

Exploration in a dark open field: a shift from directional to positional progression and a proposed model of acquiring spatial information

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Abstract

Exploration in a dark open field undergoes three progressive changes: i) an initial phase of spending equal amount of time in various zones of the arena changes to staying at corners, and ultimately spending most of the time at one corner; ii) traveling paths are first circular and scattered all over the arena, but then gradually become anchored to one corner at which they start and end; iii) traveling distance gradually decreases to the initial level seen in light. Altogether, rodents shift from a 'looping' exploration mechanism with feeble coupling with the environment, to 'home base' exploration which is firmly anchored to the environment. This shift also involves switching from momentary and sporadic to repeated returns to a specific, presumably familiar place to which the animal navigates back from various places. This switching illustrates navigating first by directional and then by positional environmental cues, as hypothesized in the 'parallel map theory'. We also suggest that the transition from looping to home base behavior is part of a hierarchal construction of space representation via three modes of spatial information processing: i) **piloting** - sequential processing, based on moving from one landmark to the next; ii) **orienting** - parallel processing, based on moving from one point to the next, with the same starting and ending point; and iii) **navigating** - continuous processing, based on continuously updating position in relation to several locations in the environment (map navigation).

Key words: cognitive map - dead reckoning - piloting – orientation - systematic search - navigation -
- internal cues - external cues.

Introduction

To navigate in the world, animals usually need to determine a heading direction [26]. That is, to know which way it is facing with respect to some frame that specifies directions [7]. This capacity to get organized in time and space rests on two mechanisms: i) dead reckoning (also termed path integration; [20, 23, 41]); and ii) perception of the direction and distance of landmarks in relation to the animal [31]. Dead reckoning relies on internal (idiothetic) cues generated by self movement of the animal (e.g. vestibular and kinesthetic cues), with the navigator continuously integrating and updating its position in reference to a fixed location; for example, the starting point of progression [23]. In other words, dead reckoning is viewed as an integrated vector that points from the actual location of the navigator to the starting point of integration. On the other hand, landmarks are external (allothetic) cues in the layout of the environment, in reference to which an animal may locate itself [10, 21, 26]. Hence, internal and external cues are utilized by animals in navigating and constructing spatial representation [4, 24-26, 48, 49]. One approach in studying spatial representation is to train animals to reach a goal depending on specific cues, and then to alter these cues [37, 50]. Another approach, which was utilized in the present study, is to introduce an animal into an unfamiliar environment, follow its movements and routes, and from these conclude on the representation of the environment by that the animal [51, 55]. In the latter procedure of following a freely moving animal, familiarity with a specific place is represented by repeated visits to that place. Indeed, Wise [61] suggested that *"the space through which we move and interact, home and elsewhere, is made up partly through habitual action, and is bodily space as well as cognitive one"*. Locomotor behavior is, apparently, a tool in assessing the degree of familiarity or learning a route, as described by Konrad Lorenz [36] (p.126): *"it is noticeable that the animal moves along much faster whenever it is repeating what it has already learned"*.

The open field is the most common tool in animal psychology [57]. It is a relatively simple environment, constructed of a table (with cliffs as boundaries) or enclosure (with walls as boundaries). When a rodent is introduced into an open field, it soon establishes a home base - a location from which it sets out to round trips in the environment. At the home-base location, rodents

display typical behaviors: they stay there for extended periods and display a high incidence of grooming, crouching and rearing [18]. Round trips to the home base are carried out in a typical form: the outbound segment of the trip is slow and comprises frequent stops, whereas the inbound segment frequently takes the form of a direct and fast shortcut through the center back to home-base location. This behavior was nicely described by Konrad Lorenz ([36]; p.119): *"Exactly as mice and many other small rodents would do under similar conditions, the shrews interrupted their careful exploration of their new surroundings every few minutes to dash wildly back into the safe cover of their nest box. The survival value of this peculiar behaviour is evident: the animal makes sure, from time to time, that it has not lost its way and that it can, at a moment's notice, retreat to the one place it knows to be safe"*. It should be noted that 'home base' relates to a behavior which is superimposed on a specific location, typically near a salient landmark. In other words, it is the behavior, and not necessarily the physical structure that makes a corner a home base. This is reminiscent of home definition in humans, which is based on the way of using the house and not on its physical properties [61].

Home base behavior as a process of learning and settling in an unfamiliar environment was demonstrated in numerous studies and with various species [1, 2, 14, 16-18, 28, 62]. Nevertheless, little is known on the procedure of establishing a home base, except that it is typically established at a distinctly featured landmark [2, 14, 28, 35, 52]. In an illuminated empty arena the corners stand against the background and are the salient spatial cue. Therefore, the home base is typically located at a corner [17, 18, 28]. However, establishment of a home base in the illuminated arena is almost immediate, making it hard to characterize the settling process.

The present study was conducted in a dark open field, under the presumption that the lack of visual cues will extend the duration of settling. Indeed, in a previous study we found that when jirds (a species of gerbil) were introduced for 10 minutes into a dark arena, they did not establish a home base, rather they explored the arena in a mechanism termed 'looping' [62]. In looping, the animal travels slowly in circular paths that progressively spread over larger areas with only momentary and sporadic returns to certain places. Looping however, was not a result of lacking the ability to return (navigate) in the dark to a certain place since rodents are capable of returning to a starting point in

dark [15, 20, 37, 60], and may do that repeatedly [55], probably by using dead reckoning or scent marks. We assumed that looping is an exploration mechanism in a pattern of scattered, seemingly chaotic behavior [62]. A looping-like traveling or flying pattern was described in insects and suggested as an effective low risk strategy of searching for suitable habitats [3, 11, 12]. These studies suggest that looping may serve as a model-case for learning a new environment, especially under poor visibility [11].

In light of the above studies we assumed that if rodents (jirds) would be exposed to a dark arena for an extended period (compared with the 10 minutes of [62], they may gradually switch from looping to home base behavior. Accordingly, the present study was designed to expose jirds to a dark arena for 50 minutes in order to deduce from the structure of their routes how they gradually learn and obtain a spatial representation of the arena. This structure could then serve as a heuristic ground in unveiling the underlying mechanisms of navigation and of spatial information processing.

MATERIALS AND METHODS

Animals:- Tristram's jird (*Meriones tristrami*), a nocturnal rodent of the Gerbillidae family was used in this study. It is a burrow dweller rodent, feeding mainly on green vegetation and seeds [40]. Twenty-one adult male jirds were obtained from captive colonies at the *I. Meier Segal's Garden of Zoological Research* in Tel-Aviv University, and were housed in 120cm x 63cm x 45cm cages, located outdoors under natural temperature and light conditions. Overturned ceramic pots and wooden boxes were located inside the cages to provide shelter. The jirds were provided daily with fresh vegetation, seeds and rodent pellets. At all times, animals were maintained and treated according to the guidelines for animal care and use of animals in research (permit L-05-048).

Apparatus:- The open-field was a 200 x 200cm arena with 50cm high walls of opaque plexiglas and a white linoleum floor. The arena was located in a quiet, light-proofed and air-conditioned (24°C) room. According to the specific test, the room was illuminated with either: 1) two 300W light bulbs directed to the white ceiling in order to provide diffused illumination of the arena ('light' test); or 2) two infrared lights (*Tracksys*, IR LED Illuminator; UK) with 830 nm filters that emit light not visible to animals, and are known as 'covert' IR ('dark' test). We were not able to find direct information on spectral sensitivity in jirds, but in rats it is known to be limited to 510nm [43], well below the infrared filter that was used here. A video camera (Ikegami B/W ICD-47E) was located 2.5m above the center of the arena, providing a top view of the arena. The video signal was recorded onto a VCR (JVC HR-J737). When testing with lights on, room structure was visible to the jirds, providing various landmarks (e.g. location of monitor, closet, door, etc.). In dark testing the room was in complete darkness, and all light sources (e.g. indicator lights of video, camera, air-conditioner, etc.) were sealed by opaque tape.

