearned. This is critical for interpreting certain neurochemical experiments in which cued navigation learning is used as a control condition for hidden goal navigation (ignoring for a moment the important implications for inferring hippocampal contributions to memory from anterograde amnesia experiments alone).

Leaving aside inferred neurobiological mechanism, if we only consider the information processing components underlying navigation, again there is a tendency in the literature to shoe-horn all of navigation into one or another falsely dichotomous categories. For example, it is often supposed that, depending upon task conditions, rats are using either a spatial mapping (or distal cue) strategy or a landmark (or proximal cue) based strategy. In fact it is known that both strategies can be simultaneously acquired and then rats, even on a single trial, can switch between them [4]. Furthermore, how does one classify processes of navigation that are dependent on a sequence of motor responses, not tied to a place or landmark? Similarly, some investigators prefer the place vs response dichotomy, but then how are trajectories controlled by approaching landmarks classified? Finally, two closely related dichotomies, allocentric vs egocentric or allothetic vs idiothetic, share the same defects. For example, allothetic navigation is defined by the use of stable relationships among exteroceptive cues and idiothetic by the use of internal cues generates by self-movement. A serious problem in this dichotomy is that the allothetic category does not pick out a homogeneous class of processes. This can lead to conceptual confusion. Imagine the following though experiment. Normal rats and rats with hippocampal system damage are tested for navigation in a cue controlled room which can be illuminated or completely dark. We find that in the dark normal, but not hippocampal damaged, rats navigate to a goal accurately, but both groups navigate accurately in the light. In one buys the dichotomy then one concludes that in the absence of the hippocampus rats navigate to goals accurately using the relationship among visual cues. However, a moments reflection should reveal that in order to compel such a conclusion it would be necessary to rule out that in the light a single cue was guiding movement or that the task could be solved by moving in a ‘direction’ (using a single visible polarizing cue for example), and so on. In another vein, how can be sure that the self-movement cues in the dark do not generate accurate navigation by retrieving a mnemonic representation of the exteroceptive cue relationships and that it is this retrieval process that fails in the hippocampal damaged rats. Just because the lights are off does not mean that no visual representations can be accessed; just because the lights are on does not mean that rats are using exteroceptive cue relationships. False dichotomies of this sort turn out not to be useful in the long run, either because the categories do not pick out homogeneous classes of processes or because they are not exhaustive and mutually exclusive.

3. A descriptive model

It follows from the foregoing comments that the processes underlying spatial learning and navigation in rodents are best represented in a multidimensional space. Fig. 2 shows an example of such a representation, one that the present authors favour over the dichotomies discussed so far. We propose organizing navigational processes along three dimensions: *information, movement control,* and *reference frame*.

By information we mean the identity of the cues controlling the movement or establishing the reference

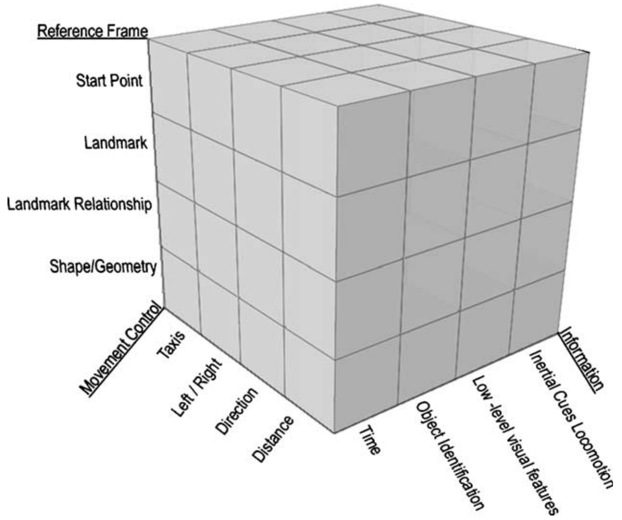

Fig. 2. Schematic representation showing the three dimensions comprising our descriptive model of constituent behavioral processes involved in spatial navigation: reference frame, information, and movement control.

frames. Clearly one source of information comes from self-movement. This can include inertial or other feedback cues from movement, or information contained in the movement command itself. ‘Low-level’ sensory features include relatively simple aspects of the stimulating environment. In the visual modality, brightness, size, textures and in the other sensory modalities there are similar, simple aspects. Next is a category of object identification in which constellations of grouped low level features can function together as a signal or cue in any sensory modality. Finally, time represents another source of information controlling navigation. Measures of duration or time interval can be used in a way not necessarily included in the other sources of information. This is particularly apparent in the case of dead reckoning in which information about the duration of movement in a particular direction provides an essential component of accurate navigation.

