REVIEW

Fractionating dead reckoning: role of the compass, odometer, logbook, and home base establishment in spatial orientation

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Abstract Rats use multiple sources of information to maintain spatial orientation. Although previous work has focused on rats' use of environmental cues, a growing number of studies have demonstrated that rats also use self-movement cues to organize navigation. This review examines the extent that kinematic analysis of naturally occurring behavior has provided insight into processes that mediate dead-reckoning-based navigation. This work supports a role for separate systems in processing self-movement cues that converge on the hippocampus. The compass system is involved in deriving directional information from self-movement cues; whereas, the odometer system is involved in deriving distance information from self-movement cues. The hippocampus functions similar to a logbook in that outward path unique information from the compass and odometer is used to derive the direction and distance of a path to the point at which movement was initiated. Finally, home base establishment may function to reset this system after each excursion and anchor environmental cues to self-movement cues. The combination of natural behaviors and kinematic analysis has proven to be a robust paradigm to investigate the neural basis of spatial orientation.

Keywords Neuroethology · Path integration ·
Hippocampus · Head direction · Theta rhythm ·
Natural behaviors · Kinematics

Introduction

Rats, like many other small mammals, must obtain food from the environment while avoiding predation. These pressures are continuously in conflict. Animals that exhibit behavior solutions that optimize food procurement while minimizing risk of predation are likely to have an advantage during natural selection. Although the ability to use landmarks to accurately navigate is advantageous, the dynamic and unpredictable nature of environments precludes a single strategy solution. Rather, rats appear to use a hierarchy of navigational strategies (Maaswinkel and Whishaw 1999). Provided familiarity with an environment, rats rely on landmarks or relationships between landmarks to guide their movements (i.e., piloting-based navigation). If an environment is novel or unfamiliar (landmarks are either absent or in conflict with previous experience), then rats use self-movement cues to return to the point where movement originated (e.g., a nest). This latter navigational strategy is referred to as dead reckoning or path integration and appears to be the foundation of the spatial navigation hierarchy. This paper reviews recent advances in understanding how rats use dead reckoning to organize natural behaviors and provides a framework for investigating the contribution of sensory and higher-level neural systems to this form of navigation. The first section provides a general description of the processes involved in dead reckoning and some of the research that has been conducted to dissociate dead reckoning from other navigational strategies. Subsequent sections examine these processes in more detail and suggest potential neural correlates.

Dead reckoning

Dead reckoning involves continuous processing of self-movement cues (vestibular cues, proprioceptive cues, sensory flow, or efferent copies of motor commands) such that the animal can derive direction and distance estimates of a path back to the point where movement was initiated (Darwin 1873; Murphy 1873; Barlow 1964; Mittelstaedt

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and Mittelstaedt 1980; Etienne 1980; Potegal 1982; Etienne et al. 1986; Gallistel 1990; Séguinot et al. 1993; Maaswinkel and Whishaw 1999; Etienne and Jeffery 2004). Both invertebrate and vertebrate animals have been shown to use dead-reckoning-based navigation to maintain spatial orientation (ants, gerbils, rats, dogs, humans). Although these animals' sensory and neural systems exhibit considerable differences, several processes appear to be critical for dead reckoning: (1) Compass, the process of deriving directional information from changes in heading; (2) Odometer, the process of deriving distance information from changes in position; (3) Logbook, the set of online processes that integrate path unique information from the compass and odometer to generate a representation of the estimated distance and direction to a refuge; (4) Home base establishment, behaviors that may function to reset these systems subsequent to an excursion into the environment thereby limiting the gradual accumulation of errors. For example, consider how a rat may use each of these components during spontaneous exploration. Figure 1 presents a single exploratory trip from a rat under dark conditions (Exploratory trips reflect a subset of all exploratory behavior. Specifically, exploratory trips are selected such that the return progression is at least halfway across the table, thereby limiting the rat's ability to use proximal cues associated with the home base for guidance). The trip begins after departure from the home base. During exploration, increases in path length are associated with noncircuitous progressions, whereas changes in direction occur at fixed locations along the path. Accurate processing of self-movement information generated until the final stop enables a rat to derive an estimate of the direction and distance to the refuge. The homeward progression reflects the rat using these estimates to plot its return to the refuge. The compass, odometer, and logbook are reset after returning to the home base. This interpretation of exploratory trip organization depends on demonstrating that environmental cues are not controlling this behavior.

Multiple studies examining exploratory behavior have been designed that dissociate dead reckoning from other forms of navigation. The exploratory trip organization described above has been observed under light (Tchernichovski and Golani 1995; Tchernichovski et al. 1998; Golani et al. 1993; Drai and Golani 2001; Wallace et al. 2002b, 2006b) and dark (i.e., using near-infrared light to visualize the rat) conditions (Wallace et al. 2002b, 2006b). Although observation of exploratory trip organization under dark conditions demonstrates that visual cues are not necessary, rats may be recalling the relationships between environmental landmarks experienced during light exploration to guide behavior. To investigate this possibility, Wallace et al. (2006b) examined home base establishment and exploratory trip organization in a novel environment under dark conditions. Observing that rats established a
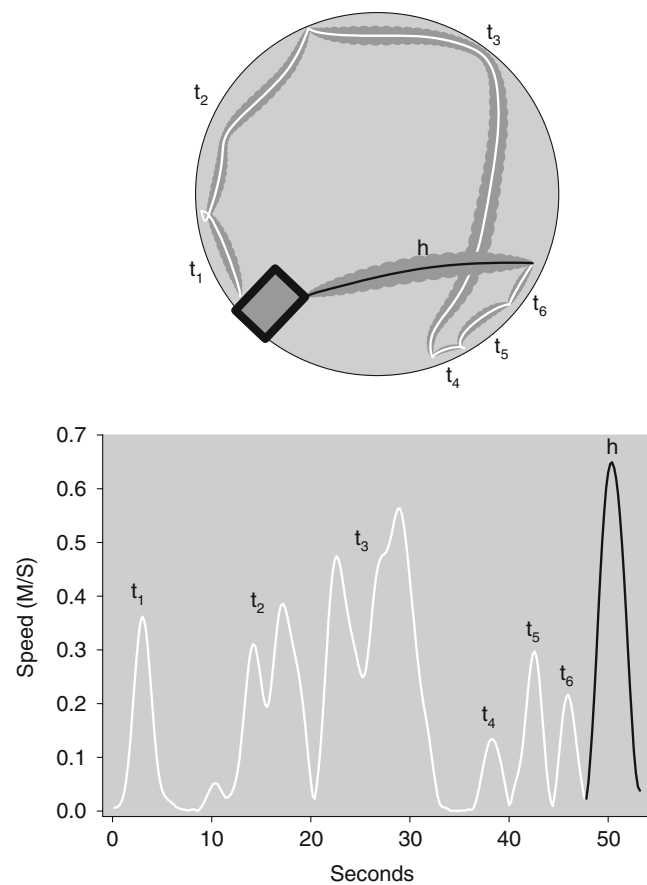