Procedure:- Ten hours before testing, jirds were housed in pairs in 33x39x16cm plastic cages with a metal mesh lid, containing sawdust and fresh vegetables. Jirds were then marked on the rear or front with a black ink marker to facilitate video tracking. The ink mark faded after 24 hours and did not seem to harm the jirds or change their behavior. Observation took place during the early hours of the dark phase of the 24 hour dark-light cycle, which are the peak-activity hours in jirds [40]. For testing,

a jird was removed from the cage into a jar, then gently placed into the center of the open-field, and videotaped for 50 min. Each jird was tested in two successive nights, being assigned to one of the following three test groups (n=7 in each group): *Dark-Light group*: tested first night under IR light, and in the following night under white light; *Light-Dark group*: tested first night under white light and in the following night under IR light; *Dark-Dark group*: tested first night under IR light and in the following night tested again under IR light. At the end of the experiment, the jirds were returned to their original breeding colony.

Data acquisition and analysis: For analysis, the arena was divided to 25 equal squares (40x40cm each). Data were then acquired by *Ethovision* tracking system (Noldus, NL), which provided the following parameters at 0.08 sec intervals (12.5 frames per second): i) *X-Y coordinates*: described the location of the center of the jird's surface; ii) *zone*: the name of zones in which the above X-Y coordinates were located; iii) *traveling distance (m.)*: the distance traveled during the 0.08 sec interval; and iv) *momentary speed (m/sec)*: the traveling speed during the 0.08 sec interval. Behavioral changes in the course of the 50-min observation period were described at 10-min intervals. After tracking, data of location per frame were exported to *Microsoft Excel* program. The above parameters then underwent further processing in order to accurately distinguish between locomotory (progressing) and non-locomotory (stopping) periods (see Appendix I).

After processing the data, behavior was comprised of progression intervals with each interval abided by stops. In the present analyses we only used the number, length and location (zone) of stops longer than 3 sec. This margin in stop-length was decided on and validated by observing the tracks, since stops shorter than 3 sec could reflect brief pauses during progression or changing direction. The sequence of stops and progressing intervals was then analyzed by a custom-designed program, *PathAnalyzer* (by E. Zadicario) to classify loops, home base and round trips, as follows:

Loops: As previously described [62], jirds explore a dark open-field by 'looping', based on returning to a recently traveled place (the 'node' of a loop-shaped path), and in the next loop return to another recently traveled place (another node). By manually screening the paths in *Ethovision*, we scored the duration (sec) and distance traveled (m) in the shortest and longest loops. These

minimum and maximum values were then fed into *PathAnalyzer* which calculated the number of loops, their start and end time, the X-Y coordinates of their closing point (nodes), their duration (sec), length (m) and location (zone). For more details see [62].

Home-base: Identification of home-base formation was assessed at 10-min intervals for each jird via *PathAnalyzer*. For each interval, a zone was defined as a home base according to jird's activity as assessed by: 1) spending extended time at that zone; 2) taking round trips in and out of this zone; and 3) performing at least some of the returns to the zone at high speed (running). If so, the jird was considered to have a home-base at that zone during that interval, and the establishment of a home-base was independently reassessed for each 10-min interval. It should be noted, that the location (zone) of the home base could change between intervals.

Round trips (Trips): Were defined as leaving the home base and traveling in the arena until returning to the home base. After scoring for the presence of a home-base in each 10-min interval, we identified the start and end time of round trips, and the number of trips in each interval. Conceptually, trips may be viewed as loops that share the same node – the home base. Round trips may also contain 'nested loops' in which the jird returned to a recently traveled place within its path, before returning to the home base.

As implied in the above definitions, in 'looping' the jirds returned only 1-2 successive times to the same node, whereas in round trips they repeatedly returned to the same node at least three times (Figure 1).

Figure 1

Statistics:- Repeated-measure ANOVA was used for comparisons (see specification of test structure in 'Results'). No transformations were required since data did not deviate from normal distribution (Kolmogorov-Smirnov test for normal distribution). Since the four tested parameters were not strictly independent, a Bonferroni correction was used, and α level was set to 0.012 (0.05 divided by 4 parameters).

RESULTS

Overall activity: - Figure 2a describes the overall distance traveled by the jirds in light and dark tests. As shown, there was no significant effect of testing order (Three-way ANOVA, between-group factor; $F_{1,12} = 0.13$, $p = 0.73$). However, traveling distance was consistently greater in dark compared with light test (Three-way ANOVA, first within-group factor; $F_{1,12} = 44.2$, $p < 0.0001$). Traveled distance was high and did not decline when jirds were tested twice in dark (Two-way ANOVA, between-group factor; $F_{1,6} = 3.23$, $p = 0.123$). In all, traveled distance in dark tests was more than three folds higher than in light tests, and this high level was preserved regardless of testing order.

Traveled distance significantly decreased in the course of the 50 minutes of the observation (Three-way ANOVA, second within-group factor; $F_{4,48} = 112$, $p < 0.0001$). Figure 2b describes traveled distance in 10-min intervals. As shown, traveled distance in the dark decreased to a level that was similar to the initial level seen in light tests (see matching levels in last dark interval and first light interval). These results indicate that light or dark test conditions had each a typical level of activity that decreased over time, that these levels were not affected by a previous exposure to the test apparatus in the dark or light (Figure 2b), and that light level started at the ending level of dark.

Figure 2

Decreased activity involved an increase in the total stopping time as accumulated in stops longer than 3 sec. While stopping time in the dark was shorter compared with light tests (Three-way ANOVA, first within-group factor; $F_{1,12} = 41.66$, $p < 0.0001$), over time, stopping time increased both in dark and in light tests (Three-way ANOVA, second within-group factor; $F_{4,48} = 39.88$, $p < 0.0001$). This increase was not affected by testing order (Three-way ANOVA, between-group factor; $F_{1,12} = 0.007$, $p = 0.93$). However, stopping time in the dark was non-significantly different when the jirds were tested repeatedly in the dark (Two-way ANOVA, first within-group factor; $F_{1,13} = 6.13$, $p < 0.048$).

In the dark, the jirds traveled in relatively slow and continuous bouts, whereas in the light they also moved in relatively high-speed traveling segments (Figure 3). The lower traveling speed was consistent during dark tests (Two-way ANOVA, within group factor; $F_{4,48} = 0.14$, $p = 0.965$); that is,

mean speed did not change over time. However, traveling speed in the dark was higher when jirds were first tested in light and then in dark compared with those tested first in dark (Two-way ANOVA, between group factor; $F_{1,12} = 9.43$, $p < 0.0097$). Thus, jirds traveled faster in the dark when they previously gained visual familiarity with the arena, whereas without that visual experience, they traveled at slower speeds.

Figure 3

Spatial distribution of activity: - Light and dark tests differed not only in activity level but also in the distribution of activity in the arena. Behavior of jirds in the arena with lights on was characterized by spending extended periods of time in one zone, typically a corner (Figure 4a), noted as early as the first 10-min in light tests. Testing in dark revealed a different pattern, with the jirds initially spending equivalent time at various arena zones. They then gradually shifted toward spending longer time in one zone, as in light tests (Figure 4a). These patterns of distribution were typical to light condition, regardless of testing order and without apparent effect of previous exposure to the arena either with lights on or off.

