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The Development of Spatial Capacity in Piloting and Dead Reckoning by Infant Rats: Use of the Huddle as a Home Base for Spatial Navigation

ABSTRACT: *Two forms of spatial navigation, piloting using external cues and dead reckoning using self-movement cues, are manifest in the outward and homeward trips of adult rats exploring from a home base. Here, the development of these two forms of spatial behavior are described for rats aged 14–65 days using a new paradigm in which a huddle of pups or an artificial huddle, a small heat pad, served as a home base on an open circular table that the rats could explore. When moving away from both home bases, the travel distance, path complexity, and number of stops of outward trips from the home base increased progressively with age from postnatal day 16 through 22. When returning to the home bases, the return trips to the home base were always more direct and had high travel velocities even though travel distance increased with age for the longest trips. The results are discussed in relation to the ideas that: (1) the pups pilot on the outward portion of their excursion and dead reckon on the homeward portion of their excursion, and (2) the two forms of navigation and associated spatial capacity are interdependent and develop in parallel and in close association with locomotor skill.*
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Animals may display at least two forms of spatial navigation, piloting and dead reckoning (Gallistel, 1990). Piloting uses allothetic or external cues, e.g., visual, olfactory, or auditory, for both guidance and for constructing representations of the environment (Morris, 1981; O'Keefe & Nadel, 1978; Redish, 1999; Sutherland & Dyck, 1984). Dead reckoning integrates idiothetic or self-movement cues, e.g., vestibular, pro-

prioceptive, and sensory flow, to allow an animal to return to a starting point (Darwin, 1873; Mittelstaedt & Mittelstaedt, 1980; Seguinot, Maurer, & Etienne, 1993; Whishaw & Gorny, 1999).

Both forms of navigation have been documented in the spontaneous exploratory behavior of rats (Wallace, Hines, Pellis, & Whishaw, 2002a; Wallace, Hines, & Whishaw, 2002b; Wallace, Hines, Gorny, & Whishaw, 2003). Rats provided with a home base located in an open environment make progressively longer exploratory trips away from the home base, and each trip is ended with a direct return to the home base. Outward trips are characterized by movements directed toward different points in the environment, and each trip consists of a number of progressions punctuated by stops, during which the animal makes head scans, suggesting that it is inspecting

its surrounding and updating its location. The relatively slow outward progressions are ended by a homeward trip that is direct with high velocity. The characteristics of the homeward trips persists in test situations in which allothetic cues are minimized or are absent, suggesting that the returns must depend upon dead reckoning. Although the presence of a home base provides a focus for exploratory behavior, it is not essential. Rats placed in a featureless environment create one or more virtual home bases from which they make outward and homeward trips (Drai, Benjamini, & Golani, 2000; Eilam & Golani, 1989; Golani, Benjamini, & Elam, 1993; Tchernichovski, Benjamini, & Golani, 1998).

Although there have been no studies of the development of dead reckoning in the rat, there are studies on the development of piloting. These studies have focused on the question of whether piloting to a landmark (proximal cue) or to a place, defined by the relationships between ambient room cues (distal cues), develops sequentially or in parallel. The onset of the behaviors have been placed together as early as Day 18 postnatal (Brown & Whishaw, 2000) and sequentially as late as Day 20 (Rudy, Stadler-Morris, & Albert, 1987), Day 22 (Rudy & Paylor, 1988), or Day 26 (Schenk, 1985). The difficulty in fixing the developmental onset of piloting relates to a number of factors including the maturation of locomotor ability, the method of motivating an animal's behavior, and the construction of the testing situation. Most previous developmental studies have used spatial swimming pool tasks (but see Rossier & Schenk, 2003). The swimming pool task has positive features in that infant rats can swim well and are motivated to escape from the water but has drawbacks in that it is difficult to control stress, fatigue, and body temperature over the series of training trials required to demonstrate task acquisition. Also, the swimming pool task does not reveal the richness of spontaneous behavior displayed by rats in open field exploratory tests.

The objective of the present study was to develop a more naturalistic paradigm for the study of spatial behavior in infant rats, and one that would be similar to the paradigms used to investigate piloting and dead reckoning in adult rats. The study was based on findings that infant rats form a huddle to assist in maintaining body temperature during a formative period of their development (Alberts, 1978a,b, 1994). Rat pups in a huddle have a rich repertoire of behavior including orienting to their mother and her nipples (Alberts, 1978a; Freeman & Rosenblatt, 1978; Kenyon, Cronin, & Malinek, 1981; Larson & Stein, 1984; Moltz, 1971). The present study examined how rat pups initiate exploratory behavior in relation to the huddle and how exploratory behavior develops. Litters of pups were placed upon a large circular table for daily tests and their behavior was video recorded. To minimize thigmotactic behavior, the open field had no walls. To control for

the use of visual cues for homeward guidance, litters were also tested in the dark. To control for use of auditory cues or odor cues from litter members, individual animals were tested with a small heating pad serving as a surrogate huddle.

METHODS

Subjects

Litters of Long–Evans hooded rats varying in age from 14 postnatal days to 65 postnatal days were used as subjects. The date of birth was recorded as Day 0. When not undergoing testing, the rats were group housed with their littermates and dam in clear, hanging cages ($45.4 \times 24 \times 19.5$ cm high) with sawdust floors. Food and water were available ad libitum in the cages. Rat pups older than 25 days had been weaned and sexed. The housing room was maintained at a temperature of $20–21°C$ and lighting was a 12-hr light, 12-hr dark cycle. All behavioral testing occurred during the light cycle.

Open Field

The open field was a wooden circular table, painted gray, 151 cm in diameter, and elevated 10 cm above the floor (Figure 1). The room normally contained a variety of visual cues including a chair, a bookcase, a tripod, etc. After each test of a litter, or pup, the open field was washed with soap and water.