Movement control refers to four different elements of guidance constancy. Movements can be made continuously toward or away from a location or cue (*taxis*). In addition, they can be made to the *left or right* (or *above or below*) of a location or cue, or in a particular *direction* relative to a location or cue, or to a spot that is a specific *distance* from a location or cue.

Reference frame represents a typically stable collection of points, features, or axes that allows an observer to efficiently organize trajectories in an environment and it would not be unreasonable to assume they reflect organizing processes involved in the trajectory generation per se. Trajectories sometimes are organized most simply by knowing the specific *starting point*, by a *specific landmark* or beacon, by a *relationship among landmarks* or beacons or by *shape or geometry* of an environmental boundary.

The three dimensional matrix defined by these axes defines a more complete set of constituent navigational processes than is provided by any of the aforementioned dichotomies. Several features of this matrix are worth noting. The specific points within the cube are not mutually exclusive within a particular task, environment, or even trajectory. It is possible that a particular trajectory could simultaneously or successively occupy several points in the cube. For example, in some examples of dead reckoning rats appear to be using time and self-movement information, controlled by direction and distance, with both starting point and landmark frames [5]. This has been shown behaviourally by Whishaw (see below) and others (see Ref. [6] for a recent review), and by Gothard, et al. [7] while recording from single hippocampal neurons. Depending upon the circumstances, the spatial mapping strategy will likely occupy a combination of object identification, landmark relationships, with control by direction and distance, but self-movement information may interact as in cases where animals generate trajectories between regions of an environment with no visual information during the transient. Some portions of the cube may never actually be occupied by a trajectory, but at least in principle we are able to think of examples that may satisfy each region.

Many might suppose that direction and distance come to control trajectories only in the case where landmark derived or geometry derived map-like representations are operative. We are aware of an especially good example of direction and distance both controlling a trajectory when the frame of reference is the start location and the information comes from self-movement. Wallace and Whishaw ([8], see Fig. 3) recorded trajectories from rats moving around a circular

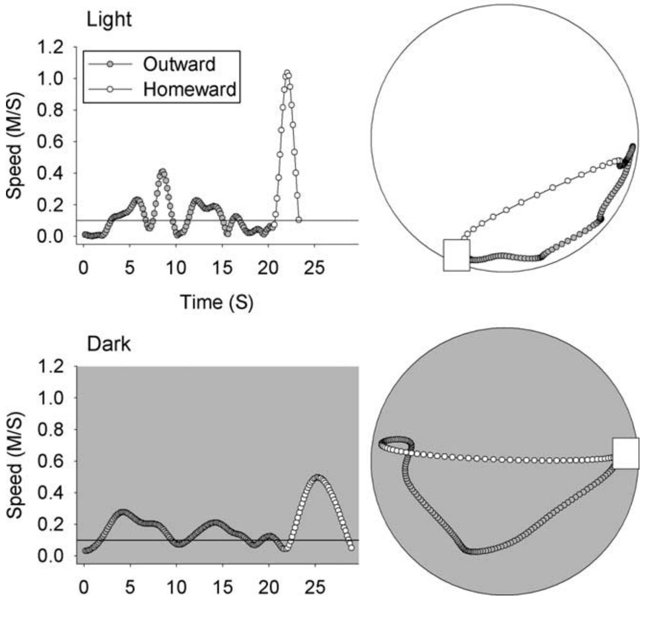

Fig. 3. Velocity (left) and path (right) for outward and return trips to a home base (square) under light and dark conditions in the dead reckoning task used by Wallace and Whishaw. The peak velocity for the return trip is reached at the midway point in both the light and dark conditions, indicating that information about direction and distance to the home base is involved in executing the homebound trip. This figure was adapted from Wallace and Whishaw [8], Fig. 4.

table-top in the light and in complete darkness. It is obvious from the typical trajectories shown on right side of the figure that the rats are heading in the correct direction during the homeward bound trip in both lighting conditions. Of importance for our point are the measures of the momentary speed of the homeward-bound trajectory. After wandering across the table on the outbound trip in the dark when rats are unable to see the geometry of the room or any landmarks the rat turns in the direction of home and there is an acceleration and then a significant deceleration observed at the midpoint of the homeward trip, regardless of the length of the trip. In planning the trajectory homeward rats in the dark exhibit knowledge of both goal direction and goal distance. Wallace and Whishaw's demonstration is clear and compelling but it is important to realize that the phenomena they study permits measuring trajectories that tap only one region of the matrix. It is not known how often rats use the kinds of processes identified in Whishaw's work but it is very clear that these processes are certainly not obligatory in typical spatial learning tasks. For example Skinner, et al. [9] demonstrated in a 4 arm radial water maze that rats could readily learn that on a single trial first entering one arm was reinforced and than a second arm was reinforced, so that they would start from an arm, swim to reinforced arm #1 then #2 (Fig. 4). Interestingly, they tested the idea implicit in Whishaw's notion of dead reckoning (or path integration) that rats should be 'automatically' encoding distance and direction to the start point. They did this by having some of their rats trained with the start arm as reinforced arm #2. The results contradict the straightforward interpretation of the path integration idea. When reinforced arm #2 was the start arm rats found the task to be extremely difficult, more difficult than any other condition. Thus, dead reckoning or path integration represents an important set of constituent processes underlying navigation, but it may not contribute importantly to common experimental tests of spatial learning [10,11].

