Home base

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A conspicuous spatial regularity in the exploratory behavior of many organisms is the existence of a home site or home base. In the wild, animals have such site to which they return regularly after exploring their home range or territory, be they, e.g., ants, bumble bees, millipedes, small mammals, or wolves. In behavioral neuroscience experiments, the animal's "home base" refers to its most preferred place, from which it performs excursions or forays into the environment (Eilam & Golani, 1989). Upon being introduced into a novel laboratory arena, rats establish one or two places that stand out in terms of the time spent in them, the number of visits paid to them, and the incidence of grooming, and other behaviors that are typically performed in them, like crouching, turning in place around the forequarters, and the high frequency of rearing episodes performed in them. An accumulation of time acquired through a high number of visits also characterizes the home base of, e.g., mice (Fonio et al., 2009; Benjamini et al., 2011), infant rats, and zebra fish (Stewart et al., 2011).

The conspicuousness of the home base phenomenon begs an examination of its significance in spatial cognition. The currently most common ways of studying spatial cognition involve the study of map-like representations of physical space in the brain, and the computational and neural analysis of navigational strategies involving different ways of information processing like piloting, dead reckoning and the use of cognitive maps. The cognitive significance of the home base has been studied by using a complementary, ethological strategy, of obtaining a view on the organization of spatial cognition by studying the growth and differentiation of moment-to-moment spatial behavior (Gomez-Marin et al., 2016).

On a large platform placed away from walls, devoid of objects or markers, each individual rat will establish its own home base in a specific place, often at a corner but sometimes in the center area, in a location that is idiosyncratic to it. The selection of a location and the establishment of a home base in it thus reflect an endogenous constraint, characterizing the organization of exploratory behavior, independent, at least partly, of proximal features located in the environment. Home base location constrains cognitive spatial behavior.

The home base exerts its influence on the rodent's behavior across the entire explored area. Visits to 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) (Drai et al., 2000). In rats, excursions initially consist in slow outbound and fast inbound portions, the outbound one comprising intermittent progression involving multiple lingering episodes (Tchernichovski et al., 1998). With repeated performance the velocity profile is reversed, as the outbound portion becomes fast and the inbound one slow and intermittent. The speed of progression has been shown to correlate in rats with how well-trodden (familiar) the path is, exhibiting faster progression on well-trodden paths. It has been claimed that the rodents maximize novelty signal-to-noise ratio during each excursion, where novelty is defined as the accumulated information gain. In this view, the rodents maximize novelty during outbound exploration, and use novelty-triggered withdrawal-like retreat behavior, exploring the environment in a novelty-descending sequence. The piecemeal occupancy of a novel environment involving multiple repetitions of excursions characterized by incremental growth highlight how constrained behavior is during its morphogenesis. This contrasts with the view projected by mainstream studies of navigation, which study the map-like representations of physical space in the brain. These studies dispense with moment-by-moment morphogenesis, and focus on full blown behavior, at a stage when navigation appears to be relatively unconstrained. To become relatively free, spatial cognition requires, however, growth and differentiation.

The observation that the homeward trajectory of the excursion in rats is relatively straight and ballistic led to a series of studies, performed by Whishaw and colleagues of lesioned animals, demonstrating a loss of that type of trajectory in the lesioned animals. This loss has been interpreted to indicate the use, in intact animals, of the dead reckoning strategy during the inbound portion. It has been suggested that the lesioned part has been involved, when intact, in the computation of the inbound trajectory both in light and dark conditions. The brain structures claimed to be involved in computing the ballistic inbound trajectory included the hippocampus, the posterior cingulate region, the fimbria-fornix, the posterior cingulate cortex, Ammon's horn and dentate gyrus, and the vestibular system (e.g., Wallace et al., 2006).

While growth and differentiation of the exploratory repertoire in intact rats imply more freedom, dopaminergic drug stimulation induces a cognitive shutdown of freedom: amphetamine (0.5-5mg/kg Sc; Eilam&Golani 1994) and more so chronic treatment with the dopamine D2-3 stimulant quinpirole consolidates an increasingly smaller number of well-trodden routes along which increasingly shorter excursions are performed; and apomorphine (1.25mg/kg Sc) disconnects behavior from locale space (Szechtman et al., 1985). The excessive, repetitive returns to the home base and the associated compulsive checking with quinpirole have been considered an animal model for obsessive-compulsive disorder (OCD; Szechtman & Woody, 2004).

In intact mice, the growth in complexity of excursions is modular (Figure 1), first enacting in an arena surrounded by a smooth wall the terrain around the doorway (so called "garden"), (zero-dimension space; https://www.youtube.com/watch?v=Oc-JEn-j1xM), then the borderline surrounding the arena consisting of monotonical outbound and monotonical inbound movement (one-dimension space; https://www.youtube.com/watch?v=rOHzC__qWkY), then the inbound portion becomes non-monotonical, incorporating so-called shuttles on the inbound direction (https://www.youtube.com/watch?v=ykGq3jNNiBw) , and then the radial dimension, away from the borderline and towards the center (two-dimension space; https://www.youtube.com/watch?v=OqhHRCDD5nU), and only then jumping up on the wall (three-dimension space). A main feature of this process is the modularity of growth: the mice engage in building up one dimension at a time for extended bouts of behavior (Fonio et al., 2009). The fact that they enact space on a dimension by dimension basis, suggests that space is composed of locally integrated "physiological dimensions", which amalgamate into a functional unity. Modularity is thus a major built-in constraint on attention and cognition.