Heating Pad

The heating pad was made from a coil of surgical tubing covered in fabric so that its size was 6×5 cm. The fabric was black to make the heating pad a salient visual cue. The surgical tubing was attached to a water pump so that warm water ($37°C$) could be pumped through the pad.
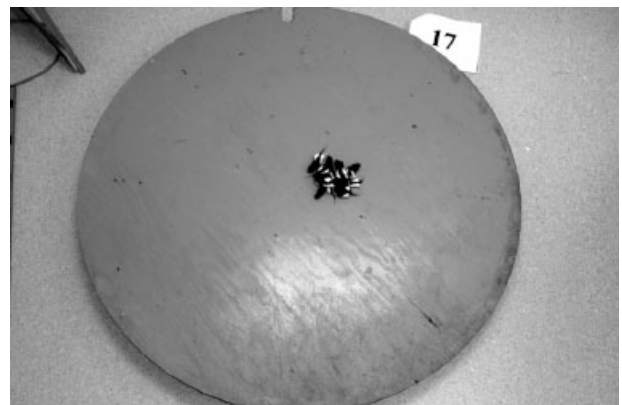

FIGURE 1 The test apparatus consisted of a circular table upon which a litter of pups were placed. An overhead camera was used to film the animals' movements.

Cues

Refuge. The refuge was a cardboard box (home base) measuring $16.5 \times 17 \times 11$ cm high with one open end. The box was placed at the edge of the table with its open end facing the center of the table.

Proximal cue. The proximal cue was a black box measuring $42 \times 48 \times 82$ cm high located 50 cm away from the edge of the circular table, with its ventral surface at the level of the circular table.

Thermal gradient. A thermal gradient was produced by placing a 23 cm diameter tin cake pan, filled with boiling water and covered with tin foil, on the circular table.

Heat source. A 250 W light was placed 62 cm over one edge of the field and remained on during the test session producing a heat gradient with a $37°C$ focal point at the table's edge.

Infrared Testing

The room was light proof for infrared testing, a wavelength to which rats are not sensitive (Neitz & Jacobs, 1986). Infrared light was reflected from two emitters onto the room walls to produce even lighting over the table. The experimenter wore infrared goggles in order to place the animals on the circular table.

Movement Tracking

A Peak Performance System (Peak Performance Technologies, Centennial, CO) was used to digitize and analyze exploratory trips using methods described by Wallace et al. (2002a,b). Briefly, video records were copied into a digital computer file for analysis with a sampling rate of 60 Hz. A trip record is acquired from the digitized file by collecting the x- and y-coordinates of the rat as it moves along its path. Acquiring the path involves manually tracking a single point (the nose) of the rat on every frame of the digitized video. The x- and y-coordinate velocity excluding stop time is computed from the sampled raw distance data. The peak velocity (m/s), resultant velocity (m/s), and cumulative distance (m) are computed for the behavioral analysis. Thus, the data reflect moment-to-moment velocities and distance traveled during each exploratory trip and during portions of exploratory trips.

Behavioral Analysis

Exploratory behavior was divided into the following components, using previously defined categories (Wallace et al., 2002a,b, 2003):

(1) *Trip.* Any movement away and back to the huddle was defined as a trip. Trip length was obtained from the digitized record.
(2) *Stop.* Stops were defined as periods in which neither hind foot moved for at least 1 s. Stop duration was timed by counting video frames, and frames were then converted into seconds (30 f/s). Stops were subdivided into: (a) *Huddle stops*, stops that occurred when a rat approached the edge of the huddle, but did not leave, (b) *First Stop*, the first stop made after leaving the huddle, (c) *Intermediate Stops*, subsequent stops excluding the last stop, and (d) *Last Stop*, the last stop made before returning to the huddle.
(3) *Outward component.* The outward component of a trip consisted of the portion of the trip after a rat left the huddle until it made its last stop prior to returning to the huddle.
(4) *Homeward component.* The homeward component of the trip consisted of that portion of the trip following the last stop until the rat arrived back at the huddle.
(5) *Circuity.* Circuity of outward and homeward components of a trip were obtained using the following formulae: circuity = actual distance traveled/distance between the starting and ending point.
(6) *Concentric analysis.* The circular table was divided into three concentric rings comprising the middle, intermediate, and outer thirds of the table for the partition of some behaviors. For partition analysis, an overlay was placed over the TV screen that partitioned the image of the table.

Procedure

Experiment 1: huddle stability. Five litters of pups were used, and each litter was placed at the center of the circular table for 30 min each day between PO Days 14 and 24. Test conditions for the respective litters were:

(1) Litter 1 ($n = 10$), the test room was in a normal configuration with room lights on.
(2) Litter 2 ($n = 13$), a thermal gradient was created by placing the cake pan of hot water at one edge of the table for 5 min prior to placing the litter at the center of the table.
(3) Litter 3 ($n = 12$), the proximal cue was placed adjacent to the table.
(4) Litter 4 ($n = 11$), the refuge was present on the table.
(5) Litter 5 ($n = 10$), the heat lamp was located above the table's edge.

On each test day, the cues were placed in a different locations on/or near the table's edge. Behavioral measures consisted of recording the movement of the huddle and of individual rats with respect to the huddle and the location of the cues.

Experiment 2: exploratory movements in relation to the huddle. Two litters of pups ($ns = 9, 13$) were tested with the room lights on and two litters of pups ($ns = 12, 13$) were tested under infra red light. Each litter was placed in the center of the table and video recorded for 50 min on postnatal days 16 through 22.

Once a litter had been on the table for 10 min, this time period allowed the huddle to stabilize, the first five trips made by pups in each litter were selected for analysis. A record was not made of which rat pups were used in the data analysis, but care was taken to ensure that a rat was not used twice in a daily analysis.

Experiment 3: exploratory movements in relation to the heated pad. Ninety rat pups, 10 from each of 8 litters aged 16, 17, 18, 19, 20, 21, 22–25, and 65 days were used. Five rat pups of each age were tested under normal room lighting and five rat

pups of each age were tested in infra red light. Single rat pups were placed on the warm heating pad on the table and video recorded for 30 min.

Once the rat pups had been on the table for 10 min, the first trip away from the heat pad was used for the behavioral analysis.