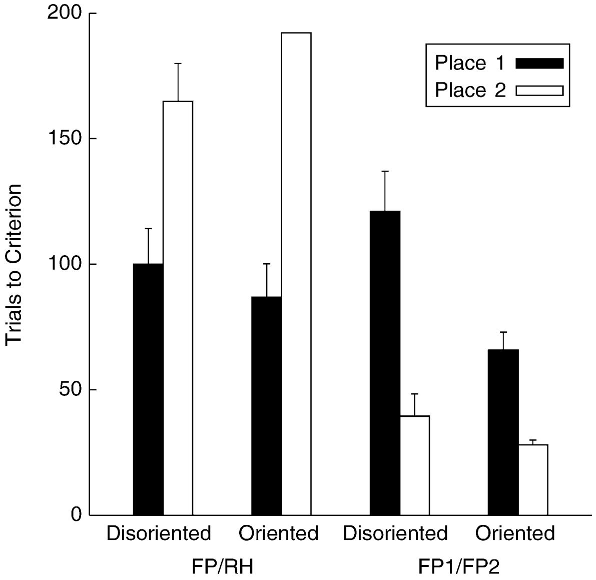

Fig. 4. Mean trials to criterion (18:20 correct + SEM) for the four groups of rats tested by Skinner at al. [9]. Animals were trained to sequentially navigate to two escape platforms in separate arms of a four-arm water maze. The first platform was always in a fixed place (FP or FP1) and the second was either in the arm where the animal released (RH) or in another arm (FP2). Half of the animals in each condition were disoriented via rotation and transport in an opaque container prior to each trial, whereas the remaining animals were not disoriented (i.e. the Oriented condition). Regardless of the orientation condition, animals were able to quickly learn to navigate to two platforms in succession (FP1 and FP2), but it took much longer to train animals to navigate to the second platform if it was located at the start location (RH). This Figure was adapted from Skinner et al. [9], Fig. 1.

When trajectories by rats appear to involve accurate direction and distance information relative to a frame of reference determined by the topographical relationships among distal landmarks or cues, there are at least two critical probe tests that should be conducted before this conclusion is firm. A simple thought experiment should demonstrate this point. Consider a rat in a T-maze centered in a large room with many large visual cues around its perimeter. The stem of the T-maze (the start arm) is always pointing southward during the rat's training experiences. On every trial the rat finds a small piece of tasty food at the end of the arm pointing eastward. The rewarded arm is white and the other (west) arm is black and, after several trials, we observe the rat efficiently running down the start arm and always making a right turn into the white goal arm. At this point, we can easily conduct a probe test to determine if the rat is navigating to the food by approaching the white arm or by making some other response. The probe should involve pitting the white cue against the right turn/place. This can be done by simply switching the white and black arms. When we conduct this 'competitive test' we discover that the rat continues to make a right turn. Next we must carry out a second probe trial in which we rotate the T-maze so that the stem (the start arm) is pointing northward, leaving the white arm in its westward position. Now the rat beginning the probe trial running southward in the stem, reaches the point where it must turn right (always rewarded) into the white arm (always rewarded), experiencing a competition between control between white and right turn vs place. If the rat's trajectory is controlled by the topographical relationship among distal cues then it should turn left into the black arm.

Thus far we have demonstrated that neither the white arm nor the right turn are constancies in the rat's trajectory, but topographical relationship among the distal cues within the room appears to be the key. One last probe trial should complete the picture. It should be noticed that not only has the rat been going to the same location in the room, even during the competitive tests, but it has also been heading in the same direction within the room (i.e. eastward) on every trial. By shifting the T-maze eastward such that the end of the west arm is exactly where the end of the east arm had been and the east arm projects much further eastward than it ever had before, we can complete our competitive testing.

If the rat heads eastward on this trial to a point in the room it had never experienced, then we can rule out location in the room as the constancy. By the same token, if the rat turns into the westward arm, we can rule out directional constancy. The fact of the matter is that with real rats and real experiments it is likely that we could arrange the complex factors influencing trajectories such that we could have some rats choosing white arms, others making only right turns, another set going to specific location in the room, and the rest always heading in a specific direction. A recent conceptually related series of experiments by Skinner et al. [12] demonstrates this point. It is only through careful probing of the controlling parts of the situation that the identity of the underlying processes can be inferred.

