The Interaction of Body Morphology, Directional Kinematics, and Environmental Structure in the Generation of Neonatal Rat (Rattus norvegicus) Locomotor Behavior

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The Interaction of Body Morphology, Directional Kinematics, and Environmental Structure in the Generation of Neonatal Rat (Rattus norvegicus) Locomotor Behavior

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We show that modeling directional kinematics is especially important for understanding spatial patterns of behavior in an arena. In rats, although patterns of locomotion appear to be under sensory control, they may be largely if not entirely explained, during early locomotor development, by the directional kinematics of random movement together with morphological/environmental constraints. Different relative probabilities of forward movement versus lateral movement (lateral:forward ratio; LFR) have dramatic consequences for the patterns of movement of modeled agents in an arena. These patterns of movement, produced by rigid-bodied agents, are also modified by increasing morphological realism in our model, wherein agents are able to bend and flex like rat pups. For both morphological designs, agents run with empirically derived LFRs matched metrics of movement for 7-day-old pups very well and 10-day-old rat pups fairly well. We conclude that LFR is an important parameter in modeling (a) patterns of dynamical behavior in an arena and (b) trajectories of behavioral development.

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Traditional approaches to the study of animal locomotion examine how an organism’s behavior varies as a function of environmental stimuli (physical, social, etc.). One influential approach, the study of “taxes” and “kineses,” was formalized by Gottfried Fraenkel and Donald Gunn in their 1940 book *The Orientation of Animals*. As part of the behaviorist tradition, taxes and kineses are classifications of observed categories of sensorimotor reactions. Taxes refer to directed locomotor responses to stimuli gradients (e.g., light, temperature, chemicals, etc.), whereas kineses are locomotor reactions to different intensities of environmental stimuli. Kineses are undirected responses. Local movement probabilities are altered by the presence of a stimulus, but unlike taxes, the movements themselves are not directed toward or away from that stimulus. Here we describe some of the effects of kineses, then introduce a novel means of producing similar effects.

Kineses, as Fraenkel and Gunn (1940) describe, have predictable, larger scale effects on the distribution and aggregation of organisms in an environment. For example, wood lice (*Porcellio scaber*) thrive in environments with humid air but quickly dry out and die in more arid environments. In humid conditions, wood lice move around very little, whereas in arid conditions, they are almost constantly active. This kinetic difference is most dramatically observed by creating a shallow humidity gradient in a controlled environment (Gunn, Kennedy, & Pielou, 1937). In doing so, Gunn et al. observed systematic changes in the speed of linear movement in response to different humidity readings along the gradient. Because low humidity caused higher movement levels, wood lice quickly exited those portions of the gradient, eventually moving toward and remaining in the high humidity end, where activity ceased. Fraenkel and Gunn referred to this proportionality of activity levels to the intensity of a stimulus as “orthokinesis.” Orthokinesis in normal environmental settings allows organisms to respond to regional environmental variations to find optimal habitats (e.g., certain organisms can be found under a rock, whereas others may be out in the sun).

In addition to orthokinesis, a second class of kineses is “klinokinesis,” wherein the rate of turning is proportional to the intensity of a stimulus. For example, Fraenkel & Gunn (1940) reported the experiments of Ullyott (1936) on a flatworm (*Dendrocoelum lacteum*). If placed on a light intensity gradient (with no directional light information), *Dendrocoelum* tended to aggregate in the dimmest intensities. Movement tracking revealed that transitions to higher intensity lights caused an increased rate of turning, whereas transitions to lower intensity lights did not. As a result, travel down the gradient resulted in straighter paths of motion, making it much more likely than travel up the gradient. Gunn (1975) later came to question the replicability of Ullyott’s experiments but not that klinokinesis could lead to gradient following as subsequently verified by simulation (Dusenbery, 2001). Kineses are illustrative here because the final environmental distributions of organisms are caused by changing local...
movement patterns rather than directed movement toward a stimulus (viz., a taxis).

van der Steen and ter Maat (1979), in their critical analysis of the usage of the terms *taxis* and *kinesis*, argued that explanations of locomotor behavior using these terms were inherently incomplete by leaving out the interaction among multiple stimuli and, as we argue, environmental and morphological constraints on locomotion. For example, Hafez, Salama, and Tolba (1971) examined taxis and kinesis responses in corn borer larvae to temperature, humidity, and light. The results, when each stimulus was tested (while the others were held constant), were clear kinetic or taxic responses. When combinations of stimuli were presented, however, orienting responses depended on the particular combinations of stimuli. Moreover, the patterns of movement of the larvae in a circular arena were shaped by the geometry of the arena. In rats, Paulus & Geyer (1997) similarly demonstrate that patterns of movement are shaped by environmental geometry. The patterns and responses to combinations of stimuli also illustrate van der Steen and ter Maat’s second point that the same patterns of behavior can be produced by different mechanisms and indeed unexpected mechanisms.