To quantify the concentration of activity in a few zones we ranked zones from high to low according to the time spent in each, and counted the number of zones that accumulated 50% of the overall time in zones. As shown in Figure 4b, the initial number of zones in the dark was about 8-10, and declined in the course of observation to 3-5 zones. In contrast, the number of zones that accumulate 50% of the overall time in zones in light tests was less than 2, and remained steady at this number throughout observation. In all, in the dark, the initial homogenous distribution of time-in-zone progressively changed to the pattern that characterized activity distribution in light.

Figure 4

Time in zone usually converged to the same particular location of the arena. In Figure 5, the duration of time in each zone is depicted for successive 10-min intervals. As shown, in the light test one zone dominated the other zones in all time intervals. In the dark test, time was initially spent evenly at various zones of the arena, and then gradually became longer and converged to the corner zones. Later on, time spent in one of these corners was extended, and by the end of 50 min dark test spatial distribution was reminiscent of that seen in light tests.

Figure 5

Figure 6 provides another illustration of the gradual convergence of time to one locale in dark tests compared with an instant convergence to one locale in light tests. Activity in light consisted of relatively long stops that converged to one or two zones. Activity in dark started with relatively short stops that were scattered over the arena. Stops then gradually became longer and converged to a few zones, and by the end of 50-min dark test, the spatial distribution of stops was reminiscent of that seen in light tests. In the repeated dark tests, convergence to one locale was faster than in the first dark test. In fact, repeated dark tests resembled more the light than the first dark test (Figure 7).

Figure 6 & 7

Spatial organization of activity: - In light, activity was almost immediately organized in relation to one of the corners, where a home base was established (Figure 5,6,7) and was a terminal for round trips to the arena. Since activity declined with time (Figure 2b), the number of trips also declined over the 50-min test. In dark, however, spatial organization was initially based on ‘looping’ with seldom trips (Figure 7, left), but then gradually changed to match the light pattern which is organized in relation to a home base (Figures 5,6,7). Indeed, in the dark-light group, the first 10-min interval was solely based on loops and did not include trips (Figure 8a). In subsequent 10-min intervals, the number of loops decreased in parallel to an increase in the number of trips. By the last interval (50 min) the number of trips matched that seen in the 20-min interval of the light test of the same jirds (Figure 8a). In other words, the number of loops diminished by the end of the dark test, and most jirds formed a home base in one of the corners, using it as trip terminal (Figure 8).

Figure 8

A decrease in the number of loops was also observed in the dark tests of the light-dark group (Figure 8b). As opposed to the dark-light group, this group had in average four trips in the first 10-min interval, with fluctuation around this average in subsequent intervals. Therefore, there was a substantial difference in the first 10-min interval between jirds that were previously exposed to the arena with lights on (light-dark group) compared with jirds lacking such experience (dark test in dark-

light group). Accordingly, all seven jirds in the light-dark group established home base by the end of the dark test, compared with only five of the dark-light group (Figure 9).

A decrease in the number of loops was also observed in both tests of the dark-dark group (Figure 8c), yet the average number of loops was initially lower in their second dark test. As in the dark-light group, the number of trips increased in the two tests of the dark-dark group. However, in terms of establishing home base, previous exposure to a dark arena had the same effect of exposure to the arena with lights on. Accordingly, all seven jirds in the second dark test established a home base by the end of the test, compared with only five in the first test of the dark-dark group (Figure 9).

Figure 9

Discussion

When introduced into a dark arena, jirds first used 'looping' - an exploratory mechanism based on slow and continuous entwined paths and seldom returns to one location. They then gradually substituted looping with another form of exploration in which behavior is based on repeated visits to the same location - the 'home-base'. In terms of progression paths, looping comprised loops that closed at different locations, indicating that behavior was not firmly linked to the environment. Home-base behavior, on the other hand, was based on repeated returns to a particular place, indicating a strong coupling with the environment. In the following discussion we describe how the gradual transition from looping to a behavioral mode in which routes are anchored in one place (the home base) represents recruitment of more composite forms of navigation. We propose that this shift is a part of a process of recruitment of navigation mechanisms via a transition from sequential, to parallel and ultimately to continuous processing of spatial information.

Looping precedes the establishment of 'home base'

Exploration in dark gradually changed to a form which is reminiscent of exploration in a lit arena. Initially, behavior in the dark was not organized in relation to a specific place, and therefore, there were neither repeated visits to the same particular place, nor a convergence of round trips to one place. Gradually, distance traveled decreased and stopping time increased, reaching activity levels similar to those measured in light. Spatial distribution of activity also changed, with more time spent

in one zone (typically a corner) to which round trips converged in increasing number, in parallel with a decrease in looping. Altogether, these changes ultimately led to a pattern of behavior in the dark which is reminiscent of home base exploration seen in light.

Home base is typically established at a distinctly featured landmark [2, 14, 28, 35, 52]. In a lit empty arena the corners stand against the background and are salient spatial cues. Indeed, exploration in a lit arena converged to a home-corner almost immediately, whereas behavior in the dark was first comprised of loops without repeated returns to the same location. The delayed emergence of home base behavior in the dark indicates that it is not exclusive to a lit environment. Rather, looping is probably an initial phase of accumulating spatial information which is necessary to establish a home base in the lack of visual spatial information. This notion is further supported by past observations on behaviors reminiscent of looping, in animals searching for a home, a den, or an adequate habitat [3, 11, 32, 59, 60]. Furthermore, looping as an initial exploration phase may rely on different navigation mechanism compared with the subsequent 'home base' phase.

Navigation mechanisms in looping and in home base behavior

Spatial behavior relies on external cues and on internal cues. External cues are compass, trails and physical features of the environment (landmarks), whereas internal cues, such as vestibular and kinesthetic sensations, are generated during self-movement of the animal. Together, these cues provide animals with means to find their way and organize their progression in time and space [44]. Relying on spatial relationship of external cues is termed piloting [26, 44] whereas relying on self-generated cues is termed dead-reckoning [21, 25, 41]. It was suggested that during home-base exploration, rodents pilot in the outbound segment, but in the homeward segment of the round-trip, they either pilot or dead-reckon [35, 60]. Piloting in the outbound segment of round-trips is preserved even in the dark [35], indicating that rodents construct the outward segment on landmarks (objects, odors). The return, however, is by piloting when the home-base is at a salient location, and by dead reckoning in the lack of landmarks [22, 23, 25, 41, 56, 60]. Indeed, the outbound segment of round trips is relatively slow and interrupted with many stops whereas the inbound segment is faster, more

direct, comprising fewer stops and typically taking the form of a short cut through the center of the open field to home base [13, 17, 18, 30, 52, 56].

'Looping' was observed immediately after introducing rodents into a dark arena, when the use of spatial cues was practically limited and dead-reckoning was probably the main navigating method. Later on, when the rodents shifted from 'looping' to 'home base' behavior, they might have been also relying on landmarks. A possible interpretation is therefore that 'looping' is a phase of scanning the environment for non-visual spatial cues and perhaps depositing scent marks. These cues are then integrated with dead-reckoning and used in subsequent piloting from and to the home base location [27, 34]. In other words, landmarks are identified or formed during looping, enabling a gradual incorporation of piloting into exploration and acquiring spatial information on the layout of the environment and on a favorable location (i.e. – a corner) for home base. Thus, shifting from looping to home-base behavior probably reflects a transition from navigation based on dead reckoning to a landmark-based navigation.