Another experiment using the Morris water task with rats makes a similar point. Compared with other apparatus used for studying spatial learning or navigation, the Morris water task has a number of advantages. One of these is geometric. Other apparatus have goal locations that are at one edge of the area within which rats can locomote. In the Morris water task the hidden goal can be placed, say, in the middle of the northwest quadrant. Rats can be released from start locations around the pool's perimeter such that correct trajectories have headings in very different directions in the room. In an apparatus with the goal at one location at the edge, place and direction are redundant, requiring additional competitive tests to disambiguate which is controlling the trajectories. But, does the Morris water task escape this sort of ambiguity? On reflecting on the matrix model of navigation it should be clear in the standard Morris water task than there are two redundant frames of reference, the distal cues of the room and the geometry of the circular pool wall. Is one or both of these used in guiding accurate swims? We know from work with head direction cells in retrohippocampal cortex, that there is a representation of head direction set up in an environment that can be based upon distal room cues. It also seems reasonable that rats can learn that the hidden goal is located a specific distance from the wall of the pool. Could it be that rats learn to navigate to a specific location in the pool by using a combination of information about global environmental direction plus local apparatus geometry/shape. This seems to be rather different than navigating to a specific location controlled by the topographical relationship among the distal features of the environment. We conducted a competitive test, pitting control by the reference frame of the pool vs that of the room (Fig. 5). After training, a no-platform probe trial was conducted during which the location of the pool in the room was shifted in such a way that if the rat was navigating using the pool it would swim to the opposite side from where it should swim relative to the room reference frame. The results could not have been more clear, all rats swam toward the location defined by global direction and pool geometry; they did not swim to the location defined by the topographical relationships among distal cues. We note here a point that we will return to at the end of the paper. If our suggestion about combined use of global direction and more local apparatus geometry is correct then it implies that the navigational system can co-register (or quickly switch between) two difference frames of reference. Thus, we conclude that it is often easy to detect ambiguities in the controlling processes when these are clearly different modalities and when they relate to well known conceptual dichotomies (e.g. visual brightness vs right or left turn vs place), but there are also more subtle ambiguities involving distance vs direction and different frames of reference.

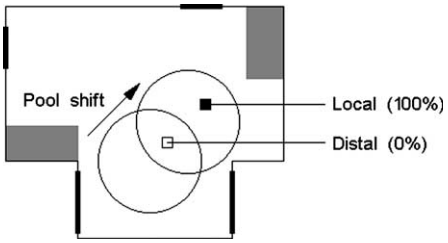

Fig. 5. Diagram of the testing room used by Weisend et al. [16] to test the control of navigation by the geometrical cues from the circular swimming pool and the constellation of distal cues (indicated by the black and grey regions). Rats were trained to navigate to a hidden escape platform in the center of the northeast quadrant of the pool. The pool was then shifted in the direction of the arrow such that the trained escape location was now centered in the southwest quadrant of the pool. All of the rats navigated to the region of the circular pool where the platform was located *relative* to the pool geometry *and* the constellation of distal cues (i.e. the northeast quadrant, indicated by the filled square), whereas none of the animals navigated to the *absolute* platform location defined by the constellation of distal cues (i.e. the southwest quadrant, indicated by the open square).

4. Cue control

When animals learn about environmental events it is known that their behaviour does not come under equivalent control by all available predictive cues. Some of the cues gain very strong control and other little or none. This phenomenon is known as *overshadowing*. There is also a form of learned overshadowing. If an animal has previously learned the predictive value of one cue (or set of cues), then when that cue co-occurs with a new and equivalently predictive cue, the new cue acquires very little control over behaviour. This is termed *blocking*. Both overshadowing and blocking are forms of cue competition. An interesting claim about spatial learning/navigation is that it does not obey the same rules of cue competition as other forms of learning. This point was clearly made by O'Keefe and Nadel [13]. According to their cognitive mapping theory through experiencing an environment there is automatic updating of stored information about topographical relationships among cues. Thus, in a typical blocking procedure, on this view of spatial learning the added cue or cues should be registered in the cognitive map and if only they are available navigation should be fine. Thus, they are holding out the possibility that this form of learning does not obey the laws of associative learning.

