Origin-related exploration in animals

(work in progress)

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Perhaps the most conspicuous spatial regularity of exploratory behavior in many organisms is the existence of a home site or a home base [25]. In the wild, animals have a home site to which they return regularly after exploring their home range or territory, be they, e.g., ants [39,65], bumble bees [74], millipedes [29], small mammals [9], or wolves [22]. In experimental behavioral neuroscience, the animal's "home base" refers to the animal's most preferred place, from which it performs excursions or forays into the environment [16]. Upon being introduced into a novel laboratory arena, rats establish one or two places that stand out in terms of the dwell time spent in them, the number of visits paid to them, the incidence of grooming, several behaviors that are typically performed in them like crouching, turning in place around the forequarters, and the incidence of rearing episodes performed in them [16]. High dwell time accumulated through a high number of visits also characterizes the home base of, e.g., mice [15,21,10], infant rats [34] and zebra fish [51,52].

On a large (160X160cm), empty, elevated, platform placed away from walls, devoid of objects or markers, each individual rat establishes its own home base in a specific place, often at a corner but sometimes at the center area, in a place that is idiosyncratic to it. The selection of a location and the establishment of a home base in it thus reflects an endogenous constraint, characterizing the organization of exploratory behavior, at least partly independent of proximal features located in the environment [25].

While home bases may be established in reference to distant environmental cues, rodents often select for a home base locations near edges, corners, objects, and shelters [16,10,11]. A home base is also often established at the location at which the rat was placed when first introduced into the novel arena (the point of entry [40]) or at one of the first locations in which the rat lingered following its introduction into the arena [16]. When allowed to explore an arena connected to their home cage through a doorway, mice use the home cage as a home base [21,5]. This property has been used to standardize home base location and provide a common origin in relation to which all the excursions performed by all the tested animals could be measured and compared [21,25]. See also [56].

The home base exerts its influence on the rodent's behavior across the whole exploratory basin [25]. Visits at the home base partition the path into excursions in the environment. The latter are further partitioned into progression segments and lingering (staying-in-place episodes) [14,15]. Excursions first consist in rats of slow outbound and fast inbound portions, the outbound portion consisting of intermittent progression involving multiple lingering episodes [16,33,56,57]. With repeated performance the velocity profile is reversed, the outbound portion becoming fast and the inbound portion slow and intermittent [57]. The speed of progression has been shown to correlate in rats with how well-trodden the path was, exhibiting faster progression on well-trodden (familiar) paths [57]. The distinction between the outbound and inbound portions of excursions is also evident in infant rats, which move in reference to a huddle of siblings [34].

Rats establish a home base and segment their exploration into excursions both under light and under dark conditions [62]. A role for the hippocampus [36], and for the posterior cingulate region [70], have been suggested by a comparison of the inbound portion of excursions in control rats and of the same portion in rats with damage to a variety of neural structures (fimbria-fornix [68], posterior cingulate cortex [70], Ammon’s horn and dentate gyrus [62], vestibular system [61]). The experiments were conducted in light and in dark conditions, sometimes also using the hoarding of food pellets response to increase the intensity of homing, while also examining as control the outbound portion of excursions. The loss of a straight ballistic inbound trajectory in the lesioned animals, suggests the use of path integration during the inbound portion [28,37,60,63,64,67,68,69,70]. Path integration, also called dead reckoning, is an online navigational strategy that involves processing self-movement cues (vestibular cues, proprioceptive cues, sensory flow, or efference copy of movement commands) for assessing an agent's position in reference to the origin where the movement has been initiated (for a review see [20]). Unlike intact controls, rats with hippocampal lesions did not exhibit habituation of home base behavior following four daily 30-min sessions of exposure to an experimental arena [11].