RESULTS

Experiment 1: Huddle Stability

When a litter of rat pups was first placed in the center of the circular table, the pups became quite active, often resulting in some fragmentation of the huddle with the occasional rat pup wandering some distance away from the huddle. Within about 10 min, however, the rats formed a compact huddle that remained in a restricted location of the table, quite close to where they had been initially placed, for the duration of the test. On postnatal days 14 and 15 there was little movement of rat pups out of the huddle, but by postnatal day 16, rats began to make excursions that became progressively longer over subsequent postnatal days up to postnatal day 22. By postnatal days 23, the rat pups did not form a single huddle but rather moved across the table haphazardly forming and unforming groups of various sizes.

For the litter for which a home base was placed on the table, two pups moved and remained at the home base on postnatal day 17. On postnatal day 18 all of the rat pups entered the home base and formed a huddle there within 6 min, and on subsequent days all of the pups entered the home base and formed a huddle there with 3 min. For the litter for which a large cue was located beside the table, by postnatal day 17, a number of rat pups made excursions in the direction of the cue and then returned to the huddle. By postnatal day 18 a preponderance of trips were in the direction of the cue, and by postnatal day 19 so many rat pups were approaching the cue that a subsidiary huddle was form at the edge of the table nearest the cue. On postnatal day 20, the rat pups quickly left the huddle at center of the table and quickly reformed a huddle at the edge of the table near the cue. For the litter that received a heated pan on the table, which formed a thermal gradient, there was no obvious tendency on the part of the rat pups to approach this location as opposed to any other location on the table. For the group for which a heat lamp was placed above the table, very few trips were in the heat lamp's direction, and indeed the rat pups appeared to avoid the location of the heat lamp.

On the basis of the results of experiment one, subsequent experiments used rat pups aged 16 days (the time at which excursions were first made) to age 22 days (the last postnatal day on which a huddle was maintained). In addition, data collection began at 10 min, thus giving the rat pups time to form a stable huddle.

Experiment 2: Exploratory Movements in Relation to the Huddle

The tracings of the trips under light and dark conditions are shown in Figures 2 and 3, respectively. Starting at day 16, the outward trip paths were short and concentrated around the huddle whereas the homeward trips were short and direct back to the huddle. Across postnatal days 16–22, although the rat pups continued to make short trips, they also began to make increasingly longer trips, and these long trips were punctuated by increases in the numbers of stops per trip. Homeward trips remained more direct and had higher velocity than outward trips. On the postnatal day 16 tests, it was observed that a few rat pups made very long trips, but rather than being organized, the rats' movements suggested that they had lost contact with the huddle and were lost. In the tests given in the light, there was a tendency of the rat pups to make trips in certain directions, which included the location of the door, a bookcase, and a tripod holding a camera. By postnatal day 20 in the light and postnatal day 19 in the dark, there were always a few rats exploring away from the huddle at one time. These pups frequently followed each other using tactile and visual cues. They also formed subsidiary huddles along the edge of the table, which they nevertheless left to return to the original huddle. After day 22 in the light and day 21 in the dark, the huddle dispersed as soon as it was placed on the table and did not reform.

Distance

In order to evaluate specific aspects of the rat pup's trips, analysis of variance (ANOVA) was used for which main effects were lighting condition, age, and direction. The dependent measures were obtained from the first five trips made by individual rats. It was not possible to identify the rats from day-to-day, nevertheless performance measures were treated as a repeated factor.

Figure 4 shows the distance traveled as rats left and returned to the huddle as a function of age. There was no difference in trip length between light and dark conditions, but trip distance did increase as a function of age, $F(6, 120) = 4.51$, $p < .001$. In both the light and the dark homeward trips were shorter than outward trips, $F(1, 20) = 63.83$, $p < .001$.

Comparisons of outward and homeward trip distances indicated that it was the outward trip distance that displayed the greatest distance increase. The homeward trip distances remained uniformly shorter, and were limited in length by the diameter of the table, giving a significant direction by age effect $F(6, 120) = 2.73$, $p < .05$. There was also a significant interaction of direction and lighting condition, $F(1, 20) = 9.881$, $p < .01$, because rats tested in the dark made longer trips at a younger age than did rat pups tested in the light.
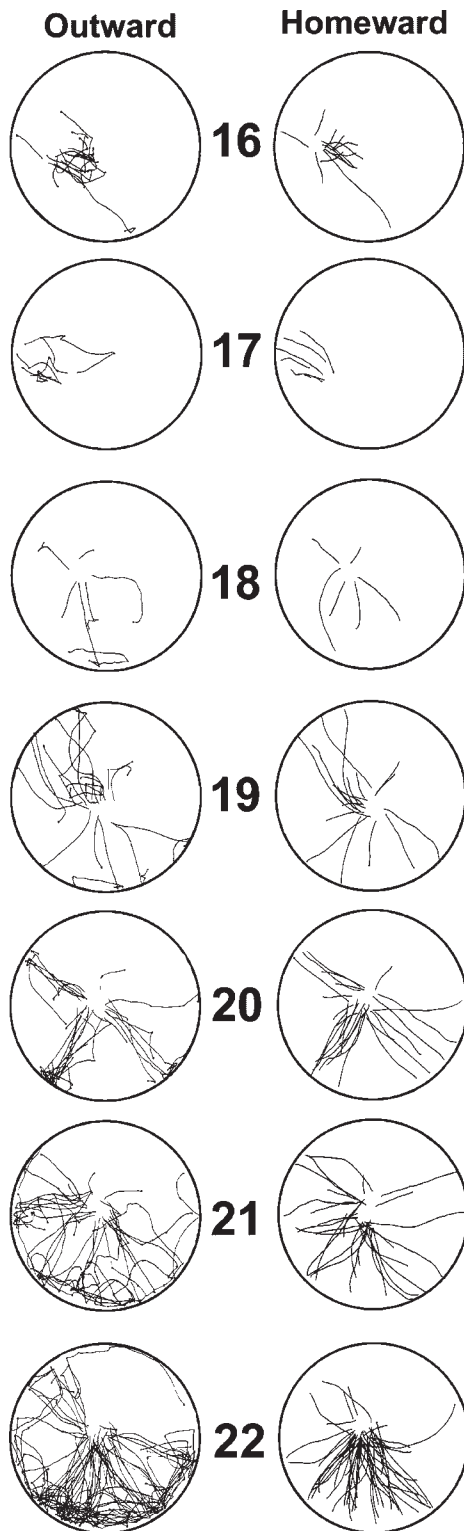
Outward   Homeward