Dead reckoning is inaccurate since it accumulates positional errors [25, 41, 42], and an obvious way to decrease the uncertainty is to re-initialize it periodically, which means that the animal has to return to the beginning of path computation. In looping, the return to the initial point occurred once or twice since successive loops are based on different starting points and behavior does not seem to be anchored to the physical structure of the environment. Then, repeated visits to the same place characterize the establishment of an arbitrary home base (arbitrary but recognizable visually, olfactorily, etc. as well as by the fact that it more or less coincides with the zero of dead reckoning) providing the animal with more accurate means in navigating either by dead reckoning or piloting [17]. Similarly, spatial representation, as reflected by place cell activity, is unstable when based only on internal cues, and is stabilized with dependence on external cues (e.g. scent marks, visual cues) [47]. Moreover, studies have shown that when external and internal cues present conflicting information, rodents favor information provided by external cues [21, 22, 37], implying a preference for piloting over dead reckoning. Thus, the transition from looping to home base behavior represents a shift from relying on internal cues to relying on external cues that are potentially more reliable.

The role of home base in navigation and exploration is comparable with the role of a nest or den. Accordingly, it was suggested that animals initially locate external cues with respect to their dead reckoned position and in relation to some environmental anchors, which in nature would be the nest or burrow [19, 27]. The similarity in the form of behavior prior to establishing a den or nest and in looping [3, 11, 59, 60] may indicate that looping is a phase in which the animal explores the area in order to gain spatial information for the establishment of home base. Once established, the home base may then serve as a stable element of the environment within the open field, which the animal may use in learning the configuration of objects in the arena [46]. In a lit arena, the distant panorama is stable and provides an orienting framework into which landmark and home base location can be placed [45, 58]. In a dark arena, however, visual distal panorama is not available, and it takes more time to establish a home base location as an organizer of motor behavior. The preceding looping phase may also serve in acquiring information on the geometry of the enclosure (open field), followed by acquiring nongeometric information (e.g. – scent marking) which is coordinated with the reference frame provided by the geometry [6, 54]. Finally, [39] described that when a landmark was located near a route along which rats were trained to travel in their way to a goal, the rats used to reach the landmark and touch it, despite the additional cost of traveling greater distance compared with direct travel to the goal. [39] referred to similar phenomena in ants, and presumed that breaking the journey into two shorter and more accurate segments, leaving less room for errors. Stopping at a specific location such as the home base may as well serve in increasing trip accuracy. Therefore, the apparently more accurate nature of piloting (compared with dead reckoning) along with the opportunity of resetting the path at the home base may be the advantage of shifting from looping to home-base behavior.

The 'parallel map theory' as an explanation for shifting from looping to home base behavior

The organization of activity in time and space is an obvious constituent of animal cognition [26]. Tolman [53], a cognitive behaviorist, suggested that both rats and humans navigate with the aid of a cognitive map, which is constructed and updated during locomotion. Further studies [44] suggested that navigation is based on two paradigms: a taxon system for route navigation and a locale system

for map-based navigation, with the space represented in the hippocampus in the form of a cognitive map. Despite being criticized [5, 38, 49, 54], the ‘cognitive map’ has remained a leading concept in animal cognition studies. In a seminal account on navigation, Jacobs and Schenk [33] suggested two parallel functions that merge together to form spatial representation: a *Bearing map* which encodes directional cues and a *Sketch map* that encodes positional cues. Accordingly, environmental cues may be directional (e.g. compass), polarizing the navigator's environment rather than identifying a specific location. Other cues are positional, used to deduce distances and directions of a specific location in the environment [33]. The bearing map is suggested to be phylogenetically ancestral, since vertebrates evolved in aquatic environment in which there was a limited capacity of visual and auditory processing. In such environment, directional cues such as chemical, magnetic, or light gradients allow animals to navigate through an unknown environment by forming a one-dimensional map (= gradient or integrated path) [33]. In contrast, the sketch map is based on positional cues that provide distances and directions of a specific location in relation to positional cues (landmarks). The present results on transition from looping to home base behavior may reflect a shift from directional to positional spatial representation. Specifically, looping in a dark environment may facilitate animals in establishing initial familiarity with the environment by using directional information such as idiothetic cues or environmental gradients like distance from start point, odor or background sound. They may then recruit specific landmarks (scent markings which they deposit or physical structures such as walls and corners), and superimpose these landmarks on the directional representation. The combined directional and positional cues are then utilized to set an anchor in the environment – the home base, which is a location from which the animal sets out for round trips in the environment. In an illuminated open field, when visual information is available, animals skip the looping phase and almost immediately establish a home base at a salient visual landmark [8, 9, 14, 62]. In all, the transition from looping to home base behavior supports the notion of parallel map [33], as if recapitulating the developmental scenario of processing first directional and then positional environmental cues.

Recruitment of navigation mechanisms: a proposed model of transition from sequential, to parallel, and ultimately to continuous processing of spatial information

In the same vein of the above hypotheses on the shift from dead reckoning to piloting, and on parallel processing of directional and positional cues, we propose that spatial learning and navigation is based on three phases of information processing: i) sequential; ii) parallel; and iii) continuous. As an example of these phases, let us assume that a traveler who is not familiar with the US needs to drive from New-York City to Boston. The instructions that he gets are "just follow the signs". Accordingly, the traveler drives from one sign to the next without knowing in which direction he will be moving next (left or right, north or west) except that heading direction will be 'Boston' at the next sign (landmark). This type of navigation is ***sequential information processing***, of traveling from one landmark to the next. A second traveling mechanism may be: "take I-95 North toward Boston". Now the traveler has two sources of spatial information: to go north and to go toward 'Boston' at the next landmark (sign). This is ***parallel information processing*** (the 'north' and 'Boston' signs). Still, the traveler has only these two sources of spatial information, not knowing what is, for example, at the left side or right side of the road, with the risk of getting lost if the north direction is not kept or if missing a sign (landmark). A third traveling mechanism may be map-based navigation in which the traveler is familiar with the road (or following it on a map), with continuous representation (update) of the environment. In this case the traveler knows that 100 miles after New-Haven he will arrive to Providence, where the road to the right leads to Fall Harbor and then Cape Cod, and that 50 miles ahead of Providence is Boston. This is ***continuous information processing***, or map-based navigation which relies on a detailed spatial representation [44], containing "*sets of connected places*" and providing "*a large choice of possible paths between any two points in the environment*" [44]; p. 89). A map, therefore, contains redundant information that allows constant validation of a location, and thus may be regarded as a more stable (accurate) navigation method compared with dead reckoning or piloting. Finally, we suggest the terminology of ***piloting*** for sequential information processing, ***orienting*** for parallel information processing, and ***navigating*** for continuous information processing (Figure 10).

Figure 10

The interpretation of the present results in light of this model will be therefore that in the first sequential phase, the animal is moving from one place to the next. In looping, the place is the node (the starting and closing point of the loop), which upon reaching it (e.g. – by dead reckoning) shifts to another location. Heading direction in that case is momentary and directed toward the node, and is changed once the animal reaches the node. The second phase, of parallel information processing,

emerges when the animal sets a home base. The animal now either dead-reckons or moves from one landmark to the next (e.g. - sequence of stops that characterize round trips ;[29], but this sequence repeatedly ends at the same location – the home base. These two phases are apparent in the present study during the transition from looping to home-base behavior. We presume that later on, the animal may establish additional bases [51] and switch between them. Progression at this ultimate phase will be flexible, representing a high degree of familiarity with the environment with the animal continuously updating its location in relation to a spatial representation. Altogether, we suggest that in exploring and navigating in an unfamiliar environment, animals gradually shift from piloting, to orienting and ultimately to navigating, and that the forms (phenotypes) of these processes are looping, home base behavior, and ultimately free (multi-base) traveling.