Fig. 1 Topographic (*top panel*) and kinematic (*bottom panel*) characteristics are plotted for a representative exploratory trip under dark conditions. The trip begins after the rat leaves the home base (*black rectangle*). Rats segment their exploration into a series of linear progressions. The width of the *dark gray* area behind the path represents the scaled speed observed at that point in the path. The tour progressions (*white lines*) vary in length and temporal pacing of linear speeds. The return progression (*black line*) occurs after the final stop and is a direct path to the home base associated with consistent temporal pacing of linear speeds

home base and organized their exploratory trips under this condition is consistent with their use of dead reckoning; however, it should be noted that olfactory cues may remain a salient feature of an environment that could be used to guide movement. For example, studies have demonstrated that rats use olfactory cues to pilot in the water maze (Means et al. 1992) and on dry mazes (Wallace et al. 2002a). Nonetheless, several experiments have demonstrated that olfactory cues are not mediating behavior during tests of dead reckoning. First, the ability to use dead reckoning to return to a home base is not influenced by displacing olfactory cues by rotating the table (Mittelstaedt and Mittelstaedt 1980; Maaswinkel and Whishaw 1999) or removal of olfactory cues associated with the home base (Whishaw et al. 2001a). Second, odor tracking and dead reckoning are associated with qualitatively different movements. Rats trained to track

odor trails move slowly, exhibit platykurtic moment-to-moment speed profiles, and make many lateral head movements (Wallace et al. 2002a; Wallace and Whishaw 2003); whereas, rats returning to the home base under dark conditions move fast, exhibit leptokurtic moment-to-moment speed profiles, and do not make lateral head movements (Wallace et al. 2006b). Finally, bulbectomized (anosmic) rats appear to establish home bases (defined as a region in which they spend a majority of their time) independent of visual cue availability (Hines and Whishaw 2005). This work demonstrates that self-movement cues provide sufficient information to maintain spatial orientation. The following sections examine the processes involved in dead reckoning and posit a role for separate systems in detecting changes in direction and position.

The Compass

Sensory systems

Changes in direction occur as an animal moves through an environment. Multiple sources of information may be used to detect changes in direction. Several lines of evidence suggest that the vestibular system is a critical source of self-movement cues associated with deriving directional information. The anatomical organization of the semicircular canals of the vestibular system is ideal for the detection of horizontal angular acceleration of the head. Although angular accelerations experienced during open field behavior are within the range of threshold values associated with the vestibular system (Fischer et al. 1979; Curthoys 1982), other sensory systems (e.g., proprioception, vibrissa flow) may be critical for detecting changes in direction associated with movements that are either below the threshold for vestibular stimulation or occur at a constant speed (i.e., no acceleration).

Behavioral studies have been critical in dissociating the role of the vestibular and proprioceptive systems in estimating direction. Golden hamsters have been shown to use angular and linear accelerations experienced while walking on an outward path to derive the homeward path (Séguinot et al. 1993). Passive transportation of the subject on the outward path stimulates the vestibular system without engaging the proprioceptive system. Provided that the hamsters are passively transported during an outward path, they appear to only use angular accelerations to derive the homeward path (Etienne et al. 1986). The difference in performance observed between active versus passive transport suggests that the vestibular system may be sufficient for detecting changes in direction (however, see section "Neural basis of the compass" for the potential role of proprioceptive cues).

Damage to the vestibular system, on the other hand, has been shown to disrupt directional estimation based on self-movement cues during a food-hoarding task (Wallace et al. 2002c). Lesions of the vestibular system involve intratympanic membrane injections of sodium arsanilate. Subsequent to recovery, rats can be trained to leave a visible refuge to search for randomly located food items. Upon locating a food item, the rat carries it back to the refuge to consume it. After rats are reliably carrying the food items to the refuge, several probes can be given that assess rats' use of environmental and self-movement cues. First, providing rats with a hidden refuge (i.e., located below the surface of the table) restricts rats to using either distal room cues or self-movement cues to maintain spatial orientation. Under these conditions in the light, both control animals and animals with vestibular lesions were able to accurately carry the food item to the refuge (see top panels of Fig. 2). Second, under dark conditions, rats are restricted to using self-movement cues when carrying food items to the hidden refuge. Although control rats carry the food pellet directly to the refuge under dark conditions, animals with vestibular lesions exhibit impairments in returning to the refuge under dark conditions (see middle panels of Fig. 2). Finally, moving the location of the hidden refuge prior to placing the rat in the refuge under light conditions creates a conflict between environmental and self-movement cues. Environmental cues signal the former location of the refuge; whereas, self-movement cues signal the new location of the refuge. Subsequent to locating the food pellet, both control animals and animals with vestibular lesions return to the former location of the refuge. Control animals then carry the food pellet to the new location of the refuge; however, animals with vestibular lesions continue to make returns to the former location of the refuge and eventually find the new refuge location after a random search (see bottom panels of Fig. 2). These observations are consistent with other work demonstrating that rats with vestibular lesions rely more on environmental cues to compensate for impairments in using self-movement cues to maintain spatial orientation (Stackman and Herbert 2002). Other studies have reported similar findings with a passive transportation task (Miller et al. 1983) or with unilateral vestibular lesions (Zheng et al. 2006).