The influence of dopaminergic stimulation on the structure of home base behavior varies: with the dopamine agonist apomorphine (1.25mg/kg Sc) the coupling of behavior to locale space is eliminated completely [53]. With amphetamine (0.5-5mg/kg Sc) the home base phenomenon is preserved and enhanced as the rats establish and then consolidate stereotypic, well-trodden routes, along which they perform excursions from the home base, reducing the number of routes in a dose dependent way, increasing the routes' stereotypy, decreasing the number of stops per excursion and increasing the number of bases [17,18]. Chronic administration of the dopamine D2-3 stimulant quinpirole profoundly increases the number of visits to the home base and reduces excursion duration [54]. The excessive, repetitive returns to the home base and the associated compulsive checking have been considered an animal model for obsessive-compulsive disorder (OCD [5554,72]).

In intact mice, repeated performance of excursions is associated with a progressive gradual growth in their extent and complexity [21]. The buildup in the extent of excursions involves a gradual increase in the length of maximal excursions, shorter and even very short excursions being performed all along [5]. Quantification of this buildup involves therefore a method that estimates the "envelope" of excursions' length rather than an estimation of means or averages of excursion length; the growth rate appears to be strain specific [5]. The growth in complexity of excursions involves several phenomena: i) a transition from monotonical excursions, consisting of a single unidirectional outbound portion and a single unidirectional inbound portion, to excursions including an increasing number of back-and-forth progression segments performed during the inbound portion of the excursion ("Shuttles" [21]), ii) a gradual increase in the number, extent, and complexity of incursions, forays away from the wall and back to it [21,33], and iii) a gradual increase in the number, extent, and complexity of ascents on the wall (in arenas including a wire mesh wall) [66].

In an arena surrounded by smooth walls the mice explore the different surfaces of the arena in a fixed order, exhausting each surface before proceeding to the next one. At first, they map the terrain around the doorway (so called "garden"), (zero-dimension space), then the borderline surrounding the arena (one-dimension space), then the radial dimension, away from the borderline and toward the center (two-dimension space), and only then proceed with jumping on the wall (three-dimension space). In this setup the mice engage in building up one dimension at a time for extended slabs of behavior [21,25] (**Figure 1**).