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Figure Captions

Figure 1.- Looping and 'home-base' behavior (top), and stops during a loop and a round trip (bottom). In looping (top left), the path comprises a simple loop (a), an 8-shaped loop (b), a 'hybrid' loop that is composed of two 8-shaped loops (c), and another 8-shaped loop (d). In home-base behavior (top right), the path comprises three round trips (a-c) that start and end at the top left home corner. In a loop (bottom left) there is only one stop (o), whereas in a round trip (bottom right) there are numerous stops (o) on the way out from the home base (here located at the top right corner), but the way back to the home base is a short cut through the center without stopping. Few stops characterize loops, whereas many stops on the out segment and a shortcut with no stops on the homeward segment characterize round trips.

Figure 2.- Total traveled distance (meters; mean \pm SEM) is shown for the entire 50-minute observation (**A.**), for light (empty bars) and dark (filled bars) tests. Total traveling distance was greater in dark compared with light (Three-way ANOVA, 1st within-group factor; $F_{1,1,4} = 44.2$, $p < 0.0001$), regardless of testing order (Three-way ANOVA, between-group factor; $F_{1,1,4} = 0.13$, $p = 0.73$). Traveled distance did not decline between repeated dark tests (Two-way ANOVA, between-group factor; $F_{1,4} = 3.23$, $p = 0.123$). Total traveling distance is also depicted for 10-minute intervals (**B.**) for the first test night (left) and second test night (right), with light tests depicted by empty symbols and dark test by filled symbols. As shown, regardless of testing night, traveled distance significantly decreased over the observation period (Three-way ANOVA, 2nd within-group factor; $F_{1,1,4} = 112$, $p < 0.00001$), and by the end of dark observation, traveled distance levels match the initial levels of light tests.

Figure 3.- Frequency distribution of traveling speed (m/sec). Data are presented for the Dark-Light group only, with only two time intervals shown for each testing day: the first 10 minutes (10) and the last 10 minutes (50). As shown, frequency of low speed traveling was greater and high speed traveling was virtually absent in the dark compared with light, both at the first and last 10 minute intervals.

Figure 4.- Distribution of time spent in the zones of the open field. **A)** Rank order of the time (sec.) spent in each of the 25 arena zones. The 25 arena zones were ranked from high to low according to

time spent at each zone. Data is shown for the group tested first in dark and then in light (top), the group tested first in light and then in dark (center), and the group tested in both days in dark (bottom). As shown, when tested with lights on, jirds spent extended time in one zone whereas when tested in dark, they initially did not spend extended period at any one zone. However, in the course of dark testing, time at one zone started to dominate, and by the end of 2nd dark test (bottom row) the rank of time in zones matched that seen in the first light interval (middle of top and center rows).

B) Number of zones in which the jirds accumulated 50% of the time. As shown, this number of zones was significantly lower in light compared with dark tests (Three-way ANOVA, first within-group factor; $F_1 = 48.8$; $p < 0.0001$), indicating that in light the jirds spent most of the time in a few zones, compared with more zones in dark. The number of zones decreased in the course of observation (Three-way ANOVA, second within-group factor; $F_4 = 24.1$; $p < 0.0001$), and by the end of the second exposure to a dark arena reached a level which was close to that seen in light tests. The interaction of light conditions (light vs. dark) and time (five observation intervals) was significant (Three way ANOVA; $F_{1,4} = 14.7$; $p < 0.0001$). The effect of testing order was not significant (Three way ANOVA, between-group factor; $F_1 = 2.6$; $p = 0.13$).

Figure 5.- Spatial distribution of time in zone (sec), shown here for one jird of the Dark-Light group. Each bar height represents the time spent at one of the 25 zones of the arena. Data are depicted from left to right at 10 minute intervals for the dark test (top) and the light test (bottom). As shown, time was almost equally distributed over the various zones at the first 10 minute of the dark test (top left). With time, time spent at the corners increased, and in the last 10-minute interval (top right) there was one corner at which the jird spent most of the time in a pattern similar of what was seen throughout the light test. Indeed, as shown, in all time intervals of the light test the jird spent extended periods at the home corner (bottom row).

Figure 6.- Convergence of stops to the home base, shown in one jird of the Dark-Light group (top) and one jird of the Dark-Dark group. Stops are represented by circles, with the diameter representing the duration: the longer the diameter the longer stop duration. The 25 arena zones are arranged along the y – axis, whereas the duration of observation is the x-axis. Only stops of at least three seconds are

depicted. As shown, stops in the first exposure to the dark are scattered over all zones (both top and bottom left hand graphs) whereas in the light test all the long stops converge to one and the same place (top right graph). Nevertheless, in the second exposure to a dark arena (bottom right), behavior is reminiscent to that seen in illuminated arena, in fact culminating a convergence to one zone which started in the course of the first dark exposure (bottom left graph).

Figure 7.- Paths of a jird in the beginning of a first dark test (left), at the end of a second dark test (center) and at the beginning of a light test (right). As shown, path diverge over the arena in the beginning of the dark test (left) but converge to the bottom right corner in the light test (right). However, behavior at the end of the second dark test (center) is similar to that seen in light (right) than to that seen in beginning of dark test (left).

Figure 8.- The shift from loops to trips. The number of loops (left y-axis) and of trips (right y-axis) as measured in 10-minute intervals are described for the 50 min of testing (x-axis), for the Dark-Light group (A.), Light-Dark group (B.), and Dark-Dark group (C.). As seen in first exposure to a dark arena (top left and bottom left), number of loops decreased and number of trips increased in the course of the session. In light test (top right and center left) there is a decrease in the number of both trips and loops, reflecting the overall decrease in activity over time in light tests.

Figure 9.- The cumulative number of jirds that established home base in each test (y-axis) is described in 10 minute intervals across the testing sessions. As shown, there was an increase in the cumulative number of jirds that established home base during the dark tests (dark symbols), whereas in light tests (clear symbols) all jirds established a home base from the beginning and preserved it throughout the light test session. Nevertheless, all jirds tested in the dark during the second session of the Light-Dark group (■) and of the Dark-Dark group (●; left) established home base toward the end of the test session.

Figure 10.- A proposed model of spatial information processing. In *piloting* (sequential information processing) the navigator travels from one landmark to the next. On the way to A, it still does not know that next it will be going to B, and has no idea in which direction is B. In *orienting* (parallel information processing) the navigator first goes east to A, knowing that when arriving to A it will

proceed east. Upon arrival to A it realizes that eastbound is to B. In *navigation*, the navigator has a representation of the location of A, B, and C in the environment. It could choose any way of traveling between them, but for some reason (e.g., taking the shortest way) it chooses to travel from A to B and then to C.

Appendix I

Distinguishing stopping and locomoting periods in output data of Ethovision

A filtration was required in order to distinguish between periods of locomoting and non-locomoting (stopping) periods, due to the measuring method of Ethovision which is based on identifying the jird's surface area and giving the x-y coordinates of its center. However, if a jird was active during stopping (e.g., rearing on its hindquarters, grooming etc.), its surface area changed, and this change was identified by Ethovision as progression, although the jird was actually stopping (noise data). To filter out this noise, we first observed some of the tracks in Ethovision, and looked for distinct progress and stop intervals, noting the start and end time and traveling distance of these intervals. The filtration process was aimed replacing traveling distances that occurred during stops with zero distance. In other words, we replaced with zero value the small values of traveling distances that reflected the small movements of the animals during stops whenever it matched one of the following:

- Smaller than 0.88 cm/frame
- 0.88 cm/frame, or 1.24 cm/frame values and followed or preceded by 0 cm/frame.
- 1.75, or 1.96, or 2.48, or 2.63 cm/frame values and followed and preceded by 0 cm/frame values.
- Streaks of two 1.75 or two 1.96 cm/frame values and followed and preceded by 0 cm/frame values.

