Neglected aspects of exploratory and investigatory behavior

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This paper consists of a review of the literature on exploratory and investigatory behavior, with special attention to aspects of behavior that are clearly part of exploration and about which little is known. In accord with previous examinations of exploration, it is argued that exploration serves the function of information gathering. In addition, it is contended that the devlopment of comprehensive models of exploration would serve to benefit greatly both the study of basic processes in cognition and studies of the neurobiology of learning and memory. Most data available as of this writing focus on the spatial character of exploration, but the open-field test most commonly used has serious conceptual and methodological flaws, which are discussed. A larger problem lies in the scarcity of knowledge about other aspects of exploration—that is, investigation of objects. Finally, this paper argues the need for extensive descriptive information about the spontaneous exploratory behavior of rats. Such an account, if available, could be used as benchmark data for establishing the basic behavioral units in spontaneous investigation and for studying the effects of diverse central nervous system interventions on behaviors previously shown to be involved in the acquisition of new information—that is, learning.

In 1961, Bindra argued that the study of nontask behaviors has been inappropriately neglected in psychology, and that spontaneous activity can reveal much about the nature of behavior. In 1990, it is still appropriate to make such a statement. The purpose of this paper is to assess the current state of knowledge about the spontaneously occurring pattern of exploration in the rat, and to propose fruitful areas for future research.

The definition of exploration has historically been determined, in effect, by what could be easily measured. This has led to a proliferation of uses of the term, including conflicting operational definitions, resulting in considerable confusion in the literature. In this paper, an alternate, expanded view of exploration will be advocated, and examples of how this view may prove useful within psychobiology will be offered. Further refinement of the concept of exploration could be achieved through a combination of two different approaches. The first is inductive, composed of identifying instances in which animals are doing what we *want to say* is exploring and describing in objective terms what is actually going on. The second approach is to define the term and then devise measurement methods consistent with that definition. Studies based on these approaches would result in the development of a detailed, conceptually based descriptive account of exploratory behavior. As described in the sections to follow, this account could serve both studies of animal cognition and the search for the neurobiological substrates of learning and memory.

Definitions of Exploratory Behavior

Rats investigate their surroundings, and will do so when satiated, placing this behavior outside the context of immediate foraging for food or water; exploratory behavior is generally considered to be a form of spontaneous, uncoerced behavior. This phenomenon has been a subject of interest for many years; both Small (1899) and Slonaker (1912) made at least brief mention of apparently inquisitive behaviors in laboratory rats. Many explanations have been proposed; most invoke some type of motivational construct such as the concept of exploratory drive or some variant (Berlyne, 1955; Fowler, 1965; Montgomery, 1955), although some have taken a broader perspective (e.g., Barnett, 1958).

In the laboratory, exploration has often been viewed as a nuisance phenomenon rather than a behavior worthy of investigation in its own right. Much of the empirical attention directed toward exploration has been in the context of attempts to limit the occurrence of this phenomenon or to place it within the context of drive-reduction interpretations of behavior (Montgomery, 1953a, 1953b, 1955). Harlow, Harlow, and Meyer (1950) proposed that curiosity was its own drive, reviving a proposal that predated the heyday of drive-reduction models (Nissen, 1930). As drive-related explanations of behavior fell out of favor, however, the primary reason given for the study of exploration in the 1950s and early 1960s disappeared, and the study of exploration practically vanished.

Although there has lately been some renewal of interest in exploration (see Archer & Birke, 1983; Voss & Keller, 1976/1983), there are still major gaps in our understanding of the structure and function of this aspect of behavior.

The use of the term "exploration" in the title or keyword list for a paper is not instantly informative; without specification of the dependent variables upon which data were collected, the term could carry any of several implied definitions. Golani, Wolgin, and Teitelbaum (1979) did elegant and detailed work on movement patterns (specifically, recovery of movement patterns after hypothalamic lesions), but used the term "exploratory" behavior to describe rats' actions while trapped on a relatively small (64 × 46 cm) platform with an overhead mirror under klieg lights and a 16-mm motion-picture camera clattering away nearby.