The latter point is dramatically illustrated by our generation of “thigmotaxic” behavior with random robotic models of infant Norway rat (pups) locomotion (May et al., 2006). Thigmotaxis refers to a directed response to contact, such as turning toward the stimulus contacted (e.g., another rat pup or a wall). Traditionally, what we call thigmotaxis has been thought to underlie observed behavioral patterns of Norway rats (*Rattus norvigicus*) to tactile stimuli from infancy to adulthood (Alberts, 1978; Patrick & Laughlin, 1934; also see Small, 1899; Vincent, 1912). Pups, when placed in an arena, tend to follow walls, burrow in corners, and aggregate (Schank, 2008; Schank & Alberts, 1997, 2001). As thigmotaxic behaviors, initial wall and corner contact should elicit further wall and corner contact, resulting in wall “following” on the one hand and corner “burrowing” on the other. Similarly, once one pup contacts another, their behaviors should subsequently be coordinated, resulting in aggregation.

In May et al. (2006), we constructed robotic analog of rat pups. Robots were designed to have a morphology similar to a pup, with a long body tapering to a rounded snout, and moved using two rear-driven wheels and a front stabilizing ball. A random control architecture was downloaded into the onboard CPU of the robot. Every 2 s, the robot randomly selected a new direction of movement, which it then executed for the duration of that interval. Unexpectedly, these robots exhibited wall following, corner burrowing, and group aggregation. In this case, random movement alone produced apparently nonrandom distributions in the environment that were both qualitatively and quantitatively similar to rat pups (May et al., 2006). These results could be explained by noting the way in which the robot’s morphology shaped and constrained its behavior in interacting with the environment or other pups. For example, when a robot
hit a wall, its tapered snout would typically cause the agent to slide along the wall. At least half of the movements that might be subsequently selected would keep the robot along the wall (e.g., forward movements or those in the direction of the wall) and produce “wall following.” In a corner, only a minority of movement options would allow the robots to escape, resulting in “corner burrowing.” In the context of groups, the coupling between two robots was even more dynamic and dramatic. Upon contact, two or more robots would so coconstrain each other’s movement that they often appeared to be following each other or be in a complicated dance. Indeed, the casual observer was often shocked to learn their behavior was random. These results illustrated several points: (a) it should not be assumed that an apparently thigmotaxic pattern of behavior is always produced by a thigmotaxic mechanism, (b) environmental structure and morphology are often essential to explaining the behavioral patterns we observe, and (c) the central nervous system of an animal is not solely responsible for producing behavior. From the standpoint of understanding behavior, the third point is especially salient: the shaping of behavior by morphology-environment interactions may effectively off-load at least some computational requirements of the brain in producing locomotor behaviors such as “wall following” and “corner burrowing” in pups.

This is consistent with other approaches which have emphasized that there may be far less internal processing by brains than previously thought. Roboticist Rodney Brooks (1999) observed that in many cases, cognition is more in the eye of the beholder than in the brain/control system of the observed organism/robot. Although this tendency to make cognitive ascriptions may have been selected for its value in navigating complex social relations for us humans (Bogdan, 1997), it tends to obscure efforts to explain, rather than simply predict, behavior. Valentino Braitenberg (1984) dramatically made this point by illustrating how appetites and aversions could be modeled as simple sensorimotor reactions to stimuli. Braitenberg’s models, however, were simply thought experiments, lacking the constraints and opportunities of real embodiment and real environments. Modeling is particularly powerful because the high level of specificity required to implement them often reveals unforeseen interactions, as demonstrated in May et al. (2006).

Here we introduce an additional factor essential for explaining patterns of locomotion. This is the kinematics of directional movement (Schank, 2008). The kinematics of directional movement can be defined by probability distributions characterizing the changes in directions or turns an animal makes independent of external stimuli. In altricial mammals such as rats, these probability distributions change developmentally (Schank, 2008). The kinematics of movement can be up or down regulated by external stimuli (kinetic or taxic responses) and they can be modified by sensory stimuli and central processing, but as we show, the kinematics of directional movement is a foundational element in modeling
behavior. How environmental stimuli alter behavioral patterns can only be fully understood relative to the behavioral patterns exhibited independently of stimuli. This is not necessarily to argue that organisms do move independently of stimuli but rather that the effects of stimuli are contingent on the unfolding capabilities of an organism. The agent-based models developed here provide a unique platform for understanding these developmental contingencies. To motivate our implementation of the kinematics of directional movement, we discuss literature on kinematic realism and highlight the limitations of previous work that did not systematically investigate directional kinematics.

**LOCOMOTOR DEVELOPMENT IN RATS**

According to Drai, Kafkafi, Benjamini, Elmer, & Golani (2001), “[forward progression and stopping-scanning] constitute locomotor behavior, a *par excellence* innate pattern” (p. 133) in rats and mice. Forward movement, they believe, is intended to take an organism from one point to the next, whereas stopping and scanning are investigatory behaviors, potentially prompting changes in direction of future forward movement. Here we refer to scanning as lateral movement to decouple behavioral from functional descriptions. The relative observed frequencies between forward and lateral locomotor movements appear to be both species and strain specific (Drai et al., 2001). Although Drai et al.’s results concern adult behavior, species and strain differences will likely be present as unique developmental trajectories as well. Indeed, by modeling the behavioral effects of different frequencies of forward and lateral movement, it may be possible to detect genotypic and species differences.