Streaks of three 1.75 or two 1.96 cm/frame values and followed and preceded by 0 cm/frame values.

Figure legends

Figure 1

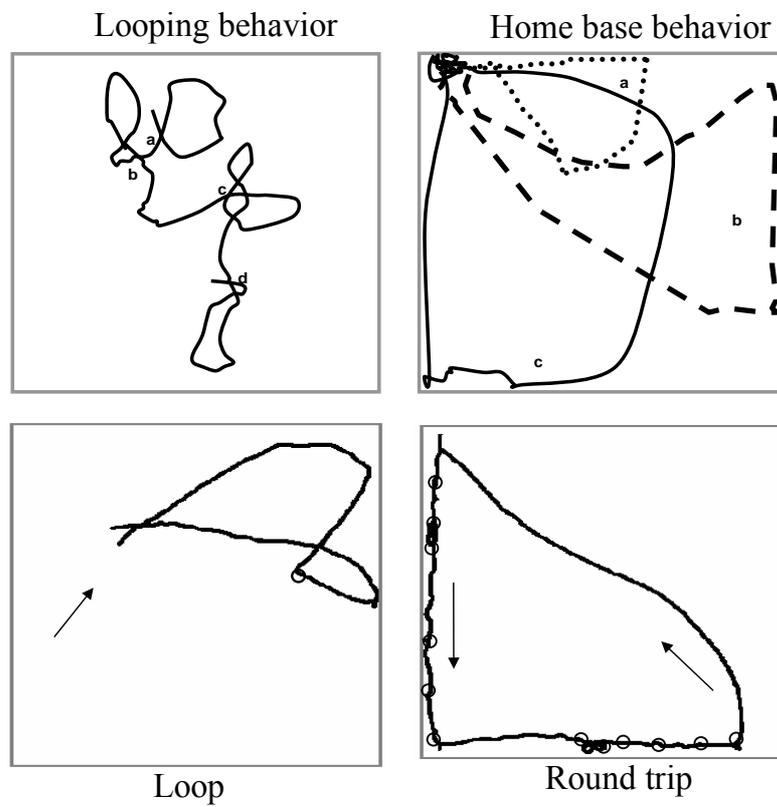


Figure 2

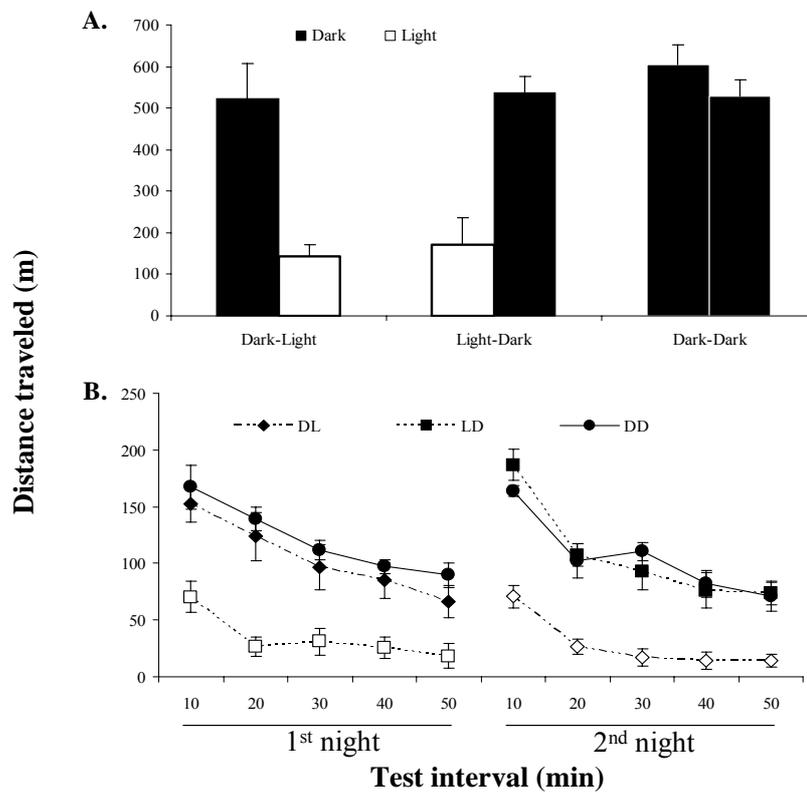


Figure 3

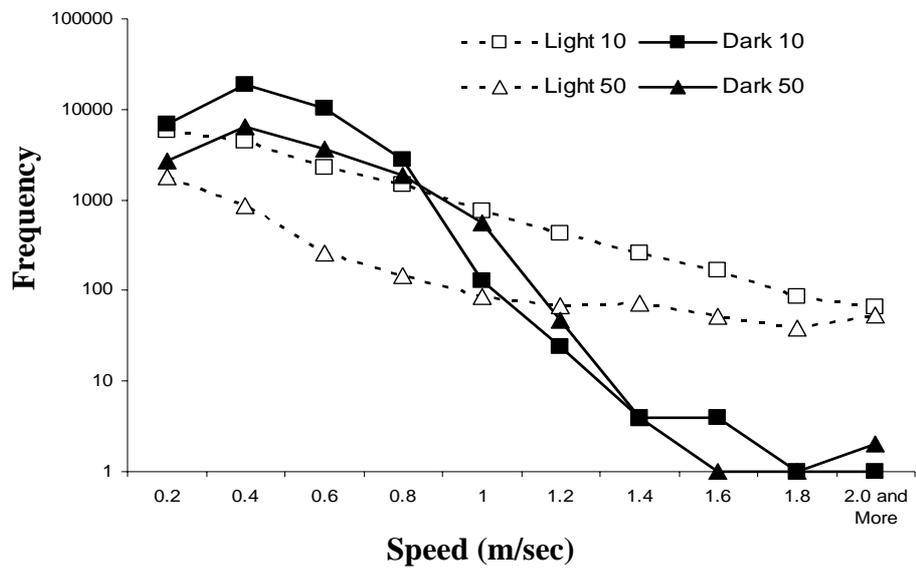
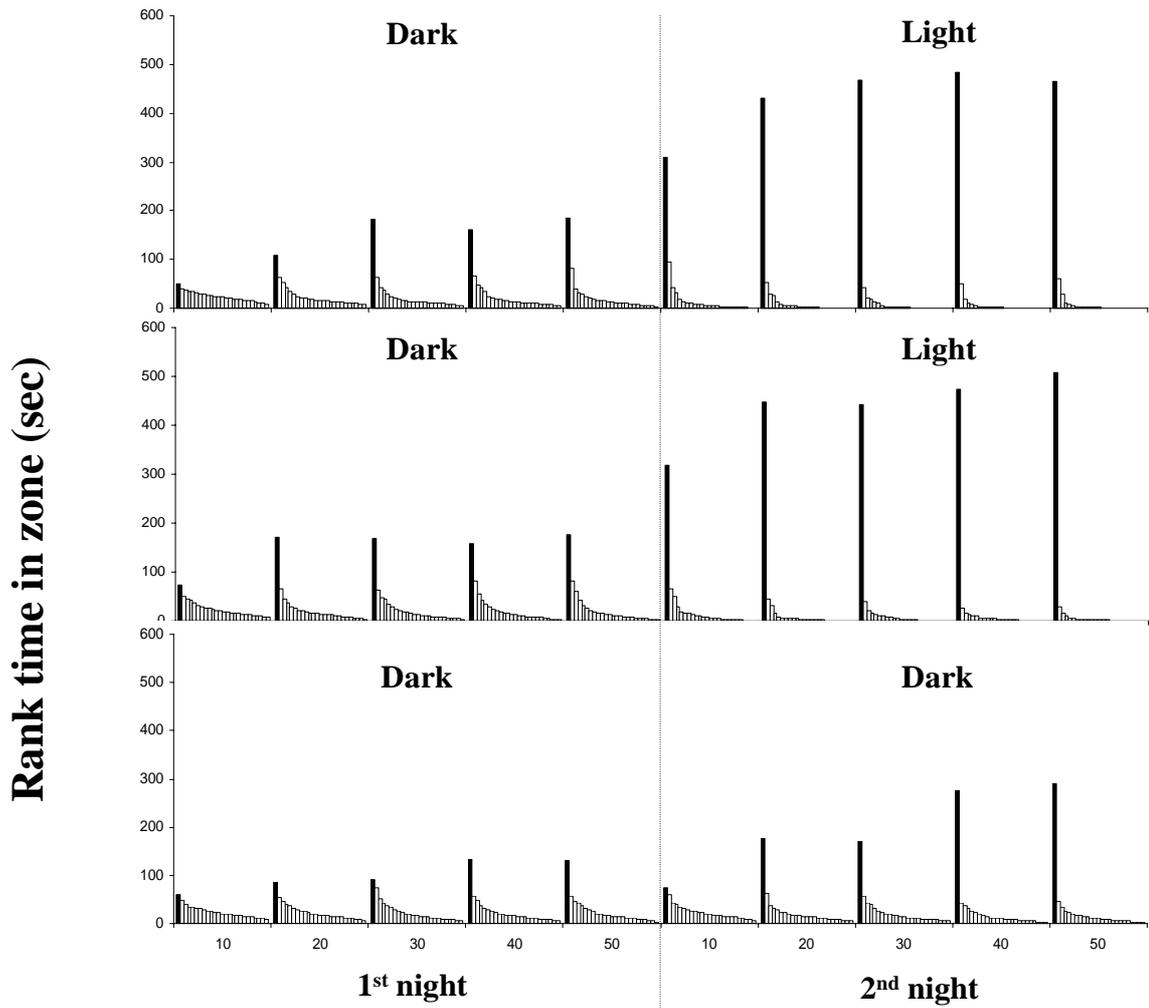