Most operational definitions of exploration have equated locomotion (i.e., change of spatial location) with exploratory behavior. O'Keefe and Nadel (1978), for example, explicitly defined exploration as "a direct response of the animal to the detection of a mismatch by the locale system" (p. 242). In most cases, however, the reader can only infer the author's definition of exploration from the dependent variables employed.

Methodological Problems with the Open-Field Test

Beginning with a definition of exploration limited to locomotion, it is not surprising that the data-gathering technique used most often is the open-field test introduced by Hall and Ballachey (1932), or some variant of it. Neither data from the open field nor the view of exploration implicit in the use of the open field to measure it is, however, complete (as will be discussed later in this paper) or free of problems. Specifically, the open-field test has serious flaws as a measure of spontaneous behavior. Considerable evidence exists that measures of locomotion in the open field may, in fact, often be measures of the subject's attempt to escape from the open field. Welker (1957) showed that in forced exploration, typical of most studies in which the subject has no option but to remain in the field, much of the rat's behavior can be reasonably interpreted as escape-related. Similarly, Suarez and Gallup (1981) have shown that, when an observer is present, the open-field situation evokes predator-avoidance reactions in chickens. Whimbey and Denenberg (1967), in a factor analysis of open-field data, reported the emergence of both "exploration" and "emotionality" factors, but did not offer a method for post hoc disentanglement of these factors. Maier, Vandenhoff, and Crowne (1988) performed an extensive principle components analysis on several behavioral tasks, including the open-field test, and were unable to clarify the relationship between emotional reactions and exploration in this test. For continuing debate on the meaning of open-field data, see the exchange between Walsh and Cummins (1976), Royce (1977), and Walsh and Cummins (1978).

It seems clear that the standard open-field paradigm is inadequate for the elicitation of unconfounded spontaneous exploration. In spite of this, the term "exploration" is still used indiscriminately in situations in which the subject may, at worst, be doing nothing of the sort and, at best, is engaged in only a situationally limited subset of exploratory behaviors. The open-field test is therefore an inappropriate technique when the full range of animal exploratory behavior is the subject of study. Conversely, use of the term "exploration" to describe studies in which gross locomotor activity is the only dependent variable should be discontinued.

Costs of Exploration

Any hypothesis about the function of exploration must also take into account the costs incurred by exploratory behavior. These costs are both logically necessary (i.e., time and energy are expended that could otherwise be used in other activities) and demonstrated by experimental evidence. Glickman and Morrison (1969) showed an inverse relationship between some measures of open-field locomotion and later survival under predation. Metzgar (1967) manipulated habitat familiarity in voles (*Microtus pennsylvanicus*) and found increased susceptibility to predation in voles unfamiliar with the territory, presumably because of increased activity in newcomer voles. Ambrose (1972) reported similar findings using white-footed mice (*Peromyscus leucopus*). Roeder, Chetcuti, and Will (1980) found higher death rates in rats that were more active and more likely to leave a protective shelter when placed in an enclosure with a polecat.

Aside from risk, animals will willingly tolerate costs for an opportunity to explore: Small (1899) reported that some food-deprived rats would choose an opportunity to investigate a new place rather than eat. Nissen (1930) showed that rats would endure electric shock (by crossing an electrified grid floor) for an opportunity to explore a novel, object-filled Dashiell maze. Both Myers and Miller (1954) and Montgomery (1954) showed that opportunity for locomotor exploration is sufficient reward to influence other behaviors. Exploration is a robust phenomenon; the simplest explanation for its existence is that the benefits of this group of activities outweigh its costs and associated risks. Exploration must, therefore, hold some intrinsic value for animals.