There are results suggesting that blocking occurs among sets of distal stimuli in the Morris water task or among

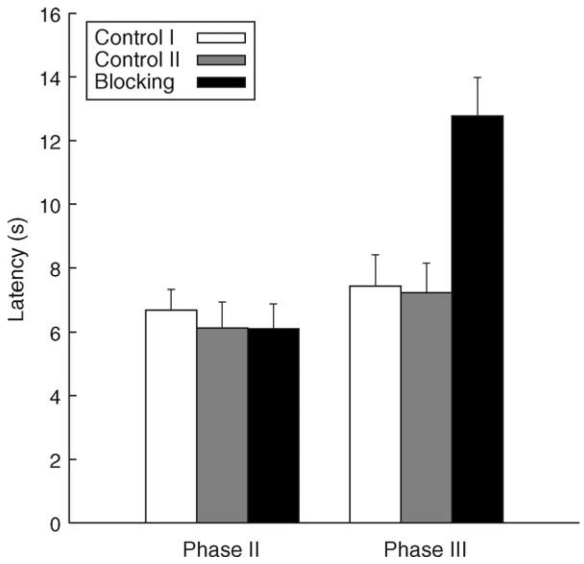

Fig. 6. Mean latency (+S.E.M.) to navigate to the escape platform in a blocking experiment conducted by Weisent et al. [16]. During Phase I (data not shown) animals in the Blocking group were given pre-training with a constellation of distal cues (A) and two control groups were given pre-training in the absence of cue-set A (Control I and Control II). During Phase II, all groups were given compound training cue-sets A and B. During Phase III cue-set A was removed, leaving cue-set B. The results indicate that prior training with cue-set A *blocked* cue-set B.

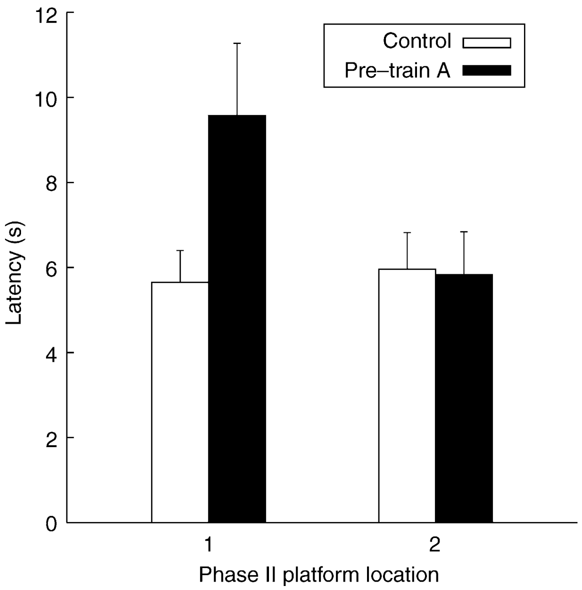

Fig. 7. Mean latency (+S.E.M.) for humans to navigate to enter the platform quadrant of a virtual pool during phase III of in a virtual Morris water task experiment (see, e.g. ref. 18 for a general description of the VMWT). During Phase I, two groups were given training with a constellation of 4 distal cues, one with cue-set A and a Control group with cue-set C (see also ref. 17). During Phase II, both groups were given compound training with cue-sets A and B. For half of the subjects from each pre-training condition the platform was moved to the diametrically opposite quadrant of the pool (location 2) at the beginning of Phase II. For the other half the platform remained in the pre-trained location (location 1). Phase III consisted of a single no-platform probe with cue-set B only (i.e., cue-set A was removed). The results indicate that pre-training with cue-set A blocked cue-set B if the platform was in the same location in pre-training and compound training, whereas changing the platform location at the outset of compound training allowed cue-set B to gain control over navigation (i.e. unblocking).

landmarks in similar open-field navigation tasks. Biegler and Morris [14] trained rats to search a region relative to several landmarks. Equally predictive landmarks were inserted during training, however, tests indicated that the animals learned less about the inserted landmarks than if the landmarks had been equally trained. Similarly, Rodrigo et al. [15] and Weisend et al. [16] (see Fig. 6) trained rats to locate a hidden platform in the Morris water task relative to the relationship among several distal visual cues. An additional set of cues was inserted into the environment and training continued. Probe trial results indicated that the inserted cue set acquired less control than in a group that received equal training with both cue sets. Using a similar method Hamilton and Sutherland [17] studied blocking in human place navigation using the virtual Morris water task (VMWT). The results obtained by Hamilton and Sutherland were consistent with reports using rats in that cues inserted later during training gained significantly less control over place navigation compared to groups that received equal training with all cues. In Fig. 7 we present data from a VMWT experiment with humans which in part replicate Hamilton and Sutherland and which show an important additional property of cue competition in spatial learning. It is established in experiments on basic associative learning that if at the time the new cues are inserted in a typical blocking procedure some aspect of the predicted event is changed, then acquisition of control by the new cues is not blocked. This phenomenon is termed *unblocking*. If the failure of inserted new cues in spatial navigation tasks is truly blocking it should be possible to observe unblocking. The way we changed the predicted event at the time of new cue insertion was by relocating the hidden platform to the other side of the pool. Unblocking is demonstrated here by the fact that the new cues acquired significantly more control over navigation when the goal was relocated than they do is the predictive value of the old cues stays the same. Thus, these results from spatial learning by rats and humans count against the idea that spatial learning is exempt from the traditional laws of associative learning.