FIGURE 2   Tracings of paths taken by rats on outward trips
(left) and homeward trips (right) on postnatal days 16–22 under
normal room lighting. Note: The progressive length and complexity
of outward trips versus direct paths of the homeward trips. In the
light the pups tended to direct trips of dominant room cues, includ-
ing the room door, a bookcase, and a tripod holding a camera.
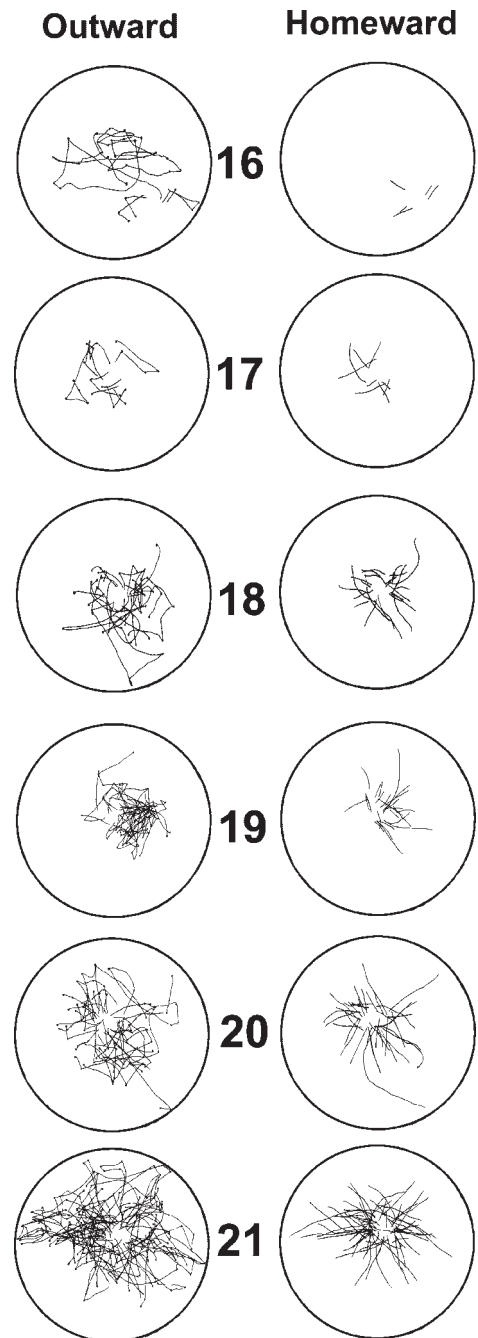
Outward   Homeward

FIGURE 3   Tracings of paths taken by rats on outward trips
(left) and homeward trips (right) on postnatal days 16–21 under
infrared lighting. Note: The progressive length and complexity
of outward trips versus direct paths of the homeward trips.

Velocity

Examination of velocity patterns showed that the outward
portions of trips, especially long trips, were characterized
by a number of velocity peaks separated by periods of
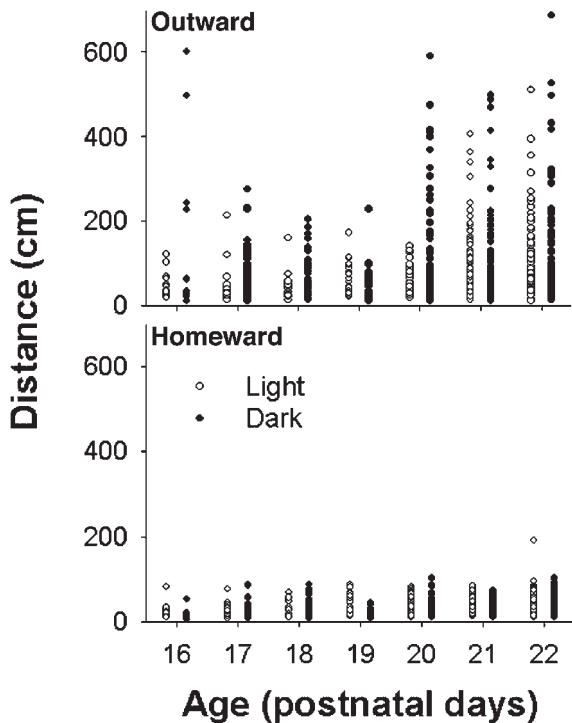low velocity, which together reflected the movements,

FIGURE 4 Travel distance of individual rats as a function of age on outward and homeward trips in the light (open circles) and in the dark (closed circles). Note: The very long trips made by a few rats in the dark on postnatal day 16 may represent rats that lost contact with the huddle.

FIGURE 5 Left: Examples of velocity of on the outward and homeward component (insert shows travel path) of a trip by an individual rat in normal room light (top) and infra red light (bottom). Note differences in x, y axis. Right: Mean velocity (mean ± standard error) on outward and homeward portions of trips in the light (top) and the dark (bottom). Note that although trip velocity was slower in the dark, velocity differences were a feature of outward and homeward trips.

pauses, and stops made by the rats. Homeward trips typically consisted of a single symmetrical peak featuring the highest velocity for a movement made on that trip. An example for a single trip in the light and a single trip in dark by 20-day-old rats is shown in Figure 5, left (note the scale differences on the x and y-axis).

Measures of mean travel velocity indicated that travel velocity increased as a function of age, $F(6, 120) = 31.2$, $p < .001$, and was higher in the light than in the dark, $F(1, 20) = 42.979$, $p < .001$. Figure 5 right illustrates average velocity of outward versus homeward trips summed across postnatal days 16 to postnatal days 22, showing that homeward trips had higher velocity than outward trips, $F(1, 20) = 123.96$, $p < .001$.