Movement organization influences detecting changes in direction

Given the role of the vestibular system in detecting changes in direction, the organization of exploratory behavior may function to increase the salience of vestibular system stimulation. For example, upon leaving the home base, an exploratory trip increases in length and path circuitry. Changes in direction occur at
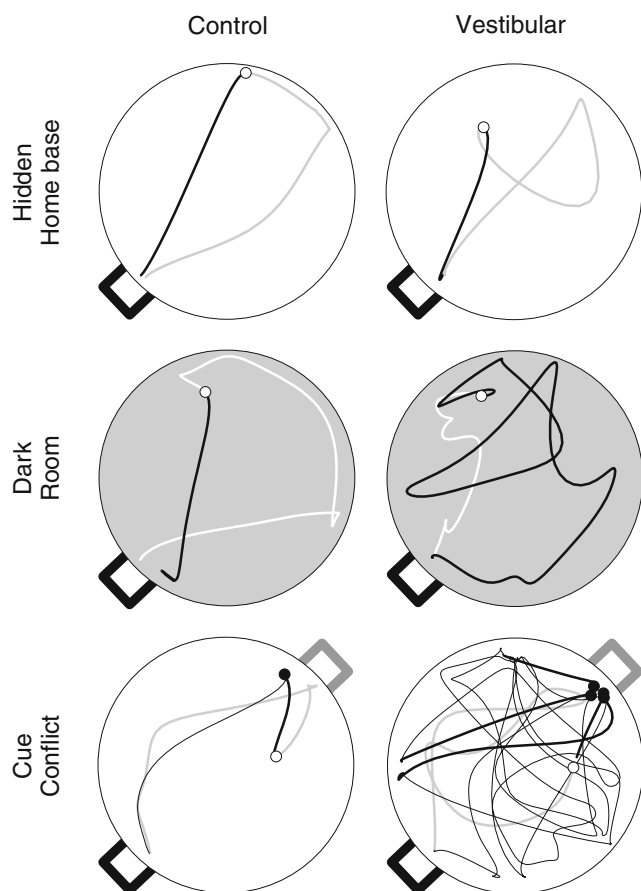
Fig. 2 Food-hoarding trips are plotted for a representative control rat (*left hand panels*) and a rat with bilateral vestibular damage (*right hand panels*). The *top row* plots the searching (*gray line*) and returning (*black line*) components of a food-hoarding trip with a hidden home base (*black box* at edge of table). After locating the food pellet (*white dot*), both rats return to the home base. The *middle row* plots the searching (*white line*) and returning (*black line*) components of a food-hoarding trip under dark conditions. Only the control animal is able to return directly to the home base after finding the food pellet. The *bottom row* plots the performance during the cue conflict test. The *black box* represents current home base location, whereas the *gray box* represents former home base location. Both rats immediately return to the former home base location (*bold black line* ending in a *black dot*) after finding the food pellet. Although the control rat returns directly to the new home base location, the vestibular rat continues to move around the table, making several returns to the former home base location and then happens to find the new location of the home base

fixed locations along the path, rather than gradually accumulating across the entire path (see Fig. 1). In general, rats appear to alternate between modes of linear progressions punctuated by periods of low linear speed and changes in direction. Provided that the relationship between linear speed and changes in direction enhance the salience of vestibular stimulation, movements that decrease this relationship should produce impairments in deriving direction information. Wallace et al. (2006a) have observed that blindfolded humans using a metal detector

to search for a hidden coin for short durations (30 or 60 s) exhibited almost an identical relationship between linear speed and changes in direction to that observed in rats. In addition, subjects accurately returned to the start location. In contrast, humans searching for the hidden coin for 120 s displayed a disruption of the relationship between linear speed and change in direction, specific to the second 60 s. Furthermore, this group was less accurate in returning to the start location relative to the other groups. One possible explanation for this observation is a gradual accumulation of direction and distance errors. As these errors accumulate, the individual becomes disorientated and is no longer able to organize his or her movements. Therefore, movements that minimize the salience associated with vestibular stimulation produce impairments in deriving directional estimates from changes in heading. Although these results demonstrate a role for movement organization in detecting changes in direction, further work is required to understand the relationship between spatial disorientation and movement organization.

Neural basis of the compass

Both electrophysiological and lesion techniques have been critical for defining the neural systems involved in deriving directional estimates from changes in heading. The discovery of neurons in the postsubiculum with firing characteristics tuned to specific directions within the horizontal plane (i.e., head direction cells) demonstrated that the representation of direction has a neural basis (Taube et al. 1990a, b). Subsequent work has demonstrated the presence of head direction cells within structures afferent to the postsubiculum: retrosplenial cortex, anterodorsal thalamic nucleus, lateral mammillary nucleus, and dorsal tegmental nucleus (Chen et al. 1994; Taube 1995; Blair et al. 1998; Sharp et al. 2001; Bassett and Taube 2001; for a thorough review of the head direction cell literature, see Wiener and Taube 2005). Several lines of evidence have suggested that self-movement cues mediate directional tuning of these structures in the head direction circuit. First, head direction cells maintain their firing characteristics under dark conditions (Taube et al. 1990b; Goodridge et al. 1998). Second, angular motion cues derived from optic flow or stimulation of vestibular system have been shown to influence the directional tuning of head direction cells (Blair and Sharp 1996). Third, damage to the vestibular system has been shown to disrupt the head direction signal (Stackman and Taube 1997; Stackman et al. 2002). Finally, there is some evidence supporting the role of proprioception in directional tuning of head direction cells, although there is little support for this in behavioral studies. When rats actively move between familiar and novel enclosures (thus providing access to both vestibular and proprioceptive information),

head direction cells maintained their preferred firing direction independent of visual cue availability (Taube and Burton 1995). Furthermore, elimination of proprioceptive cues, by passively transporting the rat between enclosures, was shown to disrupt the preferred firing direction of head direction cells under light and dark conditions (Stackman et al. 2003). These results suggest that the vestibular system is necessary but may not be sufficient for the generation of the head direction signal. However, recall that Etienne et al. (1986) reported that golden hamsters accurately returned to a nest after passive rotations in a homing task. Future work examining the effect of dorsal column lesions on directional tuning and performance on homing tasks may reconcile these conflicting lines of evidence. Considering these characteristics of head direction cells, structures within the head direction circuit may be critical for dead-reckoning-based navigation.

Lesion studies have provided additional support for the head direction cell circuit in dead-reckoning-based navigation. For example, aspiration or temporary inactivation of the retrosplenial cortex has been shown to disrupt food-hoarding performance restricted to a dark testing condition (Whishaw et al. 2001b; Cooper et al. 2001). In addition, N-methyl-D-aspartic acid (NMDA) lesions of the anterodorsal thalamic nucleus or electrolytic lesions of the dorsal tegmental nucleus have been shown to disrupt performance on a food-hoarding task in which environmental cues were made irrelevant for correct homing (Frohardt et al. 2006). These results demonstrate that the head direction circuit is necessary for dead reckoning; however, observing that lesions outside of this circuit are associated with impaired performance on similar tasks suggests that the circuit may not be sufficient for dead-reckoning-based navigation.