Classes of locomotor movement unfold ontogenetically in rat (*Rattus rattus*) exploratory behavior (Eilam & Golani, 1988). Exploratory behavior (viz., apparently undirected behavior in an open arena) begins with lateral movements in pups. Lateral movements have a rostral-caudal developmental gradient, wherein pups move their heads side to side before they can do so with their torso, and finally are capable of full-body pivoting. Following the emergence of lateral movements, pups are able to make forward movements. These too develop cephalocaudally, beginning with a craning of the neck, then the torso, and finally by full-body movement. After the onset of forward movements, pups are able to progress from strictly two-dimensional locomotion to three-dimensional locomotion with the emergence of vertical movements. Once more, these begin with the head rising up, followed later by the head and torso, and finally, full three-dimensionality (see Figure 1 for timeline of development). In addition to the initial appearance of new movement classes, there are also developmental changes in the observed frequency of each movement type in rat pups. Lateral movements are more prevalent than forward movements through 7 days of age.
At approximately that time, forward movements subsequently become more frequent.

Studies of the effect of drugs further support the division of forward and lateral movements into distinct classes of locomotor behavior, producing disso- ciable effects on the types of movement (Geyer, Russo, Segal, & Kuczenski, 1987). For example, low doses of apomorphine cause increased lateral movements, whereas high doses produce increased straight movements in an arena (Geyer et al., 1987; Paulus & Geyer, 1991). Similarly, different doses of lisuride, nicotine, MDMA, scopolamine, MBDB, heroin, and nomifensine all produce changes in the linearity of movements (Paulus & Geyer, 1991, 1997). Paulus and Geyer (1991) developed a method for quantifying movement along a spatial scale, $d$, which varies as a function of how “straightforwardly” an animal is moving and is differentially affected by different drugs. In drug-naive Sprague-Dawley rats, Paulus and Geyer (1993) report a normal distribution of $d$.

Forward movements are not only behaviorally but also neurophysiologically independent of lateral movements. For example, lateral head movements have been shown to be (a) mediated by the hypothalamus in adult rats and (b) both reciprocal and antagonistic to forward movement (Sinnamon, Karvosky, & Ilch, 1999). Neurotransmitter systems also appear to be important as the behavioral
effects of apomorphine and amphetamine were hypothesized to result from differential activation of D1 & D2 dopamine receptors (Geyer et al., 1987; Paulus & Geyer, 1991). Finally, a recent study demonstrated that the neurophysiological independence of forward and lateral movements is not unique to rats and mice. In the roundworm *C. elegans*, Suzuki et al. (2008) were able to demonstrate this decoupling at the neural level. In elucidating the mechanisms underlying positive chemotaxis (the directed response toward a chemical stimulus), they examined the effects of concentration differences of NaCl on the activity of two ASE chemosensory neurons, ASE left (ASEL) and ASE right (ASER). Increases in NaCl concentration caused increased activation of the ASEL chemosensory neuron, which subsequently increased the probability of forward movement. Conversely, ASER activity levels were increased by decreases in NaCl concentration, which thereby increased the number of turning movements. These behavioral results were confirmed by selective ablation of ASEL and ASER neurons.

Eilam and Golani’s (1988) observations, Paulus and Geyer’s (1991) drug manipulations, and demonstrations of neural dissociations (Sinnamon et al., 1999; Suzuki et al., 2008) all suggest that a biological model of locomotor movement should decouple lateral from forward movement. More lateral than forward movement would be expected early in development (i.e., Day 7 and earlier) with a rapid transition to more forward movements by Day 10 (Eilam & Golani, 1988). Given that 7-day-old pups exhibit different patterns of movement in an arena from 10-day-old pups (Schank, 2008), this raises the possibility that a diversity of macrolevel environmental distributions may arise, not by the sensory-mediated kineses described by Fraenkel and Gunn (1940) but by developmentally unfolding kinematic routines (viz., changes in local movement probabilities). Moreover, the locomotor patterns of movement and aggregation in developing rats that are sensory-mediated kineses and taxes should include the developmental constraints of locomotor kinematics.

In previous research, the robots we constructed to model rat pup locomotion and that generated apparent “thigmotaxic” behavioral patterns only implemented a single kinematics of directional movement (May et al., 2006; Schank, May, Tran, & Joshi, 2004). For all types of turns, one wheel spun faster than the other. A left turn, for example, required that the right wheel spin faster than the left. The relative speed difference between wheels determined the degree of the turn. One consequence of this kinematic implementation was that robots could not turn “in place,” namely, around an axis of rotation. This limited the patterns of movement observed. It is important to note that 7-day-old pups do turn along an axis of rotation (see Figure 1). Our kinematic implementation, however, was not capable of this kind of movement (i.e., punting; Altman & Sudarshan, 1975). Thus, our initial efforts at modeling movement could not produce punting, which is particularly prominent in 7-day-old rat pups (Schank, 2008). This suggests
that a thorough analysis of locomotor kinematics in developing pups should begin with a systematic analysis of kinematic implementations. In addition, as we make clear shortly, such an analysis must be combined with an analysis of body morphology and flexibility.