Figure 4

A.



B.

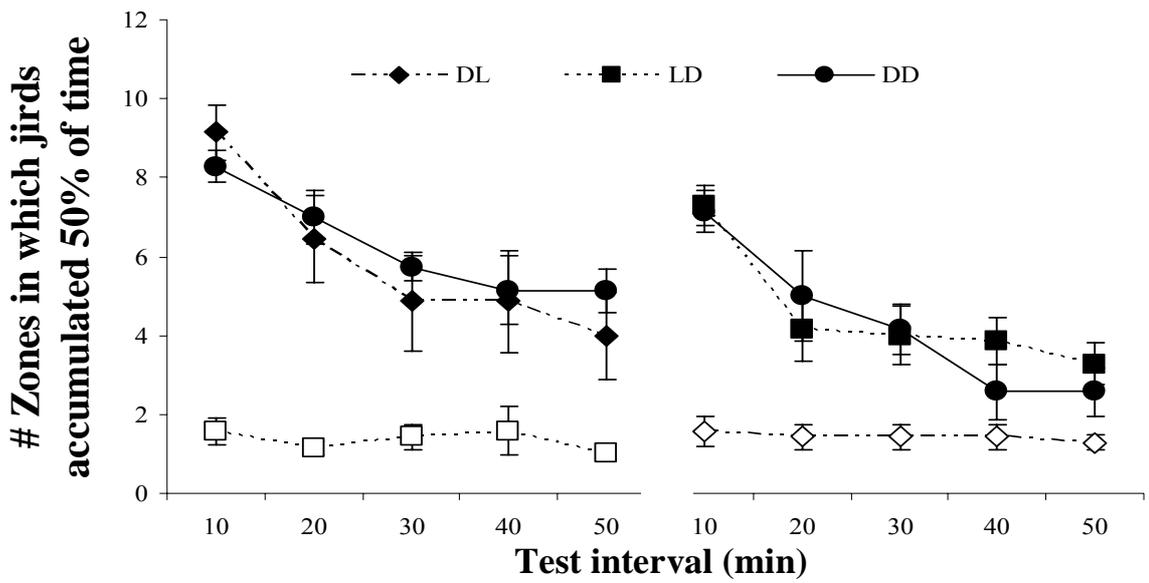


Figure 5

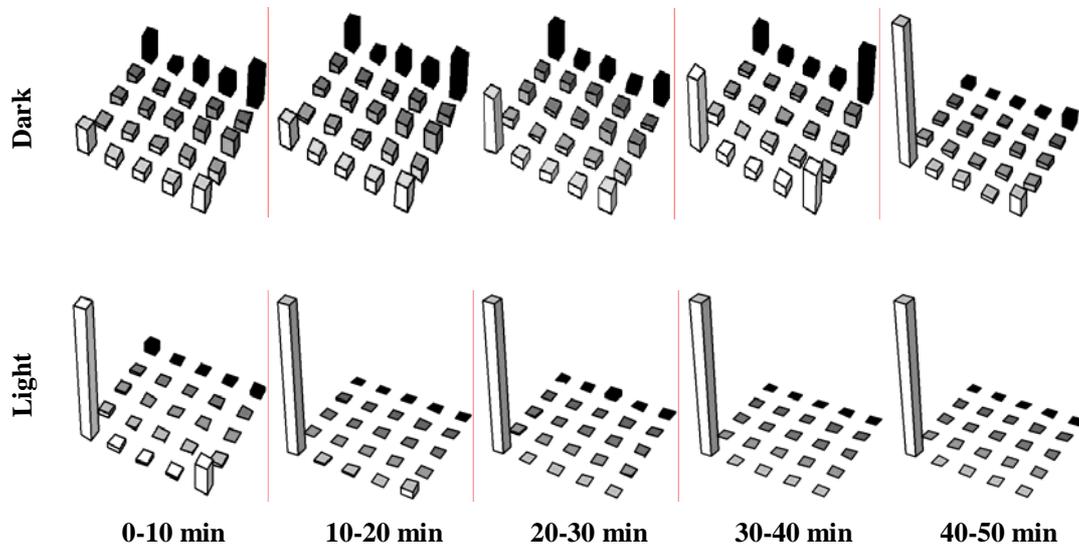


Figure 6

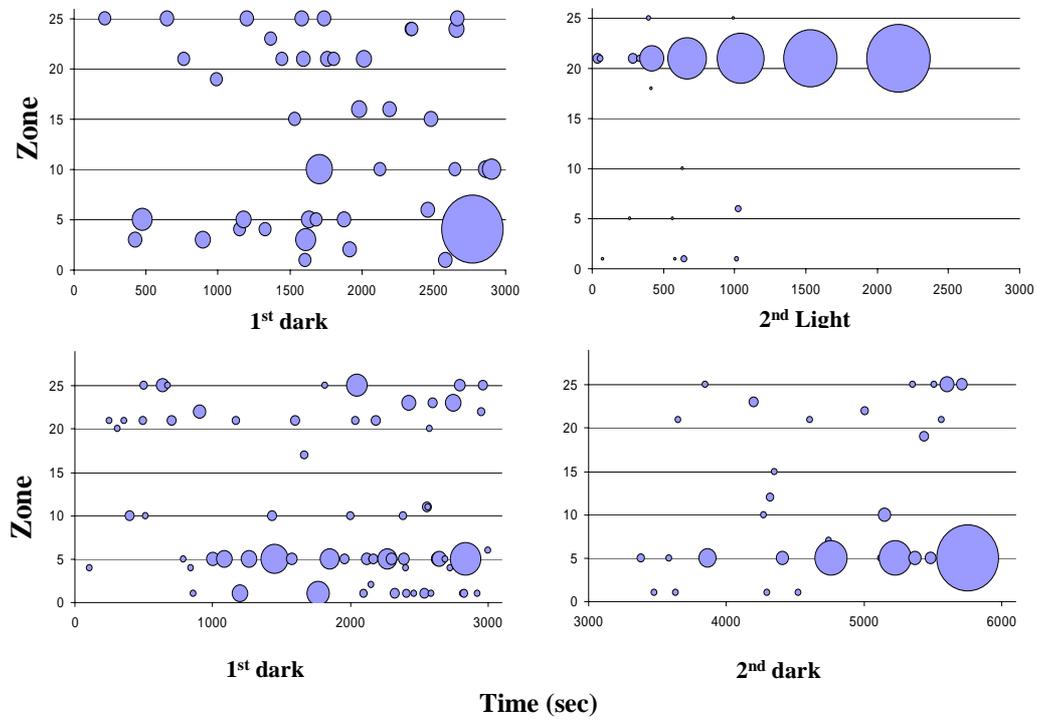


Figure 7

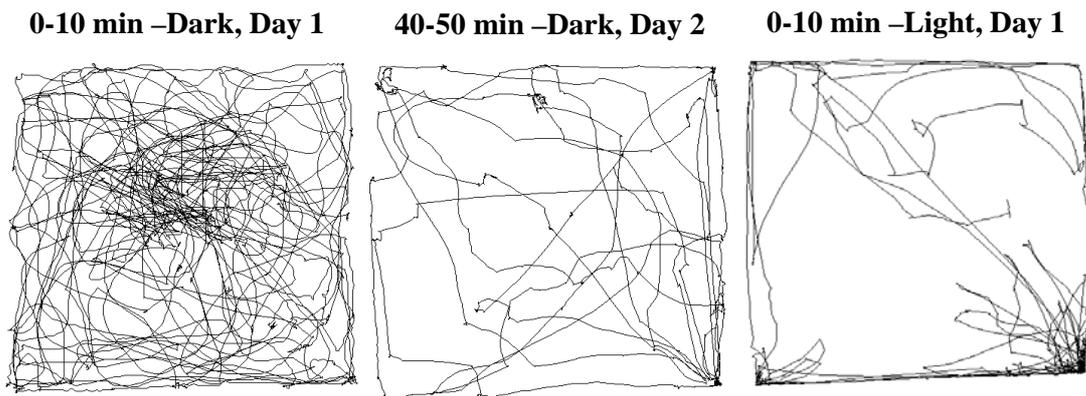


Figure 8