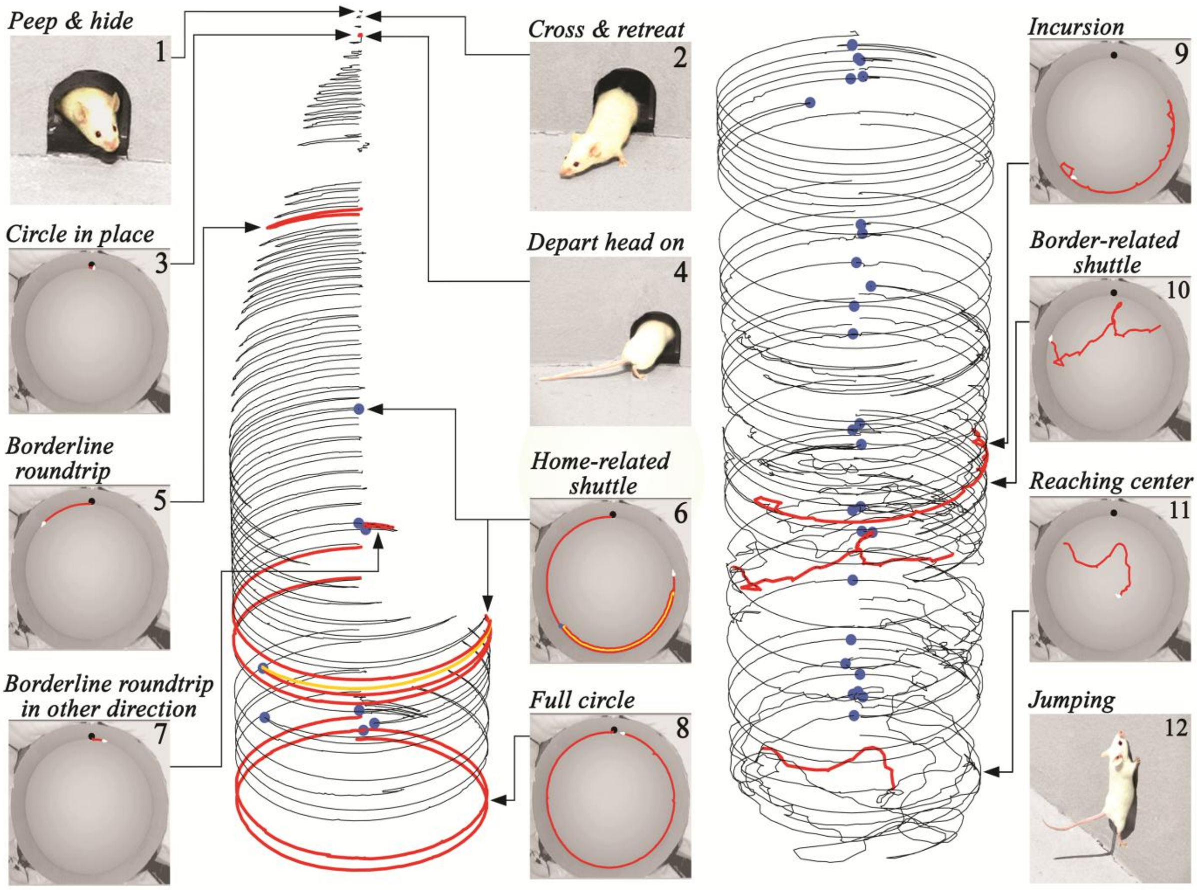

Figure 1. The moment-to-moment developmental sequence of free exploration from a sheltered homebase. The developmental landmarks in a specific BALB/c mouse-session performed across a 3-h period. The spiral proceeding from top to bottom, first in the left and then in the right column, presents the time-series of 2-D locations on the path traced by the mouse. The enumerated figure-inserts show the 12 landmark motions described in the text, traced in red within the arena, and on the spiral. Blue dots indicate instances in which the mouse approached the cage doorway and did not enter the cage (cage-skips), or stopped short of returning all of the way home during a return (Home-related-shuttle). Absence of a blue dot implies departure into home-cage. Yellow path stands for the return portion within a Home-related-shuttle. Courtesy of Fonio et al., PNAS [21].

Changing the affordance of the vertical wall by attaching a wire mesh to it to enable climbing disrupts the absolute order but preserves modularity: the mice start with mapping the garden and the borderline dimension, but then alternate between the radial dimension ("incursions") and the vertical dimension ("ascents"). Most important, exploring each dimension involves separate, sustained attention to it: an initial series ("bout") of borderline segments precedes alternating bouts of incursions and bouts of ascents (Video demonstrating the modular performance of incursions and ascents). Single occurrences of these motion types are rare. The performance of bouts as an integral part of the buildup in excursions supports the view that exploratory behaviour is modular, consisting, in this setup, of three distinct components (dimensions), all of which grow and differentiate independently of each other [66].

Another feature demonstrating the connectedness between the home base and movement in the environment surrounding it is present in rats but not in mice: it is the slow and then fast increase in home base attraction with every additional lingering (stopping) episode, also expressed as the existence of an intrinsic upper bound on the number of stops [25]. The upper bound is not increasable by increasing arena size. As a rat leaves the home base, home base attraction increases with every additional stop performed by it, first slowly and then fast. This cumulative process of attraction may be concluded after each stop, as long as the number of stops does not exceed an intrinsic upper bound; once the upper bound is reached, the rat concludes that excursion and returns to base without stopping even when far away from the home base. In a large arena, the rats extend inter stop distances rather than cross the upper bound on the number of stops per excursion [23]. The same phenomenon has been observed in voles [19]. The existence of an upper bound is demonstrated by showing that the number of stops per excursion is following a uniform distribution: however large the number of observations, the upper bound is hardly crossed. This observation supports stopping (lingering) as a kinematic quantity indicating some form of measurement by the animal in reference to the home base. It also validates visits at the home base as a natural suture between excursions, and demarcates excursions as particulate processes of exploratory behavior [24].

