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Behavioral and neural subsystems of rodent exploration

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ABSTRACT

Animals occupy territories in which resources such as food and shelter are often distributed unevenly. While studies of exploratory behavior have typically involved the laboratory rodent as an experimental subject, questions regarding what constitutes exploration have dominated. A recent line of research has utilized a descriptive approach to the study of rodent exploration, which has revealed that this behavior is organized into movement subsystems that can be readily quantified. The movements include home base behavior, which serves as a central point of attraction from which rats and mice organize exploratory trips into the remaining environment. In this review, we describe some of the features of this organized behavior pattern as well as its modulation by sensory cues and previous experience. We conclude the review by summarizing research investigating the neurobiological bases of exploration, which we hope will stimulate renewed interest and research on the neural systems mediating these behaviors.

1. Introduction

Animals occupy territories in which resources such as food and shelter are often distributed unevenly. Given the challenges involved in securing resources while at the same time minimizing the risk of predation, it is critical that animals optimize their movements to efficiently explore the space. While studies of exploratory behavior have been conducted in a wide number of animal species (Berlyne, 1960; Menzel, 1973; Renner, 1990), research involving the laboratory rodent as an experimental subject has largely dominated the field (Barnett, 1963; Drai, Kafkafi, Benjamini, Elmer, & Golani, 2001; Eilam & Golani, 1989; Whishaw & Whishaw, 1996). The concentration on rodent research stems from the fact that their exploratory activity can be assessed in a variety of test situations including multi-choice mazes, cylinders, open-fields, and in response to brain manipulation (Clark, Hines, Hamilton, & Whishaw, 2005; File, 1985; Gharbawie, Whishaw, & Whishaw, 2004; Hall, 1934; O'Keefe & Nadel, 1978; Renner, 1990; Whishaw, 1974). An additional advantage of using rodents as subjects for experimental study is that, although behavior is variable from animal to animal, some movements are identifiable across tasks and rodent species. For instance, orientation responses towards environmental stimuli have been well characterized (Pavlov, 1927; Sokolov, 1963). Other movements that can be readily measured include the vertical movements made by animals when rearing up on their hind legs or against surfaces (Gharbawie et al., 2004; Lever, Burton, & O'Keefe, 2006), and general locomotor activity that takes an animal from one location to another (O'Keefe & Nadel, 1978).

Nevertheless, several challenges to the quantification of exploratory behavior remain. For example, rodent exploratory movements are often described as stochastic or random, and lacking moment-to-moment consistency (Morris, 1983; Tchernichovski & Golani, 1995). Others have argued that rodent behavior in open-fields and complex mazes are difficult to describe quantitatively, and much of the focus has remained on simple end-point measures such as the cumulative distance traveled, the number of photobeam crossings during a test, and locomotor speed. A second difficulty in quantification is whether exploratory

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behavior should be formulated in terms of the movements involved (Teitelbaum, Schallert, DeRyck, Whishaw, & Golani, 1980), or in relation to the underlying motivations or goals (Morris, 1983; Renner, 1990; Whishaw, Gharbawie, Clark, & Lehmann, 2006). Indeed, exploratory activity is often described in terms of concepts such as fear and anxiety (Blanchard, Kelly, & Blanchard, 1974; Gray, 1982; Montgomery, 1955; Russell, 1973), curiosity and information-gathering (Berlyne, 1960), and the acquisition of spatial "maps" of the environment (Nadel, 1991; O'Keefe & Nadel, 1978).

A recent line of investigation has utilized a descriptive approach to the study of rodent exploratory behavior, which involves breaking the movements down into simpler behavioral subsystems which, when recombined, reconstitute the original full pattern of exploratory behavior (Golani, 2012; Teitelbaum et al., 1980; Whishaw, Cassal, & Majchrzak, 1994). Such descriptions have revealed that the structure of exploration is far from random, and is composed of movement subsystems that can be readily quantified (Eilam & Golani, 1989; Golani, 2012; Golani, Benjamini, & Eilam, 1993; Hines & Whishaw, 2005; Wallace, Hines, Pellis, Whishaw, 2002; Wallace, Hines, Whishaw, 2002; Whishaw, Hines, & Wallace, 2001). In this review, we describe some of the central features of this organized behavior pattern. Much of our discussion will center on the observation that rodent exploratory behavior is organized around specific environmental locations termed "home bases" (Chance & Mead, 1955; Eilam & Golani, 1989). It has been argued that home bases serve as an organizational feature of rodent locomotor activity from which exploratory trips or excursions are made into the remaining environment. Although this rodent behavior pattern appears early in development and is likely a behavioral primitive (Loewen, Wallace, & Whishaw, 2005), the organization of these movements can be modulated by sensory cues as well as previous experience with environment stimuli (Clark et al., 2005; Lehmann, Clark, & Whishaw, 2007). We conclude this review by summarizing work on the neurobiological bases of rodent exploration, which we hope will stimulate renewed interest and organize future thinking for the study of exploratory behavior.

