Autonomous Robots 11, 249–254, 2001

Active Sensing Capabilities of the Rat Whisker System

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Abstract. The rat whisker system may be a good model for approaching the design of robust robotic active sensing and exploratory systems. Here we examine how rats use their whiskers (vibrissae) during free exploratory behavior and during a texture discrimination task. Results show that during free exploration, the rat rhythmically moves its head to place its small (micro) vibrissae on the surfaces it is exploring. These periodic "microvibrissal placements" are temporally synchronized with the whisking movements of the large (macro) vibrissae. The periodic microvibrissal placements occurred even during a texture discrimination task, in which a smooth, continuous movement might have been equally effective at extracting the required information. Finally, it was found that rats may sometimes use their micro and macro vibrissae *consecutively*, instead of simultaneously. This suggests that, like humans, rats' exploration consists of a series of movement sequences in which increasingly refined information is gathered about an object. Some implications of these results for the design of artificial exploratory systems are discussed.

Keywords: vibrissae, exploratory behavior, exploration, tactile discrimination, active sensing, texture

1. Introduction

Future NASA missions could greatly benefit from robotic systems that can act autonomously, and this will require that the systems be able to efficiently detect, explore, and recognize objects in the environment. Such systems should operate in a robust fashion under a wide variety of environmental conditions, including darkness and noise. Rats, as nocturnal, burrowing animals, have evolved a highly-sensitive whisker system that can extract information about object properties even when vision and audition are difficult or impossible. For example, it is known that rats use active movements of their whiskers to identify object position, orientation, size, shape, and texture (Vincent, 1913; Carvell and Simons, 1990; Brecht et al., 1997). The rat whisker system may therefore be a good model for approaching the design of robust artificial active sensing and exploratory systems.

As shown in Fig. 1, rats have two types of whiskers—large whiskers (macrovibrissae), and small whiskers (microvibrissae). When exploring their environment, rats sweep their macrovibrissae back and forth against objects at frequencies between 5 and 12 Hz, in a well-studied behavior known as "whisking" (Vincent, 1913; Welker, 1964; Carvell and Simons, 1990). In contrast, the fine microvibrissae that cover the rat's lip surfaces cannot be actively moved, and are much less well studied than the macrovibrissae.

Although numerous studies have examined the neurophysiology and tactile capacities of the whisker system (reviewed in Paxinos, 1995; Kleinfeld et al., 1999), most have focused exclusively on the macrovibrissae. However, some of the earliest work on the whisker system suggested that micro and macrovibrissal use were closely intertwined (Welker, 1964). If that were true, then studying the two sets of whiskers in isolation from each other might actually preclude an accurate characterization of the way the rat whisker system operates. It may therefore be useful to treat the micro and macro vibrissae as a unified sensory system, and to examine their relative, perhaps differential, use during exploratory behaviors.

Figure 1. Backlit view of the micro- and macrovibrissae.

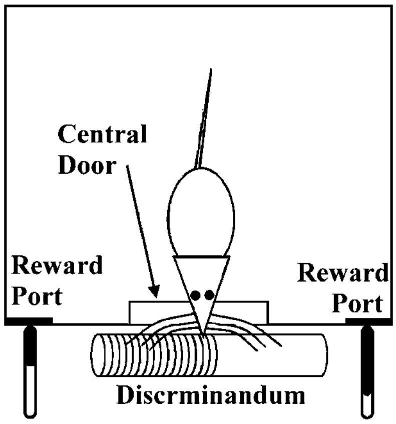

Figure 2. Bird's eye view of the behavioral cage and discriminandum. Drawing not to scale.

This paper examines rats' use of their micro and macrovibrissae during free exploratory behavior, and during a texture discrimination task. The results show that the rat's use of micro and macrovibrissae are in fact closely entwined: as the rat whisks with its macrovibrissae, it also rhythmically moves its head in such a way as to place its microvibrissae on the surfaces it is exploring. Furthermore, these periodic "microvibrissal placements" are temporally synchronized with, but not necessarily one-to-one with, the macrovibrissal whisking movements. The periodic microvibrissal placements occurred even during a texture discrimination task, in which a smooth, continuous movement might have been equally effective at extracting the required information. Finally, it was found that under some conditions, the rat may use its two whisker systems *consecutively*, instead of simultaneously.

2. Methods

2.1. Free Exploration

To examine whisker use during tactile sensory exploration, rats were videotaped as they freely explored an unfamiliar cage and objects. The rat's whiskers and lip surfaces were in extensive contact with the cage floor and objects during this behavior.

2.2. Behavioral Apparatus for Tactual Discrimination

Two rats were trained to perform a texture discrimination task. Figure 2 shows a schematic of the behavioral cage in which the task was performed. One wall of the cage contained a central door, which was opened at the beginning of each trial to allow the rat access to the discriminandum. Reward ports were placed about 6 inches to either side of this central door.

The texture discriminanda consisted of bars placed in front of the central door of the behavioral cage. The bars were metal machine bolts with the head of each bolt removed: the "rough" side of the bolt had threads spaced at 16/inch, while the "smooth" side of the bolt had no threads. Before training, all bars were washed in alcohol and then distilled water to remove residual odors.