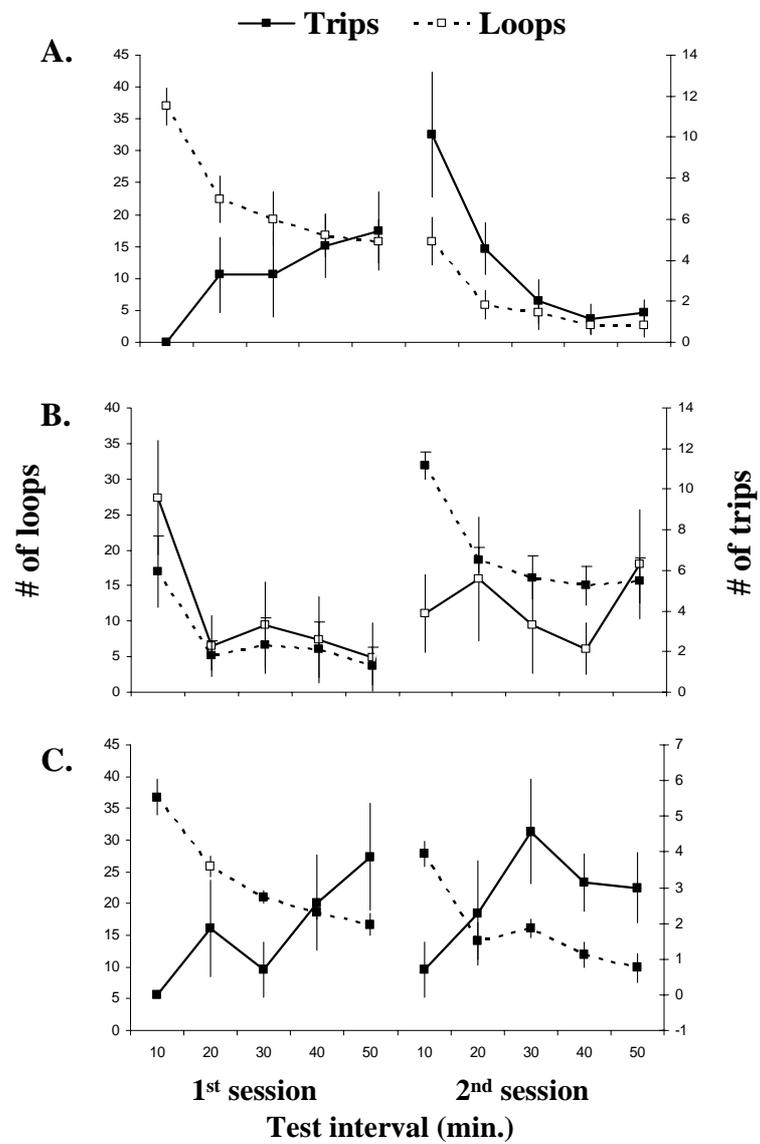


Figure 9

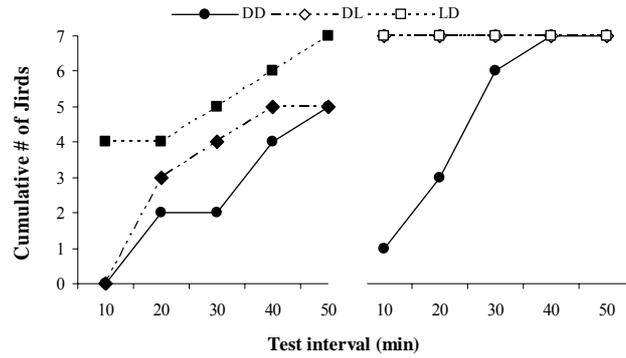


Figure 10

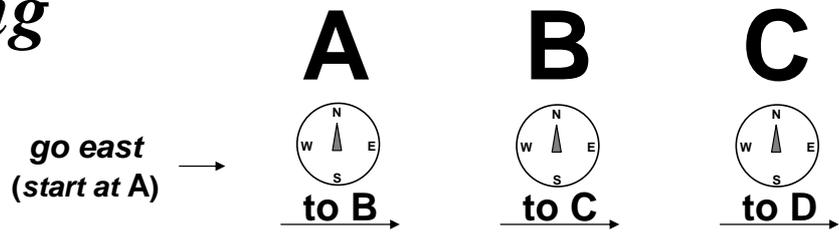
Piloting

(sequential)



Orienting

(parallel)



Navigating

(continuous)