5. Instantaneous transfer and the flexibility of spatial learning/navigation

In considering the types of behaviour that would support the existence of spatial cognitive maps, Tolman [19] proposed that favourable evidence would be demonstrated whenever an organism exhibited *flexible* use of spatial information to navigate to a goal. Morris [20] reported a result that fit nicely with Tolman's proposal and has been considered a classic demonstration of cognitive mapping in the rat. He repeatedly released rats from a single, fixed start location in the Morris water task and coined the term 'instantaneous transfer' to describe the animals' near perfect performance when released from a novel start location on the pool's perimeter. One interpretation of the instantaneous transfer phenomenon, offered by Morris, is that cognitive maps formed during initial training allowed novel trajectories to the platform to be computed without requisite, additional learning processes. However, Morris [20] did not report the amount of prior navigation in or through the region of the pool containing the 'novel' release point. It is likely that the rats in Morris' experiment did not navigate directly to the goal location at the beginning of training. Rather, they likely visited all regions of the environment and, thus, gained experience with views from those locations as well as experience navigating to the goal from various regions. Sutherland, et al. [21] suggested that behaviour described as instantaneous transfer may reflect this prior experience and presumably learning about the consequences of many trajectories, rather than the computation of novel trajectories based upon a cognitive map.

Sutherland et al. [21] tested this hypothesis in the Morris water task by systematically varying rats' ability to view and/or navigate in the half of the environment containing the novel start location (see Fig. 8 here and Fig.1 from Ref. [21]). Seven independent groups of rats were trained to locate a hidden platform located in one half of the pool (region 1). Physical and visual access to the other half of the pool (region 2) were controlled by a clear Plexiglas barrier and a black curtain. The seven experimental conditions are diagrammed in Fig. 8. Two groups (A and B) were permitted physical and visual access to the entire pool, but were started in different regions. All of the remaining groups were released from region 1. Two groups were not permitted to navigate in region 2, however, one of these group could view the environmental features in region 2 whereas the other could not. Another group could neither navigate into region 2 nor view the features in region 2. Two additional groups were treated similarly to the restricted groups, but were briefly placed in region 2 at the end of each training trial block. During this 'forced swim' period the rats could not navigate into region 1 and thus, could not navigate to the platform from region 2. The forced swim conditions allowed a test for independent effects of navigation in region 2 and navigating through region 2 on a path to the platform. In a subsequent transfer phase all viewing and navigation restrictions were removed and all groups were started from region 2. Only groups trained with unrestricted physical and visual access to the half of the pool containing the novel start location showed good transfer. Forced swim in region 2 did not significantly improve performance, suggesting that experience viewing distal cues from and navigating in this region were not sufficient to support subsequent navigation to the hidden goal. These findings suggest that groups trained without unrestricted access to the entire pool did not form cognitive maps, but, rather, learned to locate the platform within a familiar range of routes and local views of the distal cue constellation (see also Ref. [22]). Subsequently, Hamilton, Driscoll, and Sutherland [23] used the VMWT to replicate Sutherland et al. [21] in humans and found a striking similarity between the ability of rats and humans to navigate to the goal through familiar and unfamiliar regions of the pool (see Fig. 9). Like rats, humans appear to efficiently navigate to the goal from a novel release location only if they have had experience navigating in the region containing the novel release point. Because it is possible to restrict movement in the virtual domain without introducing other cues (i.e. the Plexiglas partition), a generalization decrement from the training to testing environment does not provide a parsimonious explanation of these results, as suggested by Matthews and Best [24].

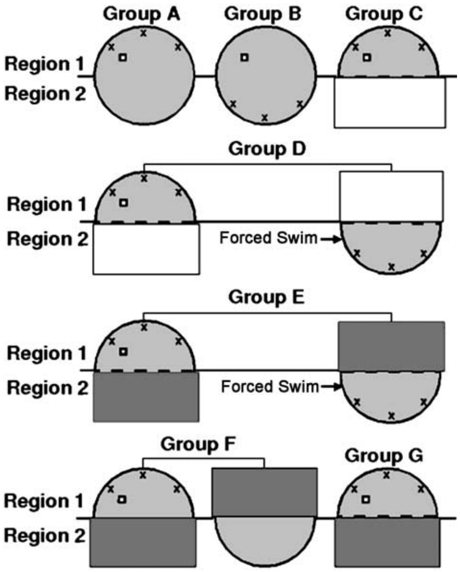

Fig. 8. Navigation and viewing restrictions during training (blocks 1–6) for each group from Sutherland et al. (Ref. [21], Experiment 1) with rats and Hamilton et al. (Ref. [23]) with humans. Subjects could navigate in and view the environment from the areas in light gray. Starting locations are marked by a small 'x'. The small, black open rectangle marks the platform location. The dashed line bisecting the pool indicates the presence of the invisible barrier which restricts navigation from the light gray region of the pool. The dark gray rectangles indicates the region of the environment that will not be visible. The large, open rectangles indicate regions that could be viewed, but where access is blocked by a plexiglass barrier (for rat) or by the virtual invisible barrier (for humans). Reprinted from Hamilton et al. [23], Fig. 3.