Circuity

Calculation of circuity indicated that trips became more circuitous as a function of age, $F(6, 20) = 11.3$, $p < .001$, and were more circuitous in the light than in the dark, $F(1, 20) = 3.45$, $p < .001$. Outward trips were more circuitous than homeward trips, $F(1, 20) = 73,2$, $p < 0/001$, and in addition there was a significant interaction between age and trip direction, $F(6, 120) = 4.23, p < .001$. The latter effect reflected the fact that homeward trips
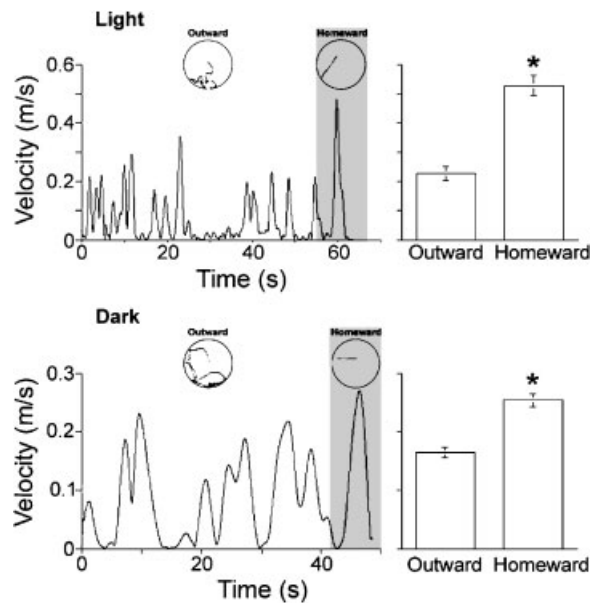
were nearly always direct whereas outward trips became more circuitous as the animals aged.

Stops

A rat pup about to leave the huddle usually began its excursion by approaching the edge of the huddle. It then extended its head from the huddle, and made a number of stretching and orienting movements away from the huddle and along the edge of the huddle. Following these orienting movements it usually left the huddle. Sometimes, however, the rat pup also retreated into the huddle, or moved to a new location in the huddle and repeated the behavior. We counted the stops made by the rat on the edge of the huddle as a "huddle stop," if the rat subsequently left the huddle. The initial movement away from the huddle was generally direct and was often ended by a brief "first stop" that was typically not associated with head orienting movements. Younger rats usually returned to the huddle after the first stop, whereas older rats frequently continued on. When the pups reached the edge of the table, they typically stopped and scanned the table's edge, a behavior that could be repeated a number of times as they moved along the edge of the table. The rat pups usually returned to the huddle after one of the stops on the edge of

the table but they also moved away from the table and stopped before returning to the huddle. The stop prior to returning to the huddle was termed the last stop.

Counts of stops that occurred after the rat pups left the huddle indicated that there were more stops made per trip as a function of age, $F(1, 20) = 2.31$, $p < .05$, and more stops made in the dark than in the light, $F(1, 20) = 4.55$, $p < .05$. There was also a significant effect of age and lighting condition, $F(6, 120) = 2.82$, $p < .05$, which indicated that the rat pups made more stops in the dark as they aged than they did in the light.

To further analyze stopping behavior, stop durations of huddle stops, first stops, intermediate stops, and last stops were measured for postnatal day 16 and postnatal day 21. The results, illustrated in Figure 6, showed that stopping durations were longer for the postnatal day 16 rat pups than for the postnatal day 21 rat pups, $F(1, 14) = 9.486$, $p < .01$, but the effect of lighting on stop duration was not significant. Huddle stops were also significantly longer than subsequent stops, $F(3, 42) = 22.120$, $p < .001$, and huddle stops were longer in postnatal day 16 pups than in postnatal day 21 pups, $F(3, 42) = 3.51$, $p < .05$.

Stop durations were also examined as a function of whether they occurred in the center third of the table (the location of the huddle), the middle third of the table, or the outer third of the table, Figure 7. There was a significant effect of stop location $F(2, 28) = 23.715$, $p < .001$. Follow-up Newman–Keuls tests indicated that with respect to duration center stops > outer stops > middle stops. The center stops were mainly huddle stops that occurred prior to the rats' excursions whereas outer stops were mainly stops along the edge of the table.

Experiment 3: Exploratory Movements in Relation to the Heated Pad

The behavior of individual rat pups in relation to the heated pad was similar to the behavior displayed by rat pups in relation to the huddle as indicated by measures of distance, velocity, and circuity.

Distance

A summary of the distance measures is illustrated in Figure 8. For postnatal day 16 rat pups, the outward trip
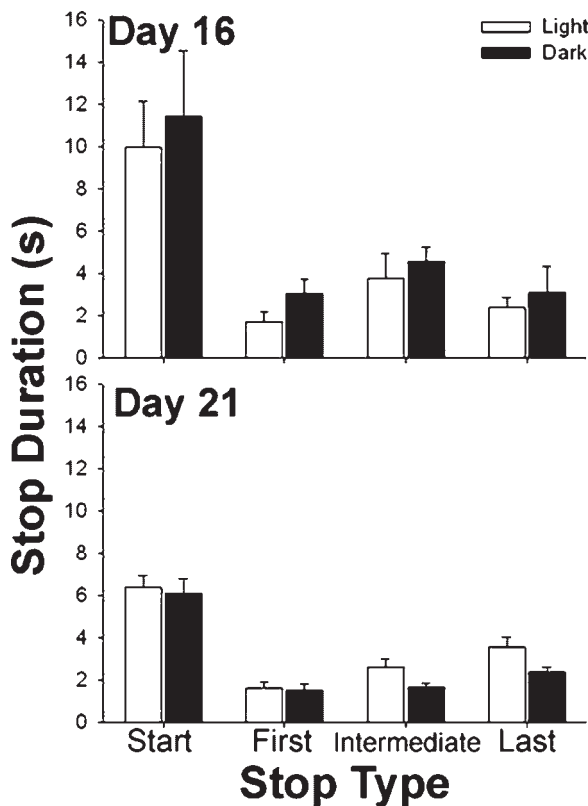