Multiple studies have examined the role of structures outside of the head direction cell circuit in dead-reckoning-based navigation. For example, cell-specific lesions of the hippocampus have been shown to produce specific impairments in the food-hoarding paradigm (Maaswinkel et al. 1999). Although sham and hippocampal animals were equivalent in their ability to carry food to a visible or hidden refuge, hippocampal rats were impaired in returning to the refuge under dark conditions. In addition, when environmental and self-movement cues were in conflict, both groups initially used environmental cues to locate the home base; whereas, only the sham rats were able to switch to self-movement cues to return to the new home base location. In contrast, Alyan and McNaugton (1999), also using selective lesion techniques, failed to observe impaired performance on several tasks in which the necessary behavior is suggested to be mediated by dead reckoning. Unlike the food-hoarding paradigm, these tasks failed to dissociate the use of environmental and self-movement cues. In the absence of this dissociation, spared performance observed in hippocampal rats may have reflected the use of environmental cues to compensate for impaired processing of self-movement cues. Independent of these conflicting results, converging lines of evidence have demonstrated a selective role for the hippocampus in dead-reckoning-based navigation. First, hippocampal lesions have been shown to disrupt head direction cell stability when rats actively move between familiar and novel enclosures (Golob and Taube 1999). Interestingly, a novel environmental cue was able to stabilize directional tuning of head direction cells, consistent with a sparing of the use of environmental cues. Next, dorsal hippocampal lesions have been shown to impair performance in a food-hoarding task in which the environmental cues were made irrelevant for homing (Save et al. 2001; Okaichi et al. 2006). Finally, NMDA lesions of Ammon's horn and dentate gyrus have been shown to disrupt topographic and kinematic characteristics of exploratory trip return progression (Wallace and Whishaw 2003). Specifically, under dark conditions, hippocampal lesions increased return progression path circuitry and variability of linear speed temporal pacing. Although return progressions remained circuitous under light conditions, rats with hippocampal lesions were less variable in the linear speed temporal pacing. The decrease in variability reflected peak speeds occurring adjacent to the home base, consistent with spared ability to use environmental cues associated with the home base. These converging lines of evidence demonstrate a role for the hippocampal formation in processing self-movement cues related to dead-reckoning-based navigation.

Several cortical areas have been implicated in dead-reckoning-based navigation. The entorhinal cortex receives projections from the postsubiculum and provides a major source of information to the hippocampus via the perforant path (Witter and Amaral 2004). Considering these connections, it is not surprising that entorhinal cortex lesions have been shown to disrupt performance during a food-hoarding task in which self-movement cues were necessary for accurate homing (Parron and Save 2004). Next, the parietal cortex, similar to the retrosplenial cortex, provides a significant source of afferent projections to the entorhinal cortex (Burwell and Amaral 1998). Therefore, observing that parietal cortex lesions impair homing accuracy on a similar food-hoarding task (Save et al. 2001; Parron and Save 2004) is consistent with a network of cortical areas involved in processing self-movement cues for dead-reckoning-based navigation. Finally, the anteromedial cortex (AMC) when directly stimulated elicits head orienting in the contralateral direction to the hemisphere being stimulated (Sinnamon and Galer 1984). Unilateral lesions of the AMC produce sensory neglect to the contralesional hemispace when located in the more caudal portion of the AMC (Barth et al. 1982; King and Corwin 1990); however,

lesions located in more rostral portions of the AMC increase perseverative head movements (Sinnamon and Charman 1988). Interestingly, work in humans has shown that current head direction is predictive of future path trajectory in various locomotor tasks (Grasso et al. 1996; Prévost et al. 2003; Hicheur et al. 2005). Therefore, the AMC may be a potential source of efferent copies of motor commands generated as a rat moves through an environment; as of yet, no studies have examined the effects of AMC lesions on dead-reckoning-based navigation.

The foregoing studies are consistent with a system of neural structures involved in deriving directional information from self-movement cues. This conclusion is based on observing that damage to these structures significantly influences the directional tuning of head direction cells and increases the head direction variability associated with homing behavior. Although these impairments are consistent with a selective loss of deriving directional information from changes in heading, these deficits may reflect a more generalized impairment in processing self-movement cues. The following section discusses the evidence that, in addition to direction, rats may use distance to guide navigation, and distance may be represented by a separate neural system.

The Odometer

Sensory systems

Change in position as the result of rectilinear movement represents a second component of movement that must be processed for successful dead reckoning. A majority of the work investigating distance estimation has been conducted on invertebrates (Collett and Collett 2000a). Optic flow has been shown to contribute to distance estimation in bees (Collett and Collett 2000b); whereas, proprioception appears to be critical for distance estimation in ants (Ronacher et al. 2000; Collett et al. 2006; Wittlinger et al. 2006). For example, a recent study investigated the role of proprioception in dead reckoning in the Saharan desert ant, *Cataglyphis fortis*, by manipulating leg length after these insects walked from their nest to a feeding station (Wittlinger et al. 2006). Decreasing leg length (i.e., removal of distal leg segments) resulted in an underestimation of distance to the nest. In contrast, increasing the length of the leg (i.e., attaching pig hairs to distal leg segments) resulted in an overestimation of the distance to the nest. Interestingly, subsequent trips to the feeding station were associated with accurate distance estimation on the return to the nest, thereby demonstrating that distance estimation is an online process. These observations demonstrate that self-movement cues are critical for deriving distance estimates in invertebrates. Although relatively fewer studies have examined distance estimation in vertebrates, they have typically supported a role for self-movement cues in deriving distance estimates (Séguinot et al. 1993; Gothard et al. 1996; Séguinot et al. 1998; Mittelstaedt and Mittelstaedt 2001; Terrazas et al. 2005; Wallace et al. 2006b). The next section considers the evidence that rats use information about distance to organize their behaviors.

Evidence of a rat odometer

Several lines of evidence have demonstrated that rats use distance information to organize their natural behaviors. First, rats engage in a variety of food protection behaviors that vary in the distance that the rat is displaced from a conspecific (Whishaw and Tomie 1988). When a rat is approached by a conspecific during the consumption of a food item, it will elicit either a dodge or brace food protection behavior. Dodging behavior involves the rat removing its forelimbs from the food item and making a lateral movement that displaces the animal a large distance from the approaching conspecific. In contrast, during bracing behavior, the rat's forelimbs maintain contact with the food item, and the animal makes relatively small lateral movements. Obviously, size is one dimension of the food item that the rats could use to guide food protection behavior; however, studies using food items of varying sizes and densities (e.g., food pellets, beans, grains) have demonstrated that time to consume the food item was the best predictor of the type of food protection behavior observed (Whishaw and Gorny 1994). In general, longer estimated eating times were associated with dodging behaviors or traveling longer distances to protect the food item. In contrast, shorter estimated eating times were associated with bracing behaviors or traveling shorter distances to protect the food item (Wallace et al. 2006c). The intensity of the approaching conspecific may have contributed to the size of the food protection behavior. However, observing that average speed of the conspecific did not vary during the consumption of the food item discounts this possibility. Therefore, the organization of food protection behavior depends on rats' ability to generate prospective distance estimates based on the time required to consume the food item. Considering that testing was conducted under normal light conditions, it remains to be determined whether distance estimates were based on environmental or self-movement cues.