2. Behavioral subsystems of rodent exploration

2.1. Rat home base behavior

Early studies investigating the exploratory movements of rodents have remarked on the natural tendency of animals to establish preferred "home" locations from which they make excursions into the remaining environment (Chance & Mead, 1955). For instance, feral rats maintain home burrows from which they organize their foraging and avoidance of predation (Barnett, 1963; Whishaw & Whishaw, 1996). Eilam and Golani (1989) provided one of the first experimental characterizations of home base behavior by placing wild rats in a large open environment devoid of a shelter or local cues. Over a 1-h period, rats visited several locations, but restricted their visits to one or two of these locations. Rats tended to spend a disproportionate amount of time stopping at a single location (10 times more than the second location). A stop or pause was defined as the absence of active movement, forward or backwards, and lasting longer than one second. The duration of stops made at this preferred home base increased as a function of test duration. Eilam and Golani additionally observed a particular set of behaviors at the home base. Grooming, for instance, was almost exclusively expressed at the home base. Bouts of grooming were typically followed by excursions into the remaining environment, or prolonged crouching in place. Other behaviors at the home base included long duration rearing movements, and circling or pivoting behavior, that latter of which likely consists of sniffing the maze substrate. In sum, Eilam and Golani's seminal study described a pattern of regionally restricted behavior characterized by grooming, rearing, and circling behaviors.

Home base behavior by rats has been reproduced in subsequent studies using featureless environments or in complete darkness (Fig. 1**A**) (Hines & Whishaw, 2005), but the behavior can also withstand changes in enclosure size and stimulus complexity (Eilam, 2004; Golani et al., 1993; Whishaw et al., 2006). Although these observations indicate that home base behavior is robust despite changing test situations and contextual features, Eilam and Golani (1989) noted a tendency for behavior to form at the edges of mazes, especially at the corners of square open-fields. Thus, home bases can be modulated to some degree by salient environmental stimuli and environment shape. Whishaw and colleagues investigated this relationship further by placing objects or small shelters in the proximity of the open-field (Clark et al., 2005; Lehmann et al., 2007; Wallace, Hines, Pellis et al., 2002; Wallace, Hines, Whishaw et al., 2002; Whishaw et al., 2001). For example, Hines and Whishaw (2005) placed a large dark cue next to an open field, but just out of reach of the rat. It has long been known that rats are attracted to dark locations in an environment (Whishaw, 1974), and it was therefore hypothesized that animals would establish their home bases near this cued location. As expected, rats rapidly visited the cued location and spent a significant amount of time in that segment of the open-field (Fig. 1**B**). Home base behavior at the cued location was similar to home base behavior in featureless environments, including the performance of circling, grooming, rearing, and slow lingering movements. In a follow-up test, the animal was removed from the field and the cue was moved to another location along the edge of the open-field. In response, rats changed their home bases locations so that it was maintained in relation to the moved cue. Hines and Whishaw (2005) reported that in some test sessions, rats would even establish home bases in relation to objects located along the testing room walls, such as a book shelf, suggesting that the behavior can be influenced by distant room cues.

In some studies, a configuration of proximal cues has been provided within the confines of the open-field or just adjacent to the field (Lehmann et al., 2007; Yaski & Eilam, 2007). Whishaw and colleagues have reported a strong tendency for animals to evenly distribute their home bases across equivalent objects (Clark, Hamilton, & Whishaw, 2006). However, when competing objects provide different sensory information, there is a clear preference for one cue over the other. For instance, Lehmann et al. (2007) placed a large black box near one side of an open field, but far enough away from the maze such that the rat could not touch the object, but could still be seen. On the opposite side of the maze, a white wall occupied a small segment of the open-field, and was close enough to the field so that it could be used as a tactile cue. The two cues were available in a 30 min exploration session repeated over four days. Although rats formed two home bases, one adjacent to the black box and another next to the white wall, by the fourth day of testing