The Function of Exploration

Although it is logically possible that exploration is nothing more than a behavioral expression of neural "noise," this seems unlikely; the idea that exploration must serve some function is compelling. The hypothesis that exploration might be a part of animal information processing has long been a common theme. Welker (1961) stated that "learning invariably occurs in any situation that evokes exploration" (p. 201). Glickman and Sroges (1966), and more recently Toates (1983), have offered similar hypotheses. It is this view of exploration that leads to the

hypothesis that exploration is an expression of a tendency to occupy time not required for satisfaction of immediate needs with the gathering of information. This hypothesis would propose that animals gain information by exploring, resulting in storage of data against future need in much the same way that feeding can result in the storage of calories against future need (similar ideas have been expressed previously by Inglis, 1983, and Cowan, 1983). The potential that learning and memory could be studied through exploratory behavior has not, however, been fully exploited.

There is evidence for learning during spontaneous exploratory activity, dating back to the latent learning studies of Blodgett (1929) and Tolman and Honzik (1930), wherein subjects form cognitive maps of spatial arrangements without the incentive of experimentally provided reward. Wilz and Bolton (1971) showed that relocation of objects within a familiar arrangement evokes increases in investigatory behavior; this result demonstrates that rats are capable of remembering object locations. Poucet, Chapuis, Durup, and Thinus-Blanc (1986) have recently discovered that hamsters share this ability. Albert and Mah (1972) extended the latent learning findings by establishing that animals can subsequently show memory for the location of an already-relevant stimulus discovered through locomotor activity. These are, however, essentially questions of spatial learning. Furthermore, these studies were designed so that even random locomotion would have exposed the subject to the information to be learned. Exploration, if we view it as functionally meaningful, cannot be treated as the animal equivalent of Brownian motion.

Studies of patrolling describe animals moving through established home ranges, often in a highly regular manner (Cowan, 1983). The function of such repeated traversals of already-familiar terrain is probably to search for new environmental features and update memory to include these features. Patrolling animals show impressive spatial memory, but useable knowledge of environmental features (i.e., objects) must involve more than encoding just object location (see Cowan, 1976, for data about reactions to new objects in familiar locations). A complete memory for objects in the environment would also include knowledge of their physical characteristics and what expectancies are associated with them. This, in turn, requires active investigation of inanimate features of the environment as well as noting their locations. Any view of exploration that sees it as related to learning must recognize that the particular behaviors of the exploring organism, or behavioral topography, can play a critical role in the nature and quantity of information obtained.

Expanded Methods of Measurement

The past decade has seen a substantial increase in the availability of techniques for automated recording of simple aspects of behavior such as location (Sanberg, 1985), from which locomotion can be inferred. Automated recording systems offer the advantage of avoiding the use of observer judgments and the possibility of accompanying observer biases. Some of these systems are quite sophisticated and can report rearing—inferred from interruptions of photobeams placed above the height of a subject engaged in normal locomotion—as well as some information about locomotor sequences (Geyer, Masten, & Segal, 1986). Video-based automated tracking of locations of unmarked subjects is also possible (e.g., Jouen & Lepecq, 1989; Lubinski, Dickson, & Cairns, 1977). However, existing video technology may constrain the experimental situation to such a degree—for example, by forcing changes in lighting—as to vitiate the ecological validity of the technique (Renner, Pierre, & Schilcher, 1990).

A slightly different technique involves modifying the walls or floor of the open-field arena to include pockets or holes, into which the subject may poke its nose or head (Boissier & Simon, 1962). The frequency and duration of such nosepokes can be readily quantified, and the behavior is amenable to automated recording. This is, however, still a forced-exploration situation, and is therefore subject to many of the same criticisms directed at the open-field method. It seems likely that much of the subject's nosepoking may reflect a search for ways to escape the arena, especially if conducted under relatively bright lighting in the presence of a human observer. In addition, even this modified open field allows an animal to express only a very limited subset of its potential behavioral repertoire.