Next, travel distance has also been shown to influence whether rats carry a food item to a refuge to eat it or consume the food item where it was found (Whishaw and Dringenberg 1991). Increasing the distance a rat traveled to locate a food item decreased the probability that the food-item was carried to the refuge. Although size of the food

item was initially shown to influence food carrying behavior (Whishaw and Tomie 1989; Whishaw et al. 1989), similar to the aforementioned food protection studies, food-carrying behavior was best predicted by the estimated eating time rather than food item size (Whishaw 1990). Food items that took less time to eat were less likely to be carried relative to food items that took longer to consume. Whishaw and colleagues suggest that rats evaluate the estimated time required to travel to the refuge in light of the time to consume the food item. Provided that estimated time to eat the food item significantly exceeds estimated travel time, the food item will be carried to the refuge. Both travel distance and consumption time have been shown to influence food carrying under dark conditions (Whishaw and Tomie 1989; Whishaw and Dringenberg 1991). This demonstrates that distance estimation is not dependent upon access to environmental cues.

Finally, movement characteristics observed during spontaneous exploration provide additional support for a role of self-movement cues in derivation of distance estimates. Subsequent to establishing a home base, rats make a series of exploratory trips though the environment (Tchernichovski et al. 1998; Whishaw et al. 2001a). Each trip can be divided into a sequence of tour and return progressions (see Fig. 1). The return progression has a temporal pacing of moment-to-moment speeds that is qualitatively different from other exploratory trip progressions (Wallace et al. 2006b). Specifically, return progression moment-to-moment speeds monotonically increase to a maximum speed at the midpoint of the progression, and then speeds monotonically decrease until the rat contacts the refuge. As return progressions vary in length, the temporal pacing of speeds adjusts such that the maximum speed occurs at the midpoint of the progression (see Fig. 3). In contrast, tour progressions of equivalent lengths were not associated with consistent temporal pacing of speeds. Differences between tour and return progression kinematics were observed under novel dark conditions and subsequent light conditions in the same room. Rats derive distance information from self-movement cues generated on the tour segment and use it to guide behavior on the return progression.

Taken together, these observations reveal two characteristics of distance estimation. First, self-movement cues are sufficient to support distance estimation. Observing organized food-carrying behavior under dark conditions demonstrates that access to environmental cues is not necessary to guide movement. Dark testing occurred subsequent to training under light conditions. Therefore, performance under dark conditions may reflect the processing of self-movement cues and retrieval of the representation of the relationship between environmental cues acquired during light training. Observing exploratory trip organization in a novel environment under dark conditions provides further support for self-movement cues being sufficient for distance estimation. Second, distance estimation operates in parallel to direction estimation. In addition to the foregoing studies, recall that restricting Golden hamster's access to vestibular-based self-movement cues produced impairments in distance-based navigation, while sparing navigation based on direction (Etienne et al. 1986). Although these results are consistent with a role for proprioceptive cues in distance estimation, an absence of empirical work leaves the sensory basis of distance estimation to be determined. The possibility that distance and direction estimations are mediated by dissociable neuronal circuits is considered in the next section.
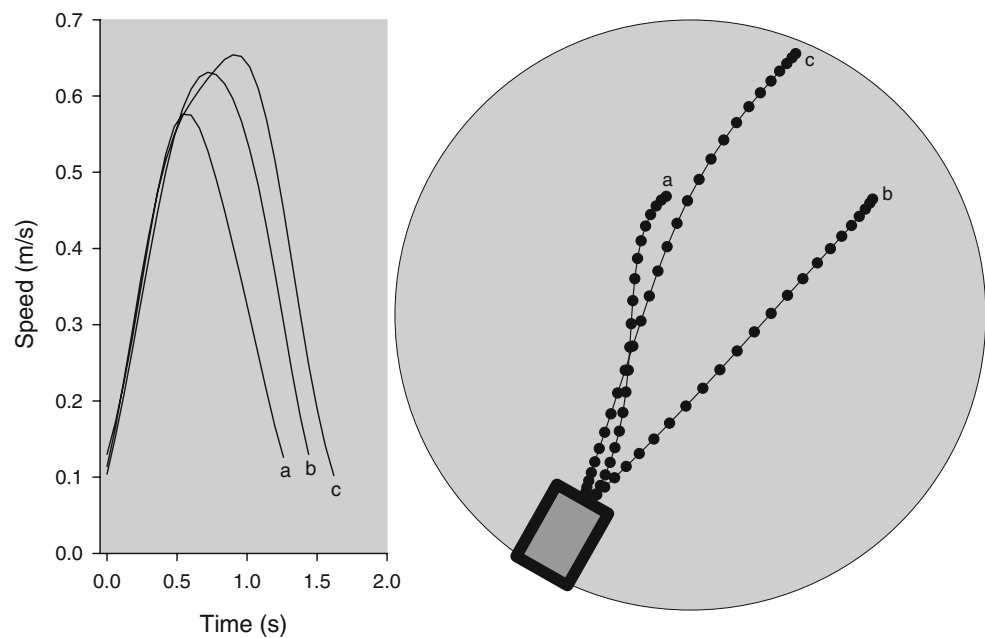
Neural basis of the odometer

The foregoing studies demonstrate that rats use distance information to organize their natural behaviors. Defining the neural basis of distance estimation will depend on observing a selective relationship between the function of a neural system and the organization of a natural behavior. In addition, this relationship should be observed in other behaviors in which rats have been shown to use distance information. The following paragraphs consider evidence that the medial septum and its projections may contribute to distance estimation.

First, ballistic movements of varying distances have been associated with quantitative changes in hippocampal field activity. For example, rats were trained to jump to a platform located a specific distance above the ground (i.e., 27.9 cm) to avoid shock. Increasing the required jump distance (i.e., 55.9 cm) was associated with a systematic increase in hippocampal theta frequency (Whishaw and Vanderwolf 1973). Although rats with fimbria–fornix lesions have been shown to learn the jump avoidance task (Myhrer 1975), their jumps were qualitatively different from control rats (Morris and Hagan 1983). These observations are consistent with a role for the medial septum in ballistic movements; however, fimbria–fornix lesions also disrupt other hippocampal subcortical afferents and efferents (e.g., mammillary bodies). In addition, these differences in performance may reflect impairments in systems that are independent of distance estimation (e.g., the motivational system). Therefore, understanding the role of the medial septum in distance estimation requires more selective lesion techniques in combination with convergent behavioral paradigms.

Second, organization of food protection behavior depends on the medial septum (Oddie et al. 1997). Hippocampal theta is observed prior to the initiation of a food protection behavior as the conspecific approaches and during the food protection behavior. Electrical stimulation

Fig. 3 Kinematic and topographic characteristics are plotted for three exploratory trip return progressions under dark conditions. Note: Peak in speed occurs at the midpoint of the progression regardless of progression length

of the posterior hypothalamus (i.e., a major medial septum afferent) has been shown to produce lateral movements similar to dodging behavior. Atropine injected directly into the medial septum abolished hippocampal theta preceding food protection behavior and disrupted the rats' ability to protect food from the approaching conspecific. Similar impairments in the organization of food protection behavior have been observed with fimbria–fornix lesions (Oddie et al. 2002). Rats with either medial septum deactivation or fimbria–fornix lesions were significantly more likely to have the food item stolen. Subsequent to the theft, rats often made attempts to steal the food item from the conspecific. This observation discounts motivational or motoric factors mediating the impaired food protection behavior associated with medial septum lesions. These observations demonstrate a role for the medial septum in organizing food protection behavior that also may depend on distance estimation.

