Behavior from the ground up: Rat behavior from the ventral perspective

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Most of the rat's behavior emanates from its ventral surface, yet rat behavior is typically studied from above or from the side. Three separate lines of research are described to illustrate the utility of studying rat behavior from a ventral perspective: (1) Grill, Berridge, Norgren, and Fentress' studies of orofacial palatability responses; (2) Whishaw and Tomie's studies of food wrestling and dodging; and (3) Pinel, Jones, Symons, and Mumby's studies of sensory-restriction-induced distortions in defensive burying. The clear view of limb movements and orofacial responses provided by the ventral perspective is its major advantage.

Much of the behavior of laboratory species is not visible from the conventional dorsal and lateral perspectives. The purpose of this paper is to illustrate the advantages of studying rat behavior from a ventral perspective. We describe three recent lines of behavioral research that have employed the ventral perspective to good advantage: (1) Grill, Berridge, Norgren, and Fentress's studies of orofacial palatability responses; (2) Whishaw and Tomie's studies of food wrestling and dodging behaviors; and (3) Pinel, Jones, Symons, and Mumby's studies of sensory-restriction-induced distortions of defensive burying.

Orofacial Indices of Palatability

Traditional measures of a food's palatability are the amount of it eaten in a particular period, the rate at which an operant response is performed to obtain it, and the degree to which it is chosen over available alternatives (see Grill & Berridge, 1985, for a discussion of these measures). One problem with these measures of palatability is that physiological and pharmacological manipulations often have general motoric, perceptual, and motivational effects that confound them. For example, brain lesions that make rats aphagic do not necessarily do so by decreasing their perception of the palatability of available food (Grill & Berridge, 1985). Grill and Norgren (1978)

developed a measure of palatability that circumvents this problem. Their idea was to assess the palatability of various flavored solutions by observing the orofacial responses of rats to intraoral infusions of the solutions through chronically implanted catheters. Because the orofacial responses of rats are not visible from above, and only partially visible from the side, Grill and Norgren videotaped the behavior of their subjects through the floor of a transparent test chamber. Using this method, Grill and Norgren identified nine stereotypic orofacial responses to intraoral infusions. Four of these patterns were labelled *ingestive* because they were typically elicited by palatable stimuli (e.g., sucrose solutions), and five were labeled *aversive* because they were typically elicited by unpalatable stimuli (e.g., quinine solutions).

Berridge and Fentress (1985) discovered that cutting the somatosensory afferent branches of the trigeminal nerve affected the rat's perception of palatability in an interesting way. The deafferented rats expressed fewer ingestive orofacial responses to sucrose solutions, but surprisingly, their aversive orofacial responses to quinine solutions remained unchanged. Berridge and Fentress (1985) concluded that trigeminal somatosensory input interacts with gustatory information to enhance the palatability of preferred, but not of unpreferred, flavors. In another study, Berridge and Treit (1986) found that chlordiazepoxide, a compound that increases eating, increased the number of ingestive responses that rats expressed to a variety of flavors but did not affect the expression of aversive responses. They concluded that chlordiazepoxide increases eating by increasing a food's ingestive palatability while having little or no effect on its aversive palatability. These and other insights into the perception of palatability (e.g., Berridge, 1988; Berridge & Fentress, 1986, 1987) could not have been gained from conventional dorsal and lateral vantage points.

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Food Wrestling and Dodging Behaviors in Rats

In the wild, rats compete with one another for resources (e.g., Barnett & Spencer, 1951; Chitty, 1954). Whishaw and Tomie (1987) and Whishaw (1988) developed a laboratory paradigm to systematically study the competition for food. Their paradigm involves introducing a food-deprived rat, designated the *robber*, into a chamber where a second food-deprived rat, designated the *victim*, is eating a food pellet. Under these conditions, the robber approaches its victim from behind, moves along the victim's side toward its head, and attempts to wrest the food pellet away. In response, the victim protects the food pellet by moving away, that is, by dodging.