SIMULATIONS

We report the results of two simulation studies and one study comparing the simulation results with rat pup data that are aimed at a better understanding of the role of whole-body kinematics of locomotion on the generation of microlevel and macrolevel patterns of behavior during early locomotor development in infant rats. In the first series of experiments, we systematically explore the consequences of different lateral and forward movement probabilities for rigid-bodied agents. The second set of simulations examines the impact of body flexibility on these consequences. The results from this exploration allow for an empirically based derivation of probability values to model different age groups of rat pups, which we report in the third study.

STUDY 1: RIGID-BODIED AGENTS

Agents

The behavioral consequences of different kinematic implementations were explored using a simulated model of infant rats. The model was created in the breve simulation platform, a three-dimensional environment with built-in physics heuristics designed for studies in artificial life (Klein, 2002). Simulated agents (hereafter agents) in this study had a long rigid-body tapering to a rounded nose (Figure 2), emulating the morphology of infant rats. Two rear-drive wheels controlled movement, and a load-bearing ball was located at the junction between the head (front third) and body (back two thirds). In a simulated arena (Figure 3), agents randomly selected a new movement every 2 s, which was then executed for the duration of the interval.

Forward and lateral movements were decoupled in the breve agents by implementing a new wheel-rotation scheme. Previously (May et al., 2006; Schank et al., 2004), agents turned by spinning one wheel faster than another. This caused the agent to arc (left, right, or back-left and back-right) across the arena. In the present study, agents turned via reciprocal wheel rotations. For example, to turn right, an agent would spin its left wheel forward and its right wheel backward at the same speed. This allowed agents to pivot rather than arc across the arena. Degree of turning (or “punting”) may be altered by changing either
the speed of reciprocal wheel rotation or the length of spin time. The speed of forward movements (or translational velocity in dynamic systems parlance) was allowed to randomly vary at each selection. As a result, some forward movements were slow and did not cause the agent to traverse much of the arena, whereas others were fast and resulted in increased distance traveled. The degree of turn for any given lateral movement was also randomly determined up to approximately 75°. Lateral movement in the same direction could be chosen

FIGURE 2 Undercarriage (left) and top view (right) of simulated agent.

FIGURE 3 Simulated agent at start of trial in a scaled arena.
in consecutive time intervals, resulting in more dramatic punting of the agent. Forward movements were implemented by matching left and right wheel output while back-left and back-right movements continued to employ differential (but nonreciprocal) wheel rotations.

Metrics

We defined a new behavioral parameter, the lateral:forward ratio (LFR), which specifies the relative proportion of each movement type. The LFR is defined by Equation 1 as the frequency of lateral movement (FLM) divided by the frequency of forward movement (FFM) and FLM:

\[
LFR = \frac{FLM}{FFM + FLM}. \tag{1}
\]

Although the LFR is not strictly a ratio between lateral and forward movements, this nomenclature is appropriately descriptive given that forward and lateral movements are reciprocally varying while other movements (e.g., stopping and backward movement) are held constant (see Table 1). A low LFR refers to a low proportion of lateral movement relative to forward movement, whereas a high LFR refers to a high proportion of lateral movement relative to forward movement. If LFR were high (i.e., close to 1.0), then most locomotor movements would be characterized by turning, which would be expected for 7-day-old pups. If LFR were lower, then we would expect to see more forward locomotor movements characteristic of 10-day-old pups (Schank, 2008).

Behavior was quantified according to the proportion of time spent in three different zones of the arena: corners, walls, and the center. Wall zones were defined as the area bounded by the wall and one “head” length from the wall, minus the area constituting a corner zone. Corner zones were defined as the area between a corner, one “head” length from the corner along each wall, and lines connecting those head length points with the intersection of two wall zone markers (see Figure 1 and Schank et al., 2004, for the development of this metric). Center zone was defined as the area spanning from the center point to the wall zone lines.

Procedure

Fifty rigid-bodied agents were run at each of 33 LFRs (Table 1) for a total of 1,650 simulations. Agents began each trial in the center of a simulated arena facing left or right and ran for 10 simulated minutes. Coordinates of the agent’s nose were sampled every 5 s and output to a text file. In subsequent analyses using Matlab, nose points were categorized as center, wall, or corner contact and the relative frequency of time spent in each zone was computed.
**TABLE 1**

Movement Probabilities for Each Lateral:Forward Ratio

<table>
<thead>
<tr>
<th>LFR</th>
<th>FLM</th>
<th>FFM</th>
<th>Fbackward</th>
<th>Fstop</th>
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*LFR* is the lateral:forward ratio, *FLM* the probability of lateral movement, and *FFM* the probability of forward movement. *Fbackward* and *Fstop* are the probabilities of backward movements and stopping, respectively.