Third, the medial septum has been implicated in the influence of travel distance on a rat's proclivity to carry a food item to its refuge. Medial septum lesions were shown to decrease the probability that a food item was carried to the refuge (Whishaw 1993). This disruption in food-carrying behavior is consistent with impaired distance estimation; however, medial septum lesions have been observed to disrupt performance on a number of tasks consistent with a reduction in anxiety (Treit and Pesold 1990; Menard and Treit 1996). For example, temporary inactivation of the medial septum produced a significant increase in the percent of time spent on the open arms of the elevated plus maze (Degroot and Treit 2004). Although administration of diazepam (also shown to increase the time spent in open arms of the elevated plus maze) has been

shown to decrease food-hoarding behavior, under certain doses, food item size continued to influence rats' food-carrying behavior (McNamara and Whishaw 1990). The interaction between food size and drug dose indicates that anxiety and distance estimation are significant factors in the organization of food-carrying behavior. Future studies are needed to determine the extent that the medial septum mediates both of these factors' contributions to food-hoarding behavior.

Fourth, aspects of exploratory trip organization have been shown to depend on distance estimation derived from self-movement cues. Rats use estimates of the distance to the refuge to guide moment-to-moment speeds on the return progression. Hippocampal lesions have been observed to significantly increase the variability of moment-to-moment speed temporal pacing under dark conditions (Wallace and Whishaw 2003). Under light conditions, no differences were observed in the variability of temporal pacing of speeds between control or hippocampal rats; however, hippocampal rats' peaks in speed were shifted towards the visible refuge. These observations are consistent with hippocampal lesions impairing self-movement processing related to distance estimation while sparing environmental-cue-based distance estimation. Medial septum lesions have also been shown to disrupt return progression moment-to-moment speed temporal pacing (Martin et al. 2007). In contrast to hippocampal lesions, rats with medial septum lesions are able to plot direct paths to the refuge. These results could also be viewed as supporting the anxiolytic explanation of the effects of medial septum lesions on food-carrying behavior (Treit and Pesold 1990; Menard and Treit 1996). For example, rats with damage to the medial septum are less motivated to return to the safety of the refuge.

Therefore, the return progression is another tour progression that happens to end at the refuge. Three aspects of the behavior conflict with this interpretation (Martin et al. 2007). First, preference for the quadrant in which the refuge is located is not influenced by medial septum lesions. Had medial septum lesions only functioned to reduce anxiety, then more time should have been spent away from the refuge, thereby influencing the quadrant preference score. Second, maximum speed observed on the return progression was not influenced by medial septum lesions. Had medial septum lesions only functioned to reduce anxiety, then the rat would have been less motivated to return to the refuge, thereby influencing return progression maximum speed. Finally, both control and medial septum rats' final stops were associated with the largest change in heading direction. Had the medial septum lesions only functioned to reduce anxiety, then the rat would have been less motivated to return to the refuge, thereby influencing changes in heading observed after each stop. These observations discount an anxiety explanation and support a role for the medial septum in exploratory trip organization. The selectivity of the disruption provides additional support for a role of the septohippocampal system in processing self-movement cues with a more selective role for the medial septum in distance estimation.

Finally, the medial septum also provides a major source of cholinergic projections to the medial entorhinal cortex (Meibach and Siegel 1997). Damage to the dorsal fornix at the level of the hippocampal flexure has been shown to selectively disrupt medial entorhinal cortex theta rhythm and cholinergic staining (Mitchell et al. 1982). These observations are important in light of the recent discovery of grid cells in the medial entorhinal cortex (Hafting et al. 2005). Grid cells fire at the nodes of a repeating triangular lattice as a rat moves across the floor of a testing apparatus. Although manipulation of environmental stimuli has been shown to influence the firing characteristics of grid cells, they maintain their firing characteristics under dark conditions (Hafting et al. 2005). In addition, grid cells in the deeper layers of the medial entorhinal cortex have been shown to have firing characteristics that are also sensitive to directional and speed components of movement (Sargolini et al. 2006). These observations in combination with previous lesion work (Parron and Save 2004) have prompted researchers to conclude a central role for the medial entorhinal cortex in dead-reckoning-based navigation (McNaughton et al. 2006). Specifically, the medial entorhinal cortex is viewed as a structure in which cortical afferents relaying multiple sources of self-movement information converge. Considering that the medial entorhinal cortex receives a majority of its cholinergic afferents from the medial septum, further work is needed to determine if this system may reflect the primary source of distance information for the hippocampus.

These studies provide converging lines of evidence for a relationship between the function of the medial septum and organization of several natural behaviors. The selectivity of the relationship is consistent with a role for the medial septum in distance estimation; however, many theories have been advanced to explain the contribution of the medial septum to ongoing behavior (Buzsáki 2005). For example, one influential view posits that the medial septum is involved in sensory processing related to the generation of voluntary behaviors (Vanderwolf 1969; Whishaw and Vanderwolf 1971; Whishaw and Vanderwolf 1973; Oddie and Bland 1998). Considering that all of the behaviors just reviewed would be defined as voluntary and the difficulty in developing a distance estimation task that would not also be classified as voluntary represents a challenge in dissociating these views, future work examining the effects of sensory deafferentation or removal of medial septum afferents on the organization of these behaviors may provide further insight into the neural basis of distance estimation.

The Log book

Thus far, this review has individually examined processes and neural systems involved in deriving directional (i.e., compass) and distance (i.e., odometer) information from self-movement cues. Information for the compass originates in the vestibular system, is processed by the dorsal tegmental nucleus and anterodorsal thalamic nucleus, and arrives at the hippocampus via the entorhinal cortex. Information for the odometer may originate from proprioceptive cues, is processed by the medial septum, and arrives at the hippocampus via the fimbria–fornix or entorhinal cortex. These observations suggest a possible double dissociation of function at lower levels of self-movement cue processing that converges at the hippocampus.

The first component of the double dissociation should involve impaired distance estimation following damage to the medial septum; whereas, direction estimation should remain intact. This prediction has been supported by the observation that medial septum lesions selectively disrupt exploratory trip organization (Martin et al. 2007). Rats with medial septum lesions displayed variable return progression temporal pacing of moment-to-moment speeds; however, these return progressions remained noncircuitous. These observations, combined with evidence that medial septum lesions disrupt the organization of food-carrying behavior (Whishaw 1993) and medial septum deactivation disrupts food protection behaviors (Oddie et al. 2002), are consistent

with a role for the medial septum in processing self-movement cues that is selective to the odometer.