Many of the methodological problems discussed here can be remedied through either modifications of procedure (e.g., removal of human observers) or advances in available technology (e.g., infrared-based motion tracking). The core problem, however, is that these techniques are limited to providing direct information about the location of the subject, and only indirect information concerning its behaviors. Automated behavioral recording is a useful tool, but it cannot replace direct observation of behavior (this point was demonstrated quite clearly by Kolb & Whishaw, 1985). It seems probable that the behaviors that are the most psychologically meaningful are those that will be least amenable to automated recording.

Timberlake (1969) provided a beginning for the study of behavioral topography in exploration by conducting a detailed examination of the behaviors of rats during repeated experience in a relatively small (Skinner box size) empty space. Timberlake reported data for self-grooming and cage investigation, as well as locomotor behaviors. Even this type of investigation falls short of providing a complete picture, however, as it does not include interactions with features of the environment other than its boundaries. Although investigations into animals' use of space can lead to insight about knowledge of space and spatial relations, animals in the real world do not typically explore empty space (especially *Rattus norvegicus*, which has long been commensal with humans and often specializes in seeking its livelihood by scavenging human refuse). Numerous objects, both animate and inanimate,

populate their worlds, and it can be shown that the animals interact with these objects. Descriptions of animals' ambulation in empty space, or even of the locomotion component of animals' behavior in object-populated space, deprive investigators of much valuable information about the behavioral strategies and information-processing abilities used by animals for gathering knowledge about a world that is not composed entirely of empty space. A complete approach to the study of exploratory behavior would involve quantification not only of locomotor behavior, but of other forms of behavior as well, including the amount and behavioral topography of object investigation and manipulation. Precious little, however, is known of the nature of object investigation as a part of exploration.

Although subject to many of the problems discussed above in regard to open-field studies, including forced presence in an arena and the presence of a potential predator (the experimenter), some investigators have included object interactions in their studies: A fair number of reports include time of contact with objects (Einon & Morgan, 1976; Lalonde, Botez, & Boivin, 1987; Maier et al., 1988; McCall, Lester, & Dolan, 1969; Misslin & Ropartz, 1981); the number of discrete bouts of contact appears less frequently (e.g., Osborne & Seggie, 1980; Thor, Harrison, Schneider, & Carr, 1988). Measurement of multiple aspects of behavior is less common still: Glickman, Higgins, & Isaacson (1970) counted instances of biting and "manipulation," although the operational definition of manipulation was not made clear.

In the 1950s, Harry Harlow and his collaborators provided rhesus monkeys with puzzles assembled from door latches, hasps, and hinges, and found that the opportunity to manipulate such puzzles was sufficient reward to motivate learning their solutions (Harlow, 1950; Harlow, Blazek, & McClearn, 1956; Harlow et al., 1950). Butler (1953, 1954) extended these results, finding that visual access to another monkey or to an electric train was sufficient reward to motivate learning of other problems, such as visual discrimination tasks. Hopf, Herzog, and Ploog (1985) quantified several types of behavior displayed during interactions with a social surrogate object, in a study of the early development of communication in squirrel monkeys.

It is important to distinguish between studies that include object-contact variables as dependent variables and studies in which the nature of interactions with objects is the focus of the study. In fact, none of the studies mentioned above was designed primarily to shed light upon investigatory behavior. For example, in the puzzle studies by Harlow et al., the dependent measures were time of contact and whether the monkeys solved the puzzles, rather than what the monkeys did in the process of solving them. No criticism of these studies is intended: Each of these studies addressed some question other than the nature of investigation, and the dependent variables in each were apparently adequate to the question at hand. On the other hand, the fact that the characteristics and

function of exploration were not the primary focus of these studies means that none of these studies included measures that can address questions of behavioral topography. (These investigations also illustrate the difficulty of obtaining records during real-time observation that are both sufficiently detailed and of adequate accuracy for analysis of the role of behavioral topography in learning during exploration.)