**Results**

Corner frequency was high (94.05) at an LFR = 0 and decreased monotonically to a value of 1.28 at an LFR = 1 (Figure 4). At low LFRs, agents made few lateral movements, quickly moving to a wall of the arena. Once reaching a wall, the agent’s rounded snout would cause it to slide along the wall, where further
movements brought the agent into a corner. Conversely, at an LFR = 0, center frequency was negligible (2.84), increasing monotonically to a value of 87.34 at LFR = 1 (Figure 5). At high LFRs, agent behavior consisted predominantly of lateral movements, causing them to remain in the center of the arena. Between these two LFR extremes, agents systematically varied in their time spent in
corners or in the center of the arena. In contrast, wall frequency tended to remain quite low. Wall frequency slowly rose from 3.1 at LFR = 0 to 31.39 at LFR = 0.6875 before falling to 11.387 at LFR = 1.

The reciprocal relationship found between the proportion of time agents spent in corners versus the proportion of time they spent in the center of the arena was quite strong. In a regression analysis, center activity predicted corner activity with $R^2 = .962 (t(32) = 27.95, p < .001; \text{Figure 6})$. These results suggest that changes in locomotor patterns of movement can be adequately characterized by the relative proportions of center and corner activity.

Discussion

These results demonstrated that patterns of movement within an arena systematically covaried with different probabilities of forward versus lateral movement. The decoupling of forward from lateral movement and exploration of a range of probability values was inspired by rat kinematics and related literature. Moreover, probability values did not incorporate feedback from any sensory stimuli.

FIGURE 6 Depiction of agent’s body flexing in response to forces produced by its interaction with the wall.
Rat movement is commonly characterized by the regions of an arena they most frequently traverse (e.g., Alberts, Motz, & Schank, 2004; Drai et al., 2001; May et al., 2006; Paulus & Geyer, 1997; Schank, 2008). Given that a diverse array of behavioral profiles are produced by random agents, it could be that different thigmotaxic-like patterns of movement observed at Days 7 and 10 are produced with little or no sensory mediation just as reported in May et al.

Nevertheless, it remains unclear how robust these results are. Unlike rat pups, both our robots and simulated agents had rigid bodies. This morphological design may shape and constrain interactions of the agent with the arena in ways that a morphologically more realistic design would not. Or perhaps a more realistic design would add new dynamics of movement that cannot be anticipated with a rigid-bodied design. For example, May and Schank (unpublished results) modified the rigid-bodied agent design used here to create two- and three-segmented agents. Two-segmented agents were negligibly different from rigid-bodied agents run on the random architecture described earlier and for the rigid-bodied robots in May et al. (2006). Three-segmented agents, however, generated a very different behavioral profile. Whereas rigid-bodied robots produced behavior intermediate to 7- and 10-day-old rat pups, three-segmented agents produced behavior better resembling 10-day-olds. The increased flexibility of the three-segmented agents allowed them to better conform to the shapes of walls and corners. As a result, agents spent more time along walls and in corners and less time in the center of the arena.

More dramatically, in a preliminary exploration of LFR, May and Schank (unpublished results) found that at an LFR = 0, agents circumnavigate the arena for an entire trial. Rigid-bodied and two-segmented agents do not do this as they spend an entire trial stuck in a single corner, just as reported here. This circumnavigating behavior was not statistically different from the same behavior produced by rigid-bodied robots whose behavior was directly caused by sensor activation (Schank et al., 2004). It also appears qualitatively similar to circumnavigating behavior observed in drug-manipulated adults and described as thigmotaxic (Gold et al., 1989). Therefore, the behavioral effects of directional kinematics must also be explored in a morphologically more realistic agent.

**STUDY 2: FLEXIBLE AGENTS**

**Agents**

Rigid-bodied agents in Study 1 were modified to create three-segmented agents. One degree of freedom was added between the head (front third) and body (back two thirds) of Study 1’s agents by implementing a revolute joint that moved side to side like a hinge. Head rotation was limited to ± 72.5 degrees from center
and joint damping (friction/resistance) was added to create inertia of movement. This joint acted as a passive joint, only moving in response to pressure from the environment (e.g., contact with a wall or corner). A second degree of freedom was created by dividing the main body into two equal-size segments and connecting them with another revolute joint. Range of motion between these two body segments was similarly restricted to $\pm 72.5$ degrees and joint damping implemented. For both revolute joints, a double spring system realigned body segments once force was no longer being exerted by the environment. For example, if an agent hit a wall at an angle, one or more body segments would flex (Figure 6). If a movement decision caused the agent to move away from the wall, body segments would realign with the pelvis (back third). In addition, a second front load-bearing ball was added in response to new instabilities created by this design (for more details, see May & Schank, unpublished results).

Procedure

Fifty three-segmented agents were run at each of 33 LFRs (Table 1) for a total of 1,650 simulations. Agents began each trial in the center of a simulated arena facing left or right and ran for 10 simulated minutes. Parameters of movement and movement decisions were the same as in Study 1. Coordinates of the agent’s nose were sampled every 5 s and output to a text file. In subsequent analyses using Matlab, nose points were categorized as center, wall, or corner contact and the relative frequency of time spent in each zone was computed.