Moving in reference to a home base is part of a more general phenomenon of organisms' movement in reference to origins (origin-related behavior [23]), be the origin a natal fruit in fruit flies [12,50]; the center of a large circular structure resembling a mandala (https://www.youtube.com/watch?v=p1PID91sEW8; BBC-Earth , Life Story Ep05 - Courtship - Puffer Fish (From Netflix)), constructed by the male pufferfish *(Torquigener sp., Tetraodontidae)* on the sea bed and playing a role in female mate choice [30]; a favorite place in the ring, to which bulls retire after being fatally wounded by the toreros in a corrida [38]; the changing location of a mother as baby chimpanzees roam across wild terrain [44]; or a stationary mother in reference to whom human infants explore a room [1,7]. Origin-related exploration is also performed in wall hugging animals, as they perform incursions, forays into the arena center that start and end near the wall [33,21], and ascents, involving climbing up and down in reference to the ground. Identification of the origins used by organisms during the performance of such *sequences of repeated motion*, the measurement of the organism's behavior in reference to these self-selected origins, and the demonstration of regular growth and differentiation in reference to them supports the establishment of their status as intrinsic natural references [24] (figure 2) [5,21].

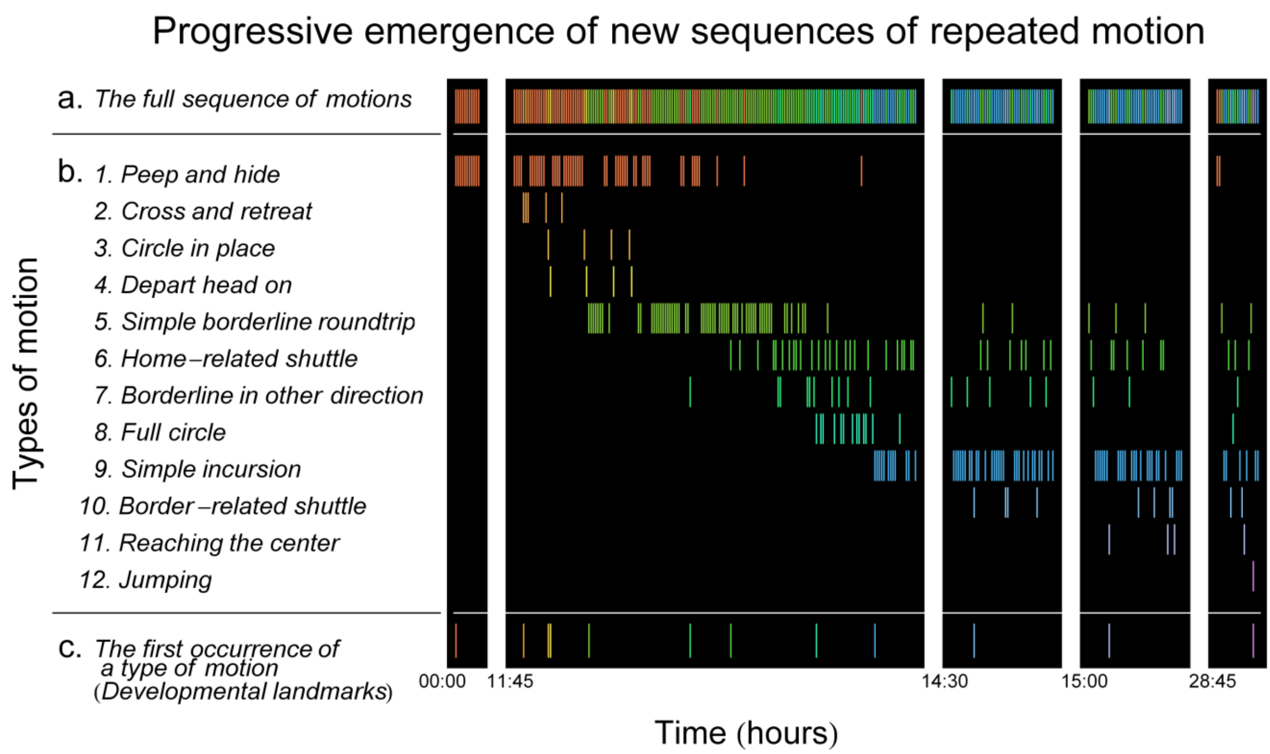

Figure 2. Four successive intervals of free exploratory behavior from a sheltered homebase in a novel arena of a selected BALB/c mouse. A sequence of motion types, each represented by a distinct color within the top horizontal line, is composed of sequences of repeated motion, each represented within an especially dedicated horizontal line. As shown, the sequences emerge successively in a prescribed order. The sequence of sequences is represented in the bottom horizontal line by the first performance of each of the landmark motion types. Courtesy of Benjamini et al., PNAS [5].

The connectedness [43,47] exhibited between the home base, the excursions, the progression segments and lingering episodes, and the outbound versus inbound portions, suggests that origin-related exploration might be homologous in vertebrates and perhaps also in arthropods [13], sharing the same architectural plan of movement in allocentric space. The connectedness that unfolds at the kinematic level calls for a search for a corresponding connectedness at the neural level. If the measures are indeed homologous then the likelihood for discovering a corresponding neural plan sharing a parallel connectedness would be increased. Such correspondence, however, has been investigated so far mostly with regard to the inbound-outbound parts of excursions, suggesting the involvement of the hippocampus in mediating the structure of the inbound portion of excursions [63].