It was not until Whishaw and Tomie began to study the competition between rats for food from the ventral perspective that they were able to fully appreciate the intricacy of the wrestling and dodging sequences. When they videotaped the behavior of their subjects from below, it became obvious that the victims usually dodged in one of two ways. In one dodging sequence, (1) the victim held the food in its forepaws and rotated its body away from the robber, (2) stepped away from the robber with the contralateral rear leg, and (3) stepped with the ipsilateral rear leg to bring the rear legs together. In the other dodging sequence, (1) the victim rotated its body away from the robber and transferred the food pellet from its forepaws to its mouth, (2) stepped away from the robber with its forepaws and rear leg contralateral to the robber, and (3) stepped with the ipsilateral rear leg to bring the two rear legs together while it transferred the food back to its forepaws. Both types of dodging sequences are normally completed in about 0.33 sec.

Whishaw and Tomie (1988) subsequently used their dodging and wrestling paradigm to study the contributions of cortical and dopaminergic processes to the control of sensorimotor sequences in the rat. They found that hemidecortication impaired the dodging responses of victims to wrestling attempts that emanated from the side contralateral to the lesion while it left intact their dodging responses to ipsilateral wrestling attempts. The wrestling attempts of hemidecorticate robbers were also impaired on the side of the body contralateral to, but not ipsilateral to, the lesion. The hemidecorticate rats recovered from both the dodging and wrestling deficits within 15 to 60 days. In contrast, Whishaw and Tomie found that unilateral 6-hydroxydopamine-induced nigrostriatal bundle lesions produced bilateral impairments of dodging and wrestling that displayed few signs of recovery within 60 days. In short, Whishaw and Tomie's adoption of the ventral perspective was an important step in their development of the wrestling and dodging paradigm.

Environmental Fine Tuning of Defensive Burying

Rats shocked by a well-defined source in the presence of a homogeneous particulate substrate (e.g., commercial bedding material or sand) subsequently spray the substrate at the source with alternating, forward-pushing movements of their forelimbs. This response is known as *defensive burying* (Pinel, Mana, & Ward, 1989; Pinel & Treit,

1978; Pinel & Wilkie, 1983). Pinel, Symons, Christensen, and Tees (1989) found that the conditions under which rats are reared profoundly affect their defensive burying behavior. Surprisingly, most rats born and reared in wire-mesh cages, with no opportunity whatsoever to interact with particulate matter, sprayed bedding at the source of the shock during their very first burying test, but they spent less time burying than did their bedding-reared counterparts. In addition, there appeared to be differences in the topography of the burying responses of the bedding-reared and wire-reared rats. However, because Pinel and his colleagues videotaped the behavior of their subjects from above, a perspective from which the rat's forelimbs are not clearly visible, they were unable to do more than comment generally on these differences.

Pinel, Jones, Symons, and Mumby (unpublished) viewed the videotaped burying responses of bedding-reared and wire-reared rats from below. To accomplish this, they covered the transparent floor of their testing chamber with only a scattering of bedding material. From the ventral perspective, the ways in which the defensive burying of wire-reared rats was distorted were apparent. Bedding-reared rats faced the shock prod and buried it with forward-thrusting, regularly alternating, forelimb strokes (i.e., right-left-right-left-right-left...). As a result, bedding-reared rats invariably sprayed a great deal of the bedding material directly at the shock source. In contrast, wire-reared rats faced the shock prod and tried to bury it with forelimb strokes that were not regularly alternating nor consistently forward thrusting. For example, the topography of the burying of several wire-reared rats parodied the breast stroke of a novice human swimmer; these rats faced the shock source but sprayed bedding material toward the sides of the chamber with laterally directed, poorly coordinated forelimb strokes. As a result of behavioral distortions such as these, wire-reared rats generally sprayed less bedding material, and only a small proportion of the material that they did spray ended up in the immediate vicinity of the shock source. Apparently, the coordination and direction of the adult rat's defensive burying response is a product of its interaction with particulate substrates during development.

Methodological Suggestions

A ventral view of an animal may be obtained with this equipment either by positioning the camera directly under the transparent floor of the test chamber or by filming indirectly through a mirror placed at an angle under the chamber floor. In this latter configuration, it is sometimes advantageous to position the camera so that a direct lateral view and an indirect ventral view (via the mirror) are recorded simultaneously. Such a configuration is illustrated in Figure 1.