Results

Corner frequency was high (75.26) at an LFR = 0 and decreased monotonically to a value of 1.37 at an LFR = 1 (Figure 7). Conversely, at an LFR = 0, center frequency was 5.74 and increased monotonically to a value of 85.6 at LFR = 1 (Figure 7). Because corner frequency was much lower for three-segmented agents at low LFRs compared with rigid-bodied agents, whereas center frequency increased much more steeply for three-segmented agents (Figures 5 & 7), center and corner activity were equiprobable at an LFR of approximately 0.3 (in contrast to an LFR of approximately 0.59375 for rigid-bodied agents). Wall frequency also started out higher (18.99 at LFR = 0) for three-segmented agents and remained above 20 from LFR = .03125 to LFR = 84375. Wall frequency, however, did not systematically change as a function of LFR.

Again, an inverse relationship was found between center frequency and corner frequency. In a regression analysis, center activity predicted corner activity with $R^2 = .969$ ($t(32) = -31.05, p < .001$; Figure 8). Corroborating Study 1, these results suggest that changes in locomotor patterns of movement can be adequately characterized by the relative proportions of center and corner activity.
Discussion

Results for three-segmented agents contained both similarities with and differences from the results for rigid-bodied agents reported in Study 1. Like rigid-bodied agents, three-segmented agents generated a range of behavioral dynamics across a spectrum of LFR values. Likewise, corner and center activity
were strongly correlated. Wall contact for three-segmented agents, however, was higher on average (24.65%) than for rigid-bodied agents (16.77%). Behavioral dynamics differed at earlier LFRs, with higher corner frequency and lower center frequency for rigid-bodied agents. However, at higher LFRs, behavioral dynamics were indistinguishable (Figure 9). For LFRs close to one, morphology should not significantly influence behavioral dynamics because there is little interaction with the walls and corners of the arena. As this interaction increases, we see a divergence in the behavior of the two models. This is consistent with results reported in May and Schank (unpublished results), where three-segmented agents with May et al.’s (2006) kinematic implementation behaved more like 10-day-old pups, which do interact more with walls and corners (Schank, 2008) than 7-day-old pups, which do not. Further evaluation of these models requires comparisons with rat pup data. However, because both models produce a range of behavioral dynamics, they both suggest that the behavior of pups at different ages may be captured by a single model with different LFR values, consistent with Eilam and Golani’s (1988) behavioral kinematic analysis of rat pups.

STUDY 3: EMPIRICAL VALIDATION

Animals

All pups used for comparison were Sprague-Dawley albino rats bred in the Psychology Department Vivarium at the University of California, Davis, from
rats obtained from Taconic Farms, Inc. (Germantown, NY, USA). One hundred twenty-seven 7-day-old and 116 10-day-old pups were tested individually. Some of the data from these pups were previously published in Schank (2008).

Procedure

Pups were removed from their mother just before testing, placed in a Styrofoam container to prevent heat loss, and transported to the testing room. Pups were placed in the temperature-controlled chamber (Alberts et al., 2004; Schank, 2008; ambient and surface temperatures were 34°C). Pups were placed in the center of the arena either facing left, right, up, or down (determined randomly). The arena surface and the Plexiglas arena were cleaned with alcohol after each session to remove odor gradients.

Data were extracted from the video recordings using algorithms developed in NIH Image (see Schank, 2008; Schank & Koehlne, 2007, for a description of these algorithms). The algorithms automatically stored a stack of images from a video stream at a specified interval (e.g., every 5 s). An observer analyzed a stack of images by identifying the head and tail location of each rat by clicking the computer mouse when the cursor was in the desired position on an image and thereby recording its xy-coordinate position. These coordinates were stored in tab-delaminated text files for each stack. Additional algorithms developed in Matlab were used to compute the same metrics described in Study 1.

To determine the best fit between the model and the data for 7- and 10-day-old pups, the sum of the squared error ($SSE$) was computed for each LFR according to Equation 2. Simulation results at the LFR with the lowest $SSE$ were then compared with the rat pups (Figure 10):

$$
SSE = [FP(\text{center}) - FM(\text{center})]^2 + [FP(\text{wall}) - FM(\text{wall})]^2
+ [FP(\text{corner}) - FM(\text{corner})]^2,
$$

where $FP$ is mean frequency as a function of center, wall, and corner occupation by the pups and $FM$ is mean frequency as a function of center, wall, and corner occupation by the model.

Fifty rigid-bodied agents were run at LFR = 0.71875 to compare with 7-day-old pups and 50 rigid-bodied agents were run at LFR = 0.4375 to compare 10-day-old pups. Fifty three-segmented agents were run at LFR = 0.4375 to compare with 7-day-old pups and 50 three-segmented agents were run at LFR = 0.09375 to compare 10-day-old pups.
Results

Seven-day-old pups had a mean center frequency of 57.5, wall frequency of 24.45, and mean corner frequency of 18. For rigid-bodied agents at an LFR of 0.71875 ($SSE = 9.88$; Figure 10), there were no significant differences from 7-day-old pups on center frequency ($M = 56.99, t(49) = 0.18, p = .86$), wall frequency ($M = 26.87, t(49) = 1.07, p = .29$), or corner frequency ($M = 16.14, t(49) = 0.77, p = .45$). Indeed, agents were 0.01 standard deviations ($SD$) from pups on center frequency, 0.1 $SD$ on wall frequency, and 0.07 on corner frequency. For three-segmented agents, at a considerably different LFR of 0.625 ($SSE = 6.7$; Figure 10), there were also no significant differences from 7-day-old pups on center frequency ($M = 59.6, t(49) = 0.66, p = .51$), wall frequency ($M = 24.18, t(49) = 0.12, p = .91$), or corner frequency ($M = 16.2, t(49) = 0.74, p = .46$). Again, simulated agent means were remarkably close to pup means, within 0.06 $SD$ on center frequency, 0.01 $SD$ on wall frequency, and 0.07 on center frequency.