FIGURE 6 Duration (s) of the four stop types for day 16 (top panel) and day 21 (bottom panel) under light and dark conditions. Note: "Start" stops made at the huddle edge before the rat leaves the huddle are longer than stops made away from the huddle.
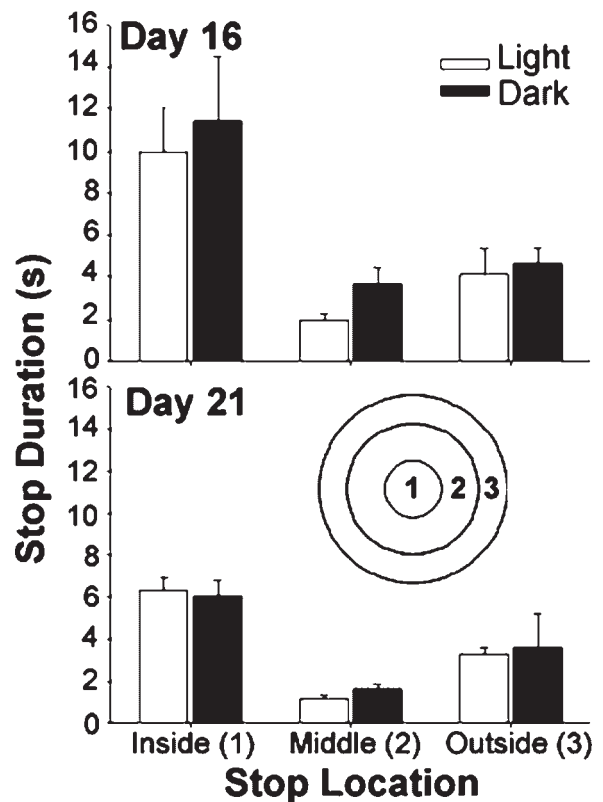

FIGURE 7 Duration (s) of stops at three locations on the table (insert) for postnatal day 16 (top panel) and postnatal day 21 (bottom panel) rats under light and dark conditions. Note: Stops on the edge of the huddle and by the table's edge are longer than stops in the middle portion of the table.
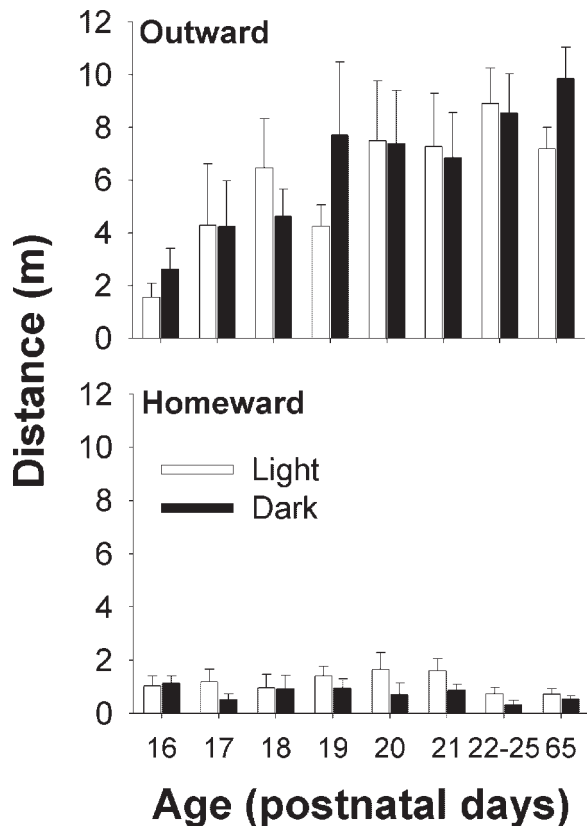
FIGURE 8 Travel distance of individual rats as a function of age on outward (top panel) and homeward (bottom panel) trips in the light and in the dark.

FIGURE 9 Velocity of rats as a function of age on outward (top panel) and homeward (bottom panel) trips in the light and in the dark.

paths were short and concentrated around the heat pad, and the homeward trips were short and direct back to the heat pad. As the rat pups aged, trip length became longer, $F(7, 64) = 2.98$, $p < .01$. On all days, the outward trips were longer than were homeward trips, $F(1, 64) = 142.05$, $p < .001$, and the outward portion of the trip increased disproportionately relative the homeward portion of the trip, age by direction $F(7, 64) = 3.27$, $p < .01$. Trip distances were not different in light and dark conditions.

Velocity

A summary of the velocity measures (excluding stops) is illustrated in Figure 9. Trip velocity was found to be higher in the light than in the dark, $F(1, 64) = 31.57$, $p < .001$, and the velocity on the homeward segment was higher than the outward segment, $F(1, 64) = 100.99$, $p < .001$. There was a significant interaction of effect of lighting condition and direction, $F(1, 64) = 12.54$, $p < .001$, reflecting the faster return trips made by the pups in the light. Finally, there was a significant interaction between velocity, direction and age, $F(7, 64) = 2.24$, $p < .05$. This appeared to be due to higher velocity
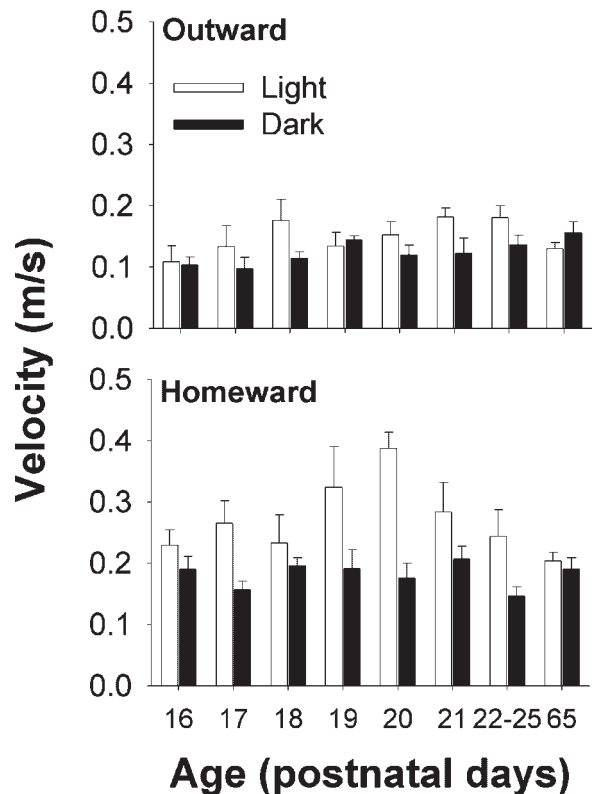
homeward trips in rat pups of postnatal ages 19–21, as compared with younger and older rat pups.