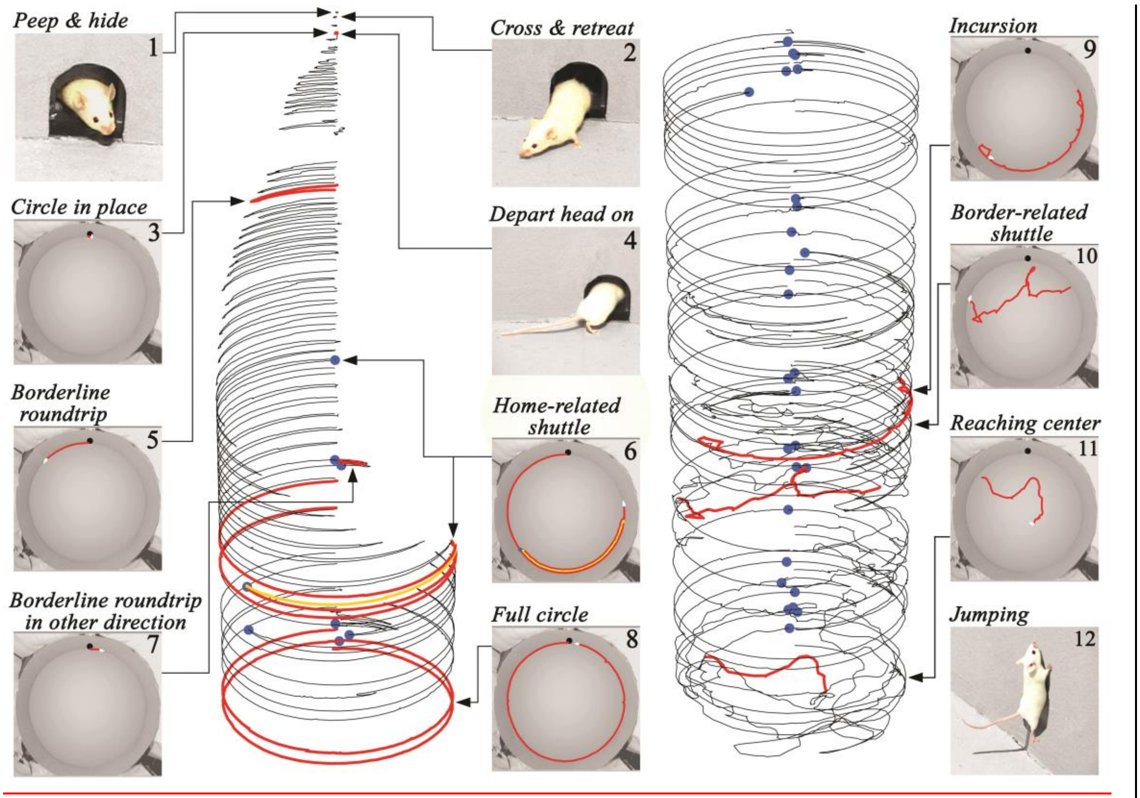

Figure 1. The moment-to-moment developmental sequence of free exploration from a sheltered homebase. The developmental landmarks in a specific BALB/c mouse-session performed across a 3-h period. The spiral proceeding from top to bottom, first in the left and then in the right column, presents the time-series 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., 2009.

Another major constraint, exhibited in rats but not in mice is the initially slow and then fast increase in home-base attraction with every additional stopping episode, also expressed as the existence of an intrinsic upper bound on the number of stops. Once the upper bound is reached, the rat concludes the excursion and returns to base without stopping, even when far away from the home base. In a large arena, rats extended inter-stop distances rather than crossing the upper bound on the number of stops per excursion (Golani et al., 1993). The same phenomenon has been observed by David

Eilam in voles. This constraint implies some form of measurement performed by the animal in reference to the home base.

The connectedness (Saint-Hillaire 1822) 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 (Cohen et al., 2015), 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 of discovering a corresponding neural plan sharing a parallel connectedness will be increased. Such correspondence, however, has been investigated to date mostly with regard to the inbound-outbound parts of excursions, suggesting the involvement of the hippocampus in mediating the structure of the inbound part of excursions (Wallace et al., 2006). Understanding the organization of a living anatomical structure by studying its morphogenesis is standard in comparative anatomy (von Baer, 1967). Since behavior, navigation included, is an extension of anatomy (Lorenz, 2013), this also applies to navigational behavior. Measuring the morphogenesis of behavior in reference to the origin(s) used by the animal can thus reasonably be expected (Golani, 2012). The home base is one such reference, shared by vertebrates and arthropods, and it is used during navigation. It would thus be expected that the home-base kinematic variables and their connectivity would be used as a search image in the pursuit of the key neurophysiological measures that support them. It would also be expected that these neurophysiological variables would be measured in reference to the animal's home base. In summary, home-base related exploration constitutes a constrained process of origin-related growth and differentiation involving the emergence of freedom of movement along specified, modulated endogenous dimensions, reflecting a gradual emancipation of the animal's exploratory path from both endogenous and environmental constraints.

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