The second component of the double dissociation should involve impaired direction estimation following damage to the vestibular system while sparing distance estimation. Vestibular lesions have been shown to disrupt head direction accuracy only when rats hoard food items under dark conditions (Wallace et al. 2002c); however, both direction and distance information are generated as the animal searches for the food item. Impairments in deriving directional heading may reflect a loss of directional information or a more generalized self-movement cue processing deficit. To further investigate whether vestibular lesions produce a more selective deficit in self-movement cue processing, in an unpublished study, we examined the effects of vestibular and fimbria–fornix lesions on food-carrying behavior. Control rats and rats that either received electrolytic fimbria–fornix lesions or chemical labyrinthectomy (i.e., produced by injecting sodium arsanilate into the tympanic membrane) were trained to leave a refuge and follow a straight 1.6-m string to locate a food item. After rats reliably followed the string, different food items (i.e., 45-mg food pellet, pearl barley, 500-mg food pellet, 750-mg food pellet, ~4-g piece of rat chow) were introduced at the end of the string. Food hoarding increased as a function of the time to eat the food item [$F_{(4, 44)}=67.851$, $p<0.001$]. In addition, groups differed in their proclivity to hoard food items [$F_{(2, 11)}=5.509$, $p<0.022$]. Specifically, control and vestibular groups were equivalent in hoarding frequencies across the different food items; whereas, fimbria–fornix animals were less likely to hoard food items that took longer to eat [$F_{(8, 44)}=4.473$, $p<0.001$] (see Fig. 4). Although travel distance was not manipulated, these results provide indirect support for vestibular lesions sparing distance estimation. Specifically, at that distance from the refuge, both control and vestibular rats were equivalent in their proclivity to carry food items. These data are consistent with direction and distance self-movement cue processing being mediated by independent neural systems; however, as of yet, no task has been developed that has a significant directional component without also generating a significant distance component. In the absence of such a task, lesions that impair heading direction accuracy may reflect a selective disruption of direction estimation or combined direction–distance estimation impairment.

Hippocampal lesions impair both direction and distance estimation. Impaired direction estimation has been observed in the food-hoarding (Maaswinkel et al. 1999) and spontaneous exploration paradigms (Wallace and Whishaw 2003). Impaired distance estimation was also suggested to mediate the inconsistent temporal pacing of moment-to-moment speeds on exploratory trip return progressions
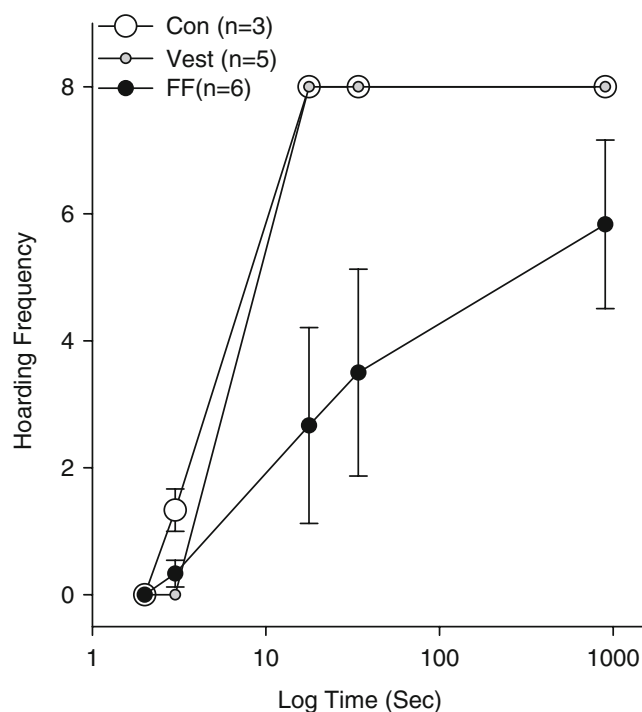

Fig. 4 Control, vestibular, and fimbria–fornix groups' average food-hoarding frequencies are plotted with respect to the average consumption time. The five food items were 45-mg food pellet, pearl barley, 500-mg food pellet, 750-mg food pellet, and ~4-g piece of rat chow (from *left* to *right* on the *x*-axis)

associated with hippocampal lesions (Wallace and Whishaw 2003). The variable temporal pacing of speeds may be related to rats following a circuitous path to the refuge rather than an additional impairment in distance estimation. Observing that hippocampal lesions also disrupt food-carrying behavior organization provides independent evidence for a role of the hippocampus in distance estimation (Whishaw 1993). Observing that hippocampal lesions spare performance on a number of environmental-cue-based navigational tasks (Whishaw and Jarrard 1995; Whishaw and Tomie 1997; Maaswinkel et al. 1999; Gaffan et al. 2000) suggests that disruptions in estimating direction and distance may be related to impaired processing of self-movement cues. Whether the disruptions in performance associated with hippocampal lesions are based on impaired processing of self-movement cues remains an area of debate.

The hippocampus has been traditionally associated with encoding the symbolic relationships between environmental cues or the cognitive map (O'Keefe and Nadel 1978). This cognitive map theory of hippocampal function has been supported by electrophysiological and lesion studies. One line of evidence supporting the cognitive map theory is the observation of cells in the hippocampus whose firing characteristics are tuned to specific locations in the environment that are controlled by environmental

cues (O'Keefe and Dostrovsky 1971; Muller and Kubie 1987; Muller et al. 1987). Another piece of evidence supporting the cognitive map theory is the impaired performance in locating a hidden platform in a water maze associated with hippocampal lesions (Morris et al. 1982; Pearce et al. 1998).

More recently, researchers began to recognize the contribution of self-movement cues to performance in these behavioral tasks. For example, place cell firing remains stable for short periods of time under dark conditions (Quirk et al. 1990). In addition, self-movement cues have been shown to contribute to learning about relationships between environmental cues. Disorientation procedures that disrupt self-movement cue processing have been shown to decrease the ability of environmental cues to control place firing (Knierim et al. 1995) and impair learning to use landmarks to find hidden food rewards (Margules and Gallistel 1988; Biegler and Morris 1996). Therefore, the development of behavioral procedures that disambiguate the use of self-movement and environmental cues has been critical in understanding the role of the hippocampus in navigation.