Circuity

A summary of the circuity measures is illustrated in Figure 10. Circuity increased as a function of age, $F(7, 64) = 2.63$, $p < .05$, and outward trips were more circuitous than homeward trips, $F(1, 64) = 540.96$, $p < .001$. In addition, a significant interaction between direction and age, $F(7, 64) = 4.07$, $p < .01$, reflected that it was mainly on outward portions of trips that circuity increased as a function of age.

DISCUSSION

Exploratory behavior was examined in infant rats as they left and returned to a huddle of pups or to a heating pad serving as a surrogate huddle. In experiments conducted in the light and in the dark, trips away from the huddle became progressively longer, more circuitous, and associated with more stops over postnatal days 16–22. Return trips to the huddle were more direct and
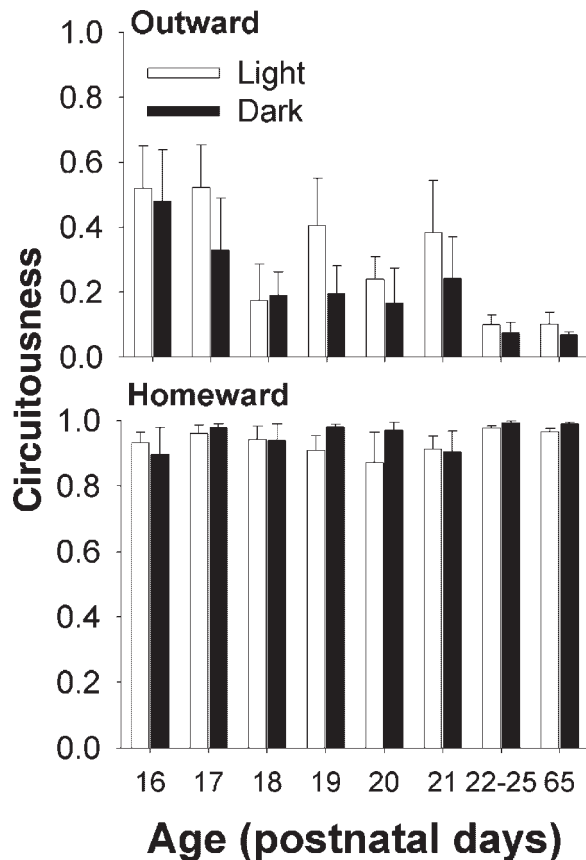
FIGURE 10 Circuity of individual rats as a function of age on outward (top panel) and homeward (bottom panel) trips in the light and in the dark.

associated with higher travel velocity than outward trips on all test days. The differences in the characteristics of outward versus homeward trips in infant rats are similar to the characteristic of the same behaviors reported in adult rats. Possibly, the differential characteristics of outward and homeward trips represent the use of the spatial navigation strategies of piloting and dead reckoning, respectively. These findings illustrating a gradual maturation of "spatial capacity" are consistent with the idea that for locomotor ability to be adaptive requires higher-level control from forebrain structures supporting spatial behavior.

The study of the development of spatial behavior in rats has proved problematic both because it is difficult to develop tasks that infant rats can perform and because it is difficult to motivate infant rats using procedures that are effective for adult rats (Brown & Whishaw, 2000; Rudy & Paylor, 1988; Rudy et al., 1987; Schenk, 1985). In the present study, a new test procedure is described for the study of the development of spatial behavior. A huddle of rat pups, or a heating pad serving as a surrogate huddle, was used as a home base from which rat pups could engage in self-paced "exploratory" trips. The examination of the outward and homeward components of trips of the rat pups in relation to the huddle provides a situation that is analogous to that in which an adult rat is given access to a home base from which to explore or forage (Wallace et al., 2002a,b, 2003; Whishaw & Pasztor, 2000). The utility of the paradigm was confirmed by the finding that the complexity of a rat's behavior increased as the animals aged. Nevertheless, huddle behavior is complex and parametric studies of rat egress from the huddle as a function of air temperature was not examined (Gerrish & Alberts, 1996). Although it is possible that the timeline of results reported here could be shifted, such shifts will be limited by the immature locomotor abilities of the rat pups at early ages and by the maturation of thermoregulatory abilities at older ages.

Previous studies with adult rats have found that exploration is organized, and consists of two component spatial behaviors, piloting and dead reckoning (Wallace et al., 2002a,b, 2003). If rats are provided with a home base in an otherwise open arena, they use the base as a center for their exploratory behavior. They make outward trips that become longer and more complex over successive trips and the trips are associated with progressively more stops. A direct, high velocity, return to the home base typically ends each trip.

Presumably, the outward trips allow an animal to collect information about an environment, while the homeward trip allows the animal to rapidly regain a safe haven. This pattern of behavior likely represents an optimizing strategy in which rats attempt to both explore an environment and to minimize their risk to predation or attacks by conspecifics (Whishaw & Whishaw, 1996). That is, because the outward trip is presumably necessary for gathering information and for that reason is difficult to truncate, an obvious way of minimizing exposure is to minimize the duration of the homeward trip. Similar direct homeward trips versus slower and more circuitous outward trips are displayed by rats in a wide array of situations, including returning to a refuge after foraging (Whishaw, Gorny, & Dringenberg, 1991).