Ten-day-old pups had a mean center frequency of 16.63, wall frequency of 22.57, and corner frequency of 60.8. For rigid-bodied agents at an LFR of 0.4375 ($SSE = 40.45$; Figure 10), there were no significant differences from 10-day-old pups on center frequency ($M = 19.39, t(49) = 1.46, p = .15$) or corner frequency ($M = 63.3, t(49) = 0.98, p = .33$). Although there was a significant difference on wall frequency ($M = 17.3, t(49) = 2.7, p < .01$), the effect size was small ($d = 0.34$; Cohen, 1992, describes effects sizes of 0.2 as
small, 0.5 as medium, and 0.8 as large), and agents were within 0.26 SDs of pups. Three-segmented agents at an LFR of 0.09375 (SSE = 23.53; Figure 10) were also not significantly different from 10-day-old pups on center frequency ($M = 14.04, t(49) = 1.37, p = .18$) or corner frequency ($M = 59.32, t(49) = 0.58, p = .57$). There was again a significant difference on wall frequency ($M = 26.63, t(49) = 2.08, p < .05$), though the effect size was again very small ($d = 0.27$) and agents were within 0.27 SD from pups. Confidence intervals (95%) for 7- and 10-day-old rats, as well as all models, are shown in Figure 11. All means were within the confidence interval of the modeled pup (except for three-segmented agents with an LFR matching 10-day-old pups on center frequency, though confidence intervals overlap).

**Discussion**

Seven-day-old pups were best modeled by LFRs of 0.71875 (rigid-bodied) and 0.625 (three-segmented), whereas 10-day-old pups were best modeled by LFRs of 0.4375 (rigid-bodied) and 0.09375 (three-segmented). For both models, the variation of a single parameter was able to account for behavioral dynamics of rat pups at two different ages. This suggests that the ontogenetic kinematic unfolding observed in rat pups (Eilam & Golani, 1988) may also account for macrolevel behavioral patterns observed in an arena. This progression of behavioral patterns need not reflect increased sensory or otherwise goal-directed engagement with the environment.

One consequence of adding morphological realism as passive flexibility is that it appears to convert forward movement into passive turning when walls are contacted. A passively flexible agent will turn left or right when it contacts a wall even with forward movement (also see May & Schank, unpublished results). Schank (2008) used a discrete agent-based model to investigate the directional kinematics of infant rats. This model made no assumptions about body morphology of physical interactions. Directional kinematics were specified by a probability matrix for moving to adjacent cells. The main results for individuals in an arena were that 7-day-old pups made greater turns (in terms of degrees of a turn over a 5-s interval) than did 10-day-old pups, which made more lateral turns (90° turns). This is consistent with both the rigid and passively flexible agents reported here. Even though the LFR for flexible agents modeling 10-day-old rats is 0.09375, which implies a high degree of forward movement, contact with walls converts forward movement into lateral movement, especially when a passively flexible agent is “following” a wall and contacts a corner. Thus, both radically different modeling approaches agree that 7-day-old pups should exhibit a greater degree of turning than 10-day-old pups, which is consistent with the data on pup development (Eilam & Golani, 1988). Finally, the analysis of the directional kinematics in both rigid and flexible-bodied agents suggest
FIGURE 11  Corner and center activity means with 95% confidence intervals of rat pups and simulated agents (SAs).
that directional kinematics generated by an animal’s active movements may not be the same as the observed kinematics. The observed kinematics in a bounded space will include interactions with boundaries, which is reflected in Schank’s (2008) analysis. Thus, the observed kinematics will depend on the nature of body morphology and the structure of the environment.

**GENERAL DISCUSSION**

We have shown that directional kinematics and body morphology appear to play an essential role in the patterns of locomotion observed in neonatal rat development. The behavioral profile of a simulated neonatal rat systematically varies as a function of the particular value of directional kinematics (LFR). At low LFRs, agents spend more time in the corners of an arena, whereas at high LFRs, agents spend more time in the center of an arena. The transition from corner activity to center activity depends on the agent’s morphology, with an earlier transition observed for three-segmented agents. In May et al. (2006), the kinematic configuration used with a random architecture yielded results intermediate to either age group. Here, implementing a new kinematic scheme based on known rat kinematic development produced models that matched each age group fairly well. For both rigid-bodied and three-segmented agents, LFR values were identified that produced behavior similar to 7- and 10-day-old rats. These new models remain random architectures in that behavior is not sensory-driven.