Based on the studies reviewed in this paper, the role of the hippocampus in navigation may be similar to the processes that are performed on information represented in a ship's logbook. During a ship's voyage, changes in direction and distance are recorded in a logbook. The direction and distance to the port of origin can be derived from the logbook by the application of a series of computations. The error in these computations will depend on the frequency in which changes in direction and distance were recorded. Less frequent updating will increase the importance of accurate temporal estimates in limiting the accumulation in error. As with this analogy, the periodicity in which an animal's representation of a path is updated determines the importance of the temporal context. More continuous updating would limit the importance of a temporal context and would provide immediate access to estimates to the direction and distance to the point of origin. Observing that startled animals immediately return to the nest location after varied amounts of exploration is consistent with continuous updating of the direction and distance to the point of origin (Siegrist et al. 2003). In contrast, less frequent updates increase the importance of the temporal context. Under this condition, representation of the path is viewed as a type of episodic memory for the entire path (Fujita et al. 1993; Whishaw and Wallace 2003). Recent work examining exploratory trip organization has suggested that updating the representation may occur during stops (Martin et al. 2007). Specifically, stops after long progressions tend to be longer in duration relative to stops after shorter progressions; this is consistent with the notion that path characteristics influence processing

demands. Both fimbria–fornix (Whishaw et al. 1994) and medial septum (Martin et al. 2007) lesions have been shown to reduce stop durations in addition to disrupting exploratory trip organization (Wallace et al. 2002b; Martin et al. 2007). These observations are consistent with a role for the hippocampus in updating changes in the representation of the path during stops, and they fit with a larger literature suggesting a role for the hippocampus in episodic memory (Vargha-Khadem et al. 1997; Tulving and Markowitsch 1998).

Home base establishment

Nest establishment is a ubiquitous characteristic of rodent behavior in the wild. Although a nest affords the animal protection from predation, this location may also play an important role in organizing navigational behavior. Rats, mice, and voles have been shown to engage in similar nest establishment behaviors when exposed to an open field in the laboratory; this is referred to as home base behavior (Eilam and Golani 1989; Drai et al. 2001; Eilam et al. 2003; Eilam 2003). Several behaviors are typically associated with the location of the home base. First, rats unevenly distribute their time across an open field, spending a majority of their time at one or two locations. Second, grooming and rearing behaviors typically occur at the home base. Finally, paths directed towards the home base are typically associated with faster speeds relative to paths directed away from the home base (Tchernichovski and Golani 1995; Tchernichovski et al. 1998; Wallace et al. 2002b; Wallace and Whishaw 2003). Although home base establishment may occur as soon as rats are introduced in the environment, researchers use these behaviors (i.e., grooming, dwell times, movement organization) to operationally define home base establishment. Approximately 15 min after introduction to a novel environment, rats begin to exhibit behaviors associated with the home base. Home base behavior has been observed across arenas of varying size and shape independent of lighting conditions (Eilam 2003; Eilam et al. 2003; Gharbawie et al. 2004; Hines and Whishaw 2005; Whishaw et al. 2006; Avni et al. 2006). Therefore, like nest establishment in wild rodents, home base behavior appears to be a fundamental component of behavior in the laboratory rat.

Several factors have been shown to influence home base location. For example, rats establish home bases next to a salient visual cue (i.e., black box) located adjacent to an open field (Hines and Whishaw 2005). In addition, rats exposed to a salient cue in the same location across several days will continue to display home base behavior in the same location on a day in which the salient cue is absent from the testing environment (Hines and Whishaw 2005;

Lehmann et al. 2007). Furthermore, tactile features of the environment have been shown to polarize home base establishment (Avni et al. 2006; Lehmann et al. 2007). Finally, the point where a rat is introduced to the testing environment has also been shown to influence home base location (Nemati and Whishaw 2007). These observations are consistent with rats learning relationships between various environmental cues and the location of the home base.

The home base may function to facilitate navigation. First, dead-reckoning-based navigation is subject to the gradual accumulation of errors (Barlow 1964). Although rats appear to structure their movements through an environment to enhance the salience of vestibular system stimulation (Wallace et al. 2006a), small errors in encoding changes in direction or distance would be amplified due to deriving estimates first from acceleration then from speed. Frequent returns to the home base may functionally reset the compass, odometer, and logbook, thereby reducing the accumulation of errors between excursions into the environment (for an implementation of this resetting idea in robotic navigation, see Neven and Schöner 1996). Manipulations that reduce the occurrence of home base behavior would be predicted to increase errors in dead-reckoning-based navigation. For example, training rats to continuously chase food pellets (as is often done in electrophysiology studies) would obviously suppress home base behavior. Therefore, it is not surprising that place and head direction cells gradually lose specificity of their firing characteristics when rats chase food pellets under dark conditions (Quirk et al. 1990; Goodridge et al. 1998). Second, the home base may function to anchor environmental cues to self-movement cues. Provided that environmental cues are experienced with consistent self-movement cues that are generated since leaving the home base, rats may learn to use environmental cues to guide navigation. Therefore, procedures that disrupt self-movement cue processing are likely to reduce environmental cue control by disrupting home base stability (Knierim et al. 1995; Margules and Gallistel 1988; Biegler and Morris 1996). Although home base behavior has never been examined under any of these procedures, all evidence indicates that rats would engage in home base behaviors during habituation sessions preceding formal pellet chasing training. Future studies combining examination of home base behavior and stimulus control of place or head direction cells could further evaluate the importance of the home base in navigation.

Conclusion

Rats use multiple sources of information to guide navigation. This review has focused on the importance of using behavioral techniques that dissociate between self-movement cues and environmental cues while investigating the neural basis of navigation. This review has also suggested that, at a lower level, two parallel systems mediate self-movement cue processing. The compass system is involved in estimating direction from self-movement cues and depends on the vestibular system and structures in the head direction circuit. The odometer system is involved in estimating distance form self-movement cues and depends on the medial septum. Both the compass and odometer converge on the hippocampus. The hippocampus, much like a logbook, is involved in integrating both of these sources of information to plot a path to the point of origin. Finally, this review has posited that home base establishment may function in two ways to facilitate navigation. First, frequent returns to the home base may function to reset systems involved in dead reckoning, thereby reducing the accumulation of errors involved in estimating direction and distance from self-movement cues. Second, the home base may function to anchor environmental cues to self-movement cues. These multiple systems have evolved to ensure that the rat maintains spatial orientation. Therefore, spatial disorientation during navigation as a result of brain damage is best viewed as a fractionation of these systems.

Neurodegenerative disorders and stroke are characterized by persistent impaired cognitive functioning within the spatial domain (e.g., wandering in Alzheimer's disease). Spatial disorientation can severely limit one's quality of life often resulting in admission into long-term care facilities (Rabins et al. 1982; Logsdon et al. 1998). Given recent advances in stem cell research and glial cell signaling, there is a potential to develop new therapies that promote repair of the central nervous system. Therefore, the effectiveness of these treatments in animal models of neurodegenerative disease or stroke will need to be evaluated. Observing that a treatment improves performance may reflect a general restoration of function or compensatory mechanisms associated with a specific system. Application of behavioral techniques presented in this review and a further understanding of the role of self-movement and environmental cues in guiding navigation will provide important insights into mechanisms of improved performance associated with central nervous system therapies.

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