6. Representations interact

It was noted above that multiple different representations could be built up as a rat experiences an environment. A wide area of investigation that is relatively untapped involves the nature of the interactions among representational systems. There are published observations that suggest that under certain circumstances different

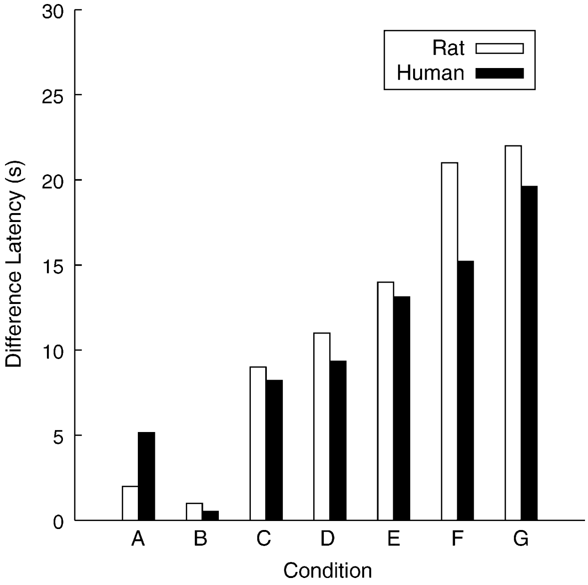

Fig. 9. Mean difference latencies (transfer test-final training block) for rats and humans in the experiments conducted bu Sutherland et al. [21] and Hamilton et al. [23]. The manipulations involving distal visual cues for both species had a similar pattern of effects on navigation in the seven independent groups (see Fig. 8). This Figure was adapted from Hamilton et al. [23], Figs. 5 and 7.

representations interfere with or inhibit one another and obviously they can be synergistic or supportive of each other. An especially clear example of the latter interaction involves the representations of head direction in a network including postsubiculum and anterior thalamus with the place field representation in the hippocampus. When the head direction system is disrupted by damage to either postsubiculum or anterior thalamus, hippocampal place fields are still intact, but aspects of their information content and stability between episodes in the same environment are degraded [25]. The representation of head direction is clearly useful in building up and maintaining a representation of where the rat is in relation to visual and other environmental cues.

We expect that representations of cues or actions could support the building of representations in downstream systems. There is, however, evidence for the counter-intuitive notion that acquiring one representation can block learning in a separate representational system and that this blocking is not due to the two systems merely driving competing movements. A nice example of this kind of interaction can be found in the work of McDonald and White [26] who studied rats learning the relationship between food reward and a particular cue in an arm of a simple maze. There was interference with this simple learning if the rats had the opportunity to explore the maze and environment. The interference effect was shown to be due to the building up of a hippocampal system representation of the environment during initial exploration and the conditioning to the cue was shown to depend upon amygdala circuitry [26–28].

In the rat we have several nice examples of synergistic and antagonistic interactions between representations in different systems. What about different representations within the same system? It is safe to say that we know little about how representations interact between systems, and we know almost nothing about within system representational interactions beyond that they occur. A recent example comes from studying contextual avoidance learning [29]. Rats are placed on a circular tabletop with salient cues around the room. When they enter a specific region on the table they receive a mild foot shock. They learn to quickly avoid entering that region. A moment's reflection reveals that, as in our preceding T-maze example, the identity of the region can be defined by more than one form of information. To consider just two, the region can be represented by its relationship to the available cues around the room or by its relationship to the available cues on the table (which would be supported by self-motion information). We know from other work measuring the place field properties of hippocampal neurons that either of these types of information can serve as a frame of reference for the hippocampal representation (e.g. Gothard et al. [7]). Which does the rat use in this situation? The answer is both.