Although including details of interactions with objects in behavioral analysis greatly increases the complexity of the analysis, an effort to incorporate this level of detail in observations is necessary if we are to achieve a functionally valid description of exploration. Previous investigations by the author have used videotape to investigate multiple behaviors in free-exploration situations, without observers whose presence might change subject behaviors. These investigations have shown that exploratory behavior in the rat (*Rattus norvegicus*) shows experience-dependent changes, and that spatial locomotion and interaction with objects are separable entities. In adolescent rats, experience-dependent changes are shown in behavioral complexity during interaction with objects without concurrent changes in the amount of object contact or amount of locomotion (Renner & Rosenzweig, 1986). In adults (Renner, 1987), changes in exploration appear in both the behavioral complexity of object investigation and on several measures of total quantity of exploration (e.g., locomotion and amount of object contact). Further investigations have shown that locomotion and the behavioral topography of interactions with objects develop according to different calendars (Renner, Pierre, & Seltzer, 1990). It should be clear from this evidence that movement in space is not the only important component of exploratory behavior; this, therefore, makes it apparent that the open-field test provides data that are not only probably confounded but also incomplete.

The studies of latent learning and the more recent work of Albert and Mah (1972) provide information about animal memory as it relates to gross locomotor activity; in such studies, the actual behaviors of the subjects themselves were of interest only incidentally. A recent study (Renner, 1988) was designed to provide data about the role played by simple features of behavioral topography in determining what information is acquired during exploration. Subjects were given differential behavioral experience and allowed to explore in a situation where predictable behavioral differences resulting from the differential experience would likely lead to differences in the information acquired. Specifically, previous work (Renner, 1987) had shown experience-dependent differences in adults in specific exploratory behaviors such as climbing on large objects; the large arena used in that study was designed to include an escape route available through climbing. Subjects were then challenged by being chased by a radio-controlled simulated predator. Escape-time differences between the groups (having different previous experience) increased with time spent in the arena prior to challenge. Also, the behavior of sub-

jects before being exposed to challenge in the arena predicted the time required for escape during the challenge. These findings show that the characteristics of an individual's exploratory behavior can exert significant influence on that individual's ability to behave adaptively; this suggests that the details of behavioral topography in exploration may be at least as important as its locomotor component for understanding its role in information processing.

These findings have been possible only through the development of techniques to quantify and classify several facets of exploratory behavior from the same observation session. Further understanding of the functional significance of exploration, and the acquisition of sufficient descriptive information to direct appropriately detailed investigations of its neural underpinnings, will rely on thorough descriptive work. These studies would ideally be carried out using existing protocols for assessing exploratory behavior at a macrobehavioral level, and by applying standardized movement notation to analysis of interactions with inanimate objects for a microanalytic view. Arguments for the need for such descriptive work across a broad variety of behavioral problems, as well as elegant examples of how such work might be carried out, have been presented recently by Jacobs et al. (1988).

Additional information would undoubtedly be provided by examination of the changes that occur in behavioral topography over time within a session or over repeated sessions. Habituation of exploration and other time-dependent processes have often proven useful in studies specifically directed at behavioral processes (Berlyne, 1955; Rosellini & Widman, 1989), as well as in studies of brain lesions (e.g., Kolb, 1974) and neurochemical intervention (e.g., Buhot, Soffie, & Poucet, 1989; Gately, Segal, & Geyer, 1986).

Neural Systems in Exploratory Behavior

If, as was argued above, exploration is important as a mechanism for acquisition of information in natural situations, then the study of the biology of learning would benefit from a knowledge of what neural systems contribute to animal information gathering through exploration. (This review leaves aside studies employing only the open-field test because of the difficulties, also discussed above, in interpreting what is measured in the open field.) The historical focus on the spatial aspects of exploration yields a tangible benefit: recent progress in the efforts of many investigators to learn something of the neural basis of spatial memory can make important contributions to our understanding of some aspects of exploration. There is much previous research on the neural underpinnings of spatial memory: early studies of the role of the hippocampal formation in spatial memory were reviewed exhaustively by O'Keefe and Nadel (1978). Although the data are clear that hippocampally lesioned rats are impaired on performance of spatial tasks, the proper interpretation of this impairment is the subject of much controversy. Included in this debate is whether deficits in

spatial tasks induced by limbic lesions are best attributed to impairment of spatial memory (Morris, 1983a; Morris, Hagan, & Rawlins, 1986; O'Keefe & Nadel, 1978) or of working memory (Walker & Olton, 1984). Although there are different current hypotheses about the exact nature of the hippocampal formation's role, most investigators seem to agree that the hippocampus plays a central role in memory for spatial relationships.