A number of technological changes have made relatively inexpensive methods for filming behavior for subsequent slow-motion analysis readily available. We have obtained success with systems that permit frame-by-frame (usually

Figure 1. A system useful for studying behavior from the ventral perspective. In this configuration, the camera is placed to provide simultaneous ventral and lateral views.

up to 30 frames per second) playback of the movement record. To avoid blurring fast movements in individual frames, we suggest the use of video cameras that have high shutter speeds. However, these require high levels of illumination. An equipment configuration that we recommend consists of a Sony Video 8 portable camera (Sony Handyman CCD-VII) with shutter speed options of 50, 100, 500, 2,000, and 4,000 frames per second (for most behavioral studies, a shutter speed of 500 frames per second is adequate). The high levels of illumination necessary for clear images at such shutter speeds can be obtained from a fiber-optic cold light source such as the Nikon MII. Although the video record may be viewed via a direct connection to a television monitor and analyzed immediately, we recommend that it first be copied onto videotape and replayed on a video recorder that has slow-motion and frame-by-frame control options. Permanent records of individual video frames or frame sequences can be obtained with a video copy processor (we have had success with the Mitsubishi P60W Video Copy Processor).

Discussion

Many of the questions now being addressed by behavioral neuroscientists cannot be answered satisfactorily without a careful analysis of behavioral sequences (see Robinson, 1983; Satinoff & Teitelbaum, 1983). We have illustrated the advantages of studying rat behavior from a ventral perspective by describing three separate lines of research. Although gross movements of the head and trunk can be observed adequately from the traditional dorsal or lateral perspectives, limb movements and orofacial movements cannot. Clearly, both limb and orofacial movements are important in orofacial palatability responses, dodging and wrestling, and defensive burying. The ventral observation of sequences of rat limb movements has provided insights into their development (Eliam & Golani, 1988) and into how brain damage (Zeigler & Szechtman, 1988) and drugs (Szechtman, 1983, 1984, 1988; Szechtman, Eliam, Teitelbaum, & Golani, 1988; Szechtman, Ornstein, Teitelbaum, & Golani, 1985) affect

them. This research has been complemented by studies that have used indirect indices of limb movement. For example, Schallert, Whishaw, Ramirez, and Teitelbaum (1978) studied the behavioral effects of anticholinergic drugs on the limb movements of akinetic, 6-hydroxy-dopamine-treated rats through their footprint patterns.

Tongue movements are a feature of rat behavior that have been largely ignored by behavioral neuroscientists, perhaps because the rat tongue is invisible from above and because in humans some of the important functions of the tongue have been taken over by the hands. Still, given the important role that tongue movements play in rat behavior and how much is known about their neural control (Lowe, 1981) and anatomy (Doran, 1975), it is surprising that they have so seldom been the focus of behavioral research. Whishaw and Kolb (1983, 1989) have studied rat tongue movements directly from both ventral and lateral perspectives, and indirectly by analyzing tongue contacts with sensing devices or patterns made by the tongue on the surfaces of objects.

Tongue movements have also recently been studied as components of orofacial response sequences (e.g., Berridge, Vernier, & Robinson, 1989; Dostrovsky, Hu, Sessle, & Sumino, 1982; Szechtman, 1983; Van Willigen, Juch, Ballintijn, & Broekhuijsen, 1986). The more widespread use of the ventral observational perspective could kindle interest in this important, but largely overlooked, rat effector organ.

Conclusion

It is paradoxical that although behavioral neuroscientists rarely study the behavior of humans and other primates from anything other than the ventral perspective, they almost always study the behavior of rats from perspectives that preclude direct observation of their ventral surfaces. We believe that one of the major reasons why the complexity of the rat's behavioral repertoire is so often underestimated is that many of the most complex and recently evolved (see Kuypers, 1981) rat behaviors are visible only from the ventral perspective. Furthermore, the failure of behavioral neuroscientists to modify their observational techniques in response to differences in the preferred postures of the different species that they study has made it difficult to compare the topography of primate and nonprimate behavioral sequences. We hope that this paper will promote the more widespread adoption of the ventral perspective in laboratory studies of animal behavior.

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