Understanding the organization of living anatomical structure by studying its morphogenesis is standard in comparative anatomy [3,4,25]. Since behavior, navigation included, is an extension of anatomy [35], this also applies to navigational behavior. Measuring the morphogenesis of behavior in reference to the origin(s) used by the animal is basic common sense [24]. The home base is one such reference, shared by vertebrates and arthropods, and it is used during navigation. Using the kinematic home base variables and their connectivity as a search image in the pursuit of the key neurophysiological measures that support them, and measuring their activity in reference to the animal's home base is only to be expected. Remarkably, however, the extensive study of map-like representations of physical space originated already one [27] and four [42] decades ago, and recently map-like representations of familiar and novel virtual space [45] in the brain focus on the neural correlates of only a small fraction of the navigational variables isolated in home base behavior. The currently prevailing method of studying the neural correlates of location [27,41], head direction [48], speed [32], and proximity to boundaries [49], while ignoring their morphogenesis in reference to the home base, and their connectivity to all the other validated home base related measures, has perhaps led to the mistake of ascribing to the hippocampus and the medial entorhinal cortex the function of representation of spatial navigation while they now appear to serve a more general mechanism, coding a broad range of diverse, continuous cognitive processes [2].

A current approach to the analysis of behavior adheres to the view that locomotor and exploratory behavior is a sequence of discrete patterns [58]. To support that view the phenotypers ignore morphogenesis by studying full blown behavior, avoid measuring behavior in reference to natural origins, segment the flow into discrete, basically fragmented patterns, and then use conditional probabilities to partly re-establish connectivity e,g., [6,8,31,73]. The morphogenetic continuity of the growth and differentiation processes characterizing home base behavior challenges this view, offering an alternative whereby excursions, incursions, and ascents are dynamic natural kinds [46,59] behaving not unlike a living anatomical tissue (Video demonstrating the growth and differentiation in the ascents of a selected mouse). The perception of behavior as an extension of anatomy and the use of morphogenesis in the study of behavior are after all old ethological imperatives yet to be implemented [26].

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