The suggestion that the outward portion of a trip is a form of piloting is inferential. Clearly, for adult rats placed in a novel environment, information gathering is a useful activity. Because adult rats increase the distance that they travel on successive outward trips and seldom traverse the same route, it is supposed that they are systematically examining their environment (Drai et al., 2000; Eilam & Golani, 1989; Gharbawie & Whishaw, 2003; Golani et al., 1993; Tchernichovski et al., 1998). A number of observations of the present study seem to confirm that the infant rats did respond to environmental cues. If there was a refuge in the environment or a prominent landmark, the rat pups moved their home base in that direction, and they

avoided a location that featured a heat lamp. Prominent features in the room also attracted the rat pups, as did the movements of other pups.

The finding that the rat pups made increasing numbers of stops as outward trips got longer, also suggests that they were using the stops to look around or confirm their location. Stops made by rat pups when they were still in contact with the huddle were relatively long and were associated with orienting (stop, look, and listen) movements as if the rat pups were making a ''safety assessment'' before leaving the huddle. Stops were also longer along the edge of the table than they were in the middle third of the table, suggesting that the rats were examining the table's edge or inspecting objects at a distance from the table. Head scans have been shown to be related to distal cue sampling (Ellard, Goodale, & Timney, 1984; Whishaw et al., 1994). Presumably, the information gathered by a rat on outward excursions not only allows the animal to learn about its environment but will also be useful for guiding subsequent trips.

Although it is possible that in the early postnatal period the short returns of rat pups are guided by local cues, for longer trips at older ages it is likely that the pups are using dead reckoning, as has been suggested for adult rats (Wallace et al., 2002a,b, 2003; Whishaw & Gorny 1999; Whishaw, Hines, & Wallace, 2001). First, direct returns persisted in infra red light, in which visual cues cannot be seen. Second, it is unlikely that homing depends simply upon vocalization from the huddle (Carden & Hofer, 1992; Clements & Kelly, 1978) because direct homing persisted in animals tested singly. Third, at older ages, when the huddle briefly fragmented into subsidiary huddles, outward-bound animals returned to their starting point and not the second huddle, suggesting the sight and smell of other rat pups was not a sole determinant in directing locomotion. Fourth, direct homing is unlikely to be mediated only by olfactory cues (Larson & Stein, 1984; Wallace & Whishaw, 2003). After making long circuitous trips, the rat pups did not follow their outward route home; the homeward trips often occurred from a distance that a rat would not be able to detect a scent from the huddle; when many rats were leaving and returning olfactory cues would not be punctuate and; the movement displayed by the homing rats does not resemble the slower velocity and back arched posture seen in tracking rats (Whishaw & Gorny, 1999; Wallace et al., 2002c). Fifth, it is also unlikely that homeward trips are mediated simply by thermal gradients (Freeman & Rosenblatt, 1978) because the distance of the animal's outward trips, at least after day 16, were such that they would preclude detection of heat generated by the huddle and because the pups did not orient to a warmed area of the table. It is noteworthy that evidence from adult rats shows that homeward trips are selectively disrupted by labrythectomy, a manipulation

that removes an animal's source of directional information (Wallace et al., 2002a,b). A more direct test of how rat pups guide their homeward trips might be obtained by examining the effects of labrythectomy.

Studies in adult rats have shown that homeward trips are distinctive in having high velocity. Peak velocity also occurs at the midpoint of the trip, regardless of trip distance and presence of visual cues, suggesting that the trip is preplanned via calculations using the self-movement cues produced on the outward excursion (Wallace et al., 2002a,b). A similar pattern of behavior occurs in relation to virtual home bases formed by rats exploring a featureless environment (Drai et al., 2000; Eilam & Golani, 1989; Golani et al., 1993; Tchernichovski et al., 1998). In the present study, it was also observed that the velocity of homeward trips was distinctively high and symmetrical in the rat pups, suggesting the movement is preplanned.

The contribution made by the present results to the understanding of the development of exploratory behavior is that that exploratory ''capacity'' matures gradually, and not abruptly. Beginning at postnatal day 16, a time point at which pups begin to spontaneously move away from the huddle, the elements of assessment, an outward trip, a stop, and a homeward trip are present. In addition, across the entire range of ages studied, outward and homeward behaviors were distinctive in that outward trips were more circuitous whereas homeward trips were more direct. This suggests that the rats' spatial capacity (both for piloting and dead reckoning) develops gradually to the point that the animals can take the long trips characteristic of adult rats. In this respect, it is interesting that locomotor skill develops over about the same time period (Altman & Sudarshan, 1975; Leblanc & Bland, 1979). Thus, it is possible to conclude that the development of spatial ''capacity'' progresses in parallel with locomotor skill, an obviously adaptive coupling.

Some research suggests that the hippocampus contributes to spatial navigation (Morris, Garrud, Rawlins, & O'Keefe, 1982; Sutherland, Whishaw, & Kolb, 1982; Wallace et al., 2002b, 2003; Whishaw & Gorny, 1999; Whishaw et al., 2001), and this raises the question of whether the hippocampus is sufficiently mature to support adult-like spatial behavior at the ages tested in the present study. A study of the electroencephalogram (EEG) of developing infant rats by Leblanc and Bland (1979) shows that the two adult forms of hippocampal theta (RSA), movement related RSA and immobility related RAS, first appear in the hippocampus at Day 10 postnatal (but see Karlsson & Blumberg, 2003) and amplitude and frequency increase progressively to reach their adult form by postnatal day 16 while atropine-sensitive RSA and atropine-resistant RSA are present by postnatal day 22. The ages of 16–22 days correspond with the ages over

which exploration from the huddle develops. This relationship suggests that the hippocampus and related structures are sufficiently developed to mediate spatial behavior.

In conclusion, the present study presents a novel way of studying the development of spatial behavior in infant rats. The study demonstrates that exploratory capacity develops gradually and in conjunction with locomotor skill between postnatal day 16 and postnatal day 22. It also shows that outward and homeward components of the exploratory trips of infant rats are distinctive. It is suggested that these results support the idea that exploration is controlled by two different spatial behaviors, piloting and dead reckoning both of which display an increasing age-related capacity.

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