In the history of the study of animal behavior, it has been recognized that random movement has a role, at least in exploratory and foraging behavior. For example, Niko Tinbergen (1950), drawing on the work of Konrad Lorenz, states,

> Instinctive behaviour often consists of two successive parts of very different kinds. An animal, in which an instinctive urge or drive is activated, starts “random,” “exploratory,” or “seeking” behaviour... Further, it is continued until the animal comes into a situation that provided the sign stimuli necessary to release the motor response of one of the centres of the lowest level. (p. 408)

Similarly, Pyke (1978) explored the extent to which random search could produce optimal foraging. In all other cases, however, the view is that behavior is instinctive or stimulus-driven. Our conjecture for locomotor behavior, a la Tinbergen and Lorenz, is that random movement is the starting point. With development or in different contexts, random movement can be shaped by changing the probabilities of turning, which we characterized by the LRF parameter. Instinctive or learned locomotor responses to stimuli are superimposed on the
directional kinematics of locomotion. This is consistent with previous work in nonmammals. For example, chemotaxis involves a random walk modified by the relative concentration of a chemogradient in both *C. elegans* (Dusenbery, 1980; Pierce-Shimomura, Morse, & Lockery, 1999) and in bacteria (Segall, Block, & Berg, 1986). In extending this conjecture to mammals, note that when, for example, a rat or mouse is trained to navigate a maze to find food, it still zigzags its way through the maze even as it follows the optimal path. Along the same lines, R. A. Hinde (1960) continues,

The central nervous system is not normally inert, having to be prodded into activity by specific stimuli external to it. Rather it is in a state of continuous activity—a state supported primarily by the non-specific effects of stimuli acting through the brainstem reticular system. Factors such as stimuli and hormones which affect specific patterns of behavior are to be thought of as controlling this activity, or increasing the probability of one pattern rather than another. Changes in strength or threshold can thus be thought of as changes in the probability of one pattern of activity rather than another. . . . (p. 212)

This contrasts with previous biorobotics studies of chemotaxis in which the robot moved forward in the absence of sensory stimulation, and concentration changes differentially modified the type of turn (toward or away from the stimulus) made by the agent (Webb, 1998). The problem of how to respond in the absence of stimulating stimuli was similarly “solved” by a default forward movement in a biorobotic study of thigmotaxis in infant rats (Schank et al., 2004) and phonotaxis in crickets (Webb, 1995). Perhaps the presumption is that as models are equipped with a larger variety of sensors and ability to integrate information, there will always be some driving stimulus. At least for some classes or organisms, this appears to be the case. For example, in describing the issues involved with developing a chemotaxis biorobotic lobster, Frank Grasso (2001) cites a number of studies of moths and blue crabs where in the absence of a chemical trail, the organism will use information from mechanoreceptors to move “cross-stream” (air or fluid) in an apparent effort to find a trail. However, these may be the exception rather than the rule.

Is mammalian behavior best characterized by kineses, taxes, or stimulus-driven behavior “all the way down”? In the absence of a complete model of single organism, it is not possible to definitively evaluate this hypothesis; however, the results here and in May et al. (2006) suggest that this may not be the case—that certain organisms, like altricial mammals, have at base random behavior, shaped by directional kinematics, body morphology, and interaction with the environment. If our conjecture is correct, then LRF may be an important control parameter we need to understand to fully explain locomotor behavior. Different patterns of movement may be explained by differences in underlying directional kinematics rather than differences in sensory processing. LFR may be
particularly important for understanding strain differences in locomotor behavior, which may aid in understanding strain differences also documented in adults (e.g., see Paulus, Geyer, & Sternberg, 1998).

LFR is one of a number of ways to characterize the directional kinematics of an animal. Our implementation of LFR employed a uniform random distribution of turns from 0 to ±72.5°. Perhaps a normal distribution of turns centered at 90° would result in different patterns of behavior. For example, in previous work on optimal foraging, Pyke (1978) measured directionality as the difference between forward and backward probabilities (i.e., \(P(\text{forward}) - P(\text{backward})\)). Directionality ranges between 0 and 1 on this measure assuming that probabilities of making discrete turns are calculated from a truncated normal distribution, which is truncated at \(-\pi\) and \(+\pi\). Thus, the variance of the normal distribution determines the directionality. If the variance approaches infinity, then probabilities are uniformly distributed 360° and directionality is 0. That is, a directionality of zero indicates that successive movements are uncorrelated (viz., the organism exhibits a lot of turns). As the variance approaches 0, the probability of moving forward approaches 1, and directionality approaches 1.

Likewise, much work is required to understand the role of morphology in locomotion. In the work presented here and in May and Schank (unpublished results), agents had a passively flexing morphology. Body flexing required interaction with the environment to create active forces on the body. In contrast, rat pups actively bend without wall or corner contact. Eilam and Golani (1988) observed that all movement types (forward, lateral, and vertical) begin with the head and conclude with the rear. The active movement of our agents was rear-driven for both three-segmented and rigid-bodied agents. If movements of the three-segmented agents progressed cephalocaudally, we might see different behavioral patterns. Ultimately, as we work out the roles of morphology (e.g., shape and flexibility) and directional kinematics, we must integrate these results with sensory input and motor output from the brain. If our hypotheses about the roles of morphology and directional kinematics are correct, then successful integrative research requires answers to these hypotheses.

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