If, however, we define exploration to include more than just features of spatial locomotion, surprisingly little is known. In a review titled "Neural Subsystems of Exploration in Rats," Morris (1983b) covered solely spatial questions. There are, however, a few reports including data concerning involvement of the hippocampal formation in more aspects of exploration than just space. Although Glickman et al. (1970) found decreases in the number of object contacts by gerbils with hippocampal lesions, Osborne and Seggie (1980) found no differences in the number of object contacts between fornix-lesioned and control rats. Jarrard (1968) reported that hippocampally lesioned rats spent more time sniffing in the home cage than did controls. Leaton (1965) found that hippocampally lesioned rats are equally as likely as controls to choose an opportunity to explore a complex environment over empty space, with hippocampals showing a decresed rate of habituation to novelty. O'Keefe and Nadel (1978) reported informal observations from which they concluded that "there is no suggestion . . . that hippocampals engage in what is clearly exploratory behavior" (p. 256). Other investigators, however (Dean, Pope, Redgrave, & Donohoe, 1980), have argued that hippocampal lesions are not sufficient to abolish exploration, and that damage to the superior colliculus is also necessary for deficits to appear in head-dipping in the hole-board test. A study by Myhrer (1988) examined the effects of combined and separate lesions to the medial and lateral portions of the perforant path on recognition of novelty (as measured by time spent investigating novel and familiar objects), and concluded that these fiber bundles play different roles in recognition memory. Neocortical lesions at the frontal pole do not influence free locomotor exploration (Glickman, Sroges, & Hunt, 1964) but do disrupt rats' ability to solve problems involving object manipulation (Gentile, Green, Nieburgs, Schmelzer, & Stein, 1978); medial parietal lesions have an opposite effect.

These bits of evidence, while intriguing, hardly present a complete picture of the neural substrates of the nonspatial components of exploratory behavior. Whishaw, Kolb, and Sutherland (1983), after an extensive review of the literature, concluded they were "unaware of any neuropsychological studies that have systematically examined the 'spontaneous' investigation of home cages or novel objects" (p. 201). Because the evidence presented here suggests that exploration is more than just an expression of spatial memory, it is reasonable to propose that different neural systems may be involved with the different components of exploratory behavior. Although we may have

a rapidly increasing knowledge of the biology underlying spatial memory, it is plain that our knowledge of other aspects of exploration is inadequate. For example, it is not even yet established whether spatial memory and object investigation are controlled by common or separate neural systems.

Conclusion

The rapidly increasing sophistication of our knowledge about biological systems underpinning learning and memory is obviously outrunning our behavioral understanding of these phenomena. This, in turn, may become an impediment to future advances in the study of the biology of learning and memory. Although cognitive models of learning and information processing must be included in theories of the neurobiological foundations of memory, existing behavioral methods rely on too limited a subset of animals' behavioral repertoires to be sufficient to this end. The study of spontaneous investigation and exploration, although highly labor-intensive at present, offers a potentially important avenue for the development of models of learning and the fundamentals of cognitive processes in a system amenable to direct neurobiological investigation.

Evidence showing functional significance of exploration, beyond its obvious link with animal cognition, speaks to the potential of using this behavioral pattern as a lever to pry loose further insight about the biology of learning and memory. This, however, will rely upon the development of thorough descriptive accounts of spontaneous exploratory and investigatory behavior, for which appropriate technology now exists.

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