Fenton and co-workers [29] demonstrated that both representations were *simultaneously* active by rotating the table in a slow and continuous manner. The rat, in the same episode, would avoid a region that rotated with the table frame and a region that was stable in the room frame. Furthermore when one records from neurons in hippocampus in this situation some neurons have place fields relative to the table frame and other to the room frame [30]. Are these two representations of the environment simultaneously active or does the hippocampal network switch quickly and coherently from one representation frame to the other? At present the answer is not known. Possibly these two frameworks could be interleaved through the network, but one could easily imagine that as the rat attends to different features of the environment these two representations are successively recalled. This latter possibility suggests that attention could be a critical process in the rat differentially allocating processing resources to different parts of the environment and hence to different representations. Several examples from ensemble neuronal recording from hippocampus by McNaughton and co-workers strongly suggest that firing can be both simultaneously and sequentially bound to two or more distinct spatial reference frames (see Fig. 10). For example, Skaggs and McNaughton [31] recorded from ensembles of hippocampal pyramidal cells in freely behaving rats while they were walking between two identical boxes via a connecting alley. If the frame of reference were starting location and self-movement information then the hippocampal place cells with fields in this environment would have fields in one box or the other. Alternatively, if landmark cues or cue relationships were the basis for the reference frame then the same place cell would tend to have similar fields in the two identical boxes. Cells recorded in the same ensemble

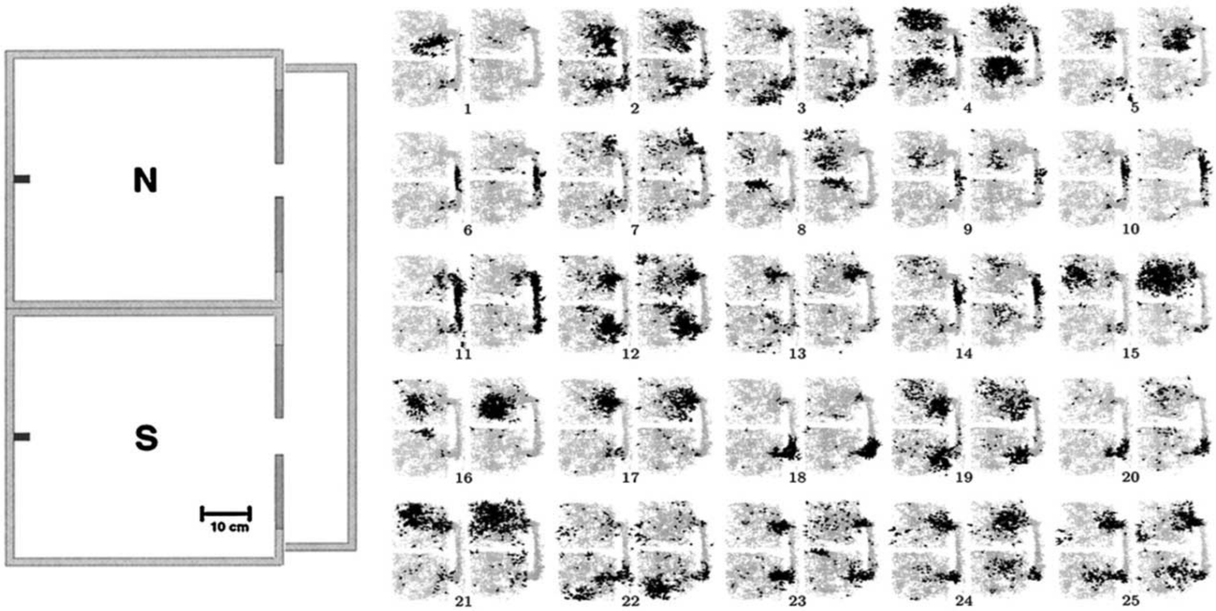

Fig. 10. To the left is a schematic layout of the environment used by Skaggs and McNaughton; Two visually identical environments (N and S) which were connected by an alley. To the right are the spatial firing plots of 25 CA1 pyramidal neurons recorded in one rat during two sessions (session 1 left and session 2 right). Black dots indicate the location where the cell spiked. Most cells had distinct firing patterns for each environment, however, there were 7 neurons with similar firing fields in both environments (cells 2, 4, 12, 15, 19, 24, and 25), suggesting that the cells had fields controlled by visual cues. This figure was recreated with permission from Ref. [31], Figs. 1 and 2.

recording session showed firing to one reference frame or the other, implying an interleaving of reference frames within the hippocampal spatial representation.

7. Conclusions

The use of spatial learning and navigation tasks as assays for underlying neurobiological processes has exploded since the mid-1990s. Nonetheless the analysis of the constituent informational processes has proceeded more slowly. Much is made in the literature of several conceptual dichotomies of spatial navigation, each one capturing an important piece of the complete picture. The dichotomous views suffer, however, from not being exhaustive or mutually exclusive in their categorization of spatial processing. A descriptive model is presented that in three dimensions attempts to map constituent processes more completely in a way that may lend itself to avoiding certain pitfalls in interpreting the results of navigation experiments. In contrast to ideas which suggest that spatial learning/navigation may be exempt from obeying the laws of learning discovered in the associative tradition, several lines of work in rats and humans suggest that it bears a fundamental family resemblance.

Acknowledgements

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