2.3. Training Procedures

At the start of each trial, a bar was randomly selected and centered in front of the central door. The door was then opened to indicate to the rat that a trial had begun. Rats were allowed to freely explore the metal bar with their lips and whiskers for as much time as necessary to perform the discrimination, and no minimum inter-trial interval was imposed. When rat had finished exploring, it was expected to remove its head from the door (at which time the door was closed), and walk to the reward port closer to the rough side of the bar. If the rat selected the correct reward port, a $\sim$1 ml sugar water reward was provided. To ensure that the rat did not base its decision on olfactory cues from the reward port(s), sugar water was present at both reward ports at all times, but was not released until the rat had begun to lick at the correct port.

Rats were trained over a period of 45 days. The number of trials per day was based on the length of time it took for the rat to satiate and ranged from 38 to 160.

2.4. *Scoring of Video Data*

Video data was time-coded and then analyzed field-by-field (16 msec resolution) on a standard Hi-8 VCR. Times of maximal protraction and retraction of the macrovibrissae were scored as well as the times of microvibrissal placement. Microvibrissal placement was defined as the time when the lip/snout was pressed most downwards and clear contact was made with the surface being explored.

3. Results

3.1. *Simultaneous Use of Micro- and Macrovibrissae During Free Exploration*

As shown in Fig. 3(A), the rat almost invariably used its micro and macrovibrissae *together* when exploring objects. The rat placed its microvibrissae on the object at the same time as it whisked over the object with its macrovibrissae. Exceptions occurred during the rat's initial detection of an object, and as the rat was moving *away* from an object it had finished exploring.

In addition, it was found that the rat's head movements, and hence microvibrissal placements, were temporally synchronized with the macrovibrissal whisking movements. However, head movements could occur over several cycles of whisking, and the microvibrissal placements did not occur on every whisking cycle. Thus the relationship between microvibrissal placements and macrovibrissal whisking is not always one-to-one; in some instances, the microvibrissae essentially sample at a subharmonic of the basic whisking frequency. These results are illustrated in Fig. 3(B).

3.2. *Consecutive Use of Micro- and Macrovibrissae During Tactile Discrimination*

As indicated in Methods, both rats were initially trained on the tactile discrimination task for 45 days. By the 30th day of training, Rat 1 had achieved an 80% correct score on the discrimination task, and the rat maintained or exceeded this score throughout the remaining 15 days of training. In contrast, Rat 2 never achieved greater than a 68% correct level during the first 30 days

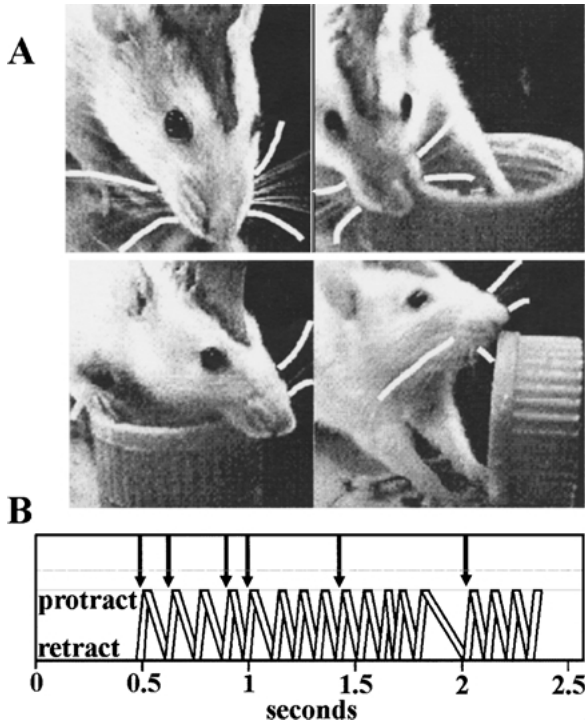

Figure 3. (A) Four video frames of a rat exploring an object. The front and back-most macrovibrissae have been highlighted in white. (B) Temporal synchronization of microvibrissal placements with macrovibrissal whisking. The triangular trace indicates the times of maximal macrovibrissal protraction and retraction, as scored in the video analysis. Black arrows indicate times that the microvibrissae contacted surfaces.

of training, and at the end of 45 days had actually returned to an almost random response choice. Given the poor performance of the second rat, we extended the training period for an additional 38 days, but the rat's performance did not improve. As will be discussed below, however, a closer inspection of the behavior of Rat 2 indicated that its overall poor performance on the discrimination task did not accurately reflect the complexity of the behavioral strategies it was employing.

Detailed video analysis indicated that the two rats differed in which regions and combinations of mouth parts were placed in contact with the bar during the discrimination task. As shown in Fig. 4(A), Rat 1 usually explored the bar with its snout and microvibrissae, while keeping its head well behind the bar. This rat rarely put its full upper lip up on the bar, and only minimal whisking activity was observed. This indicates that (in the presence of visual cues) the fine microvibrissae and sensitive snout regions may be sufficient for some rats to perform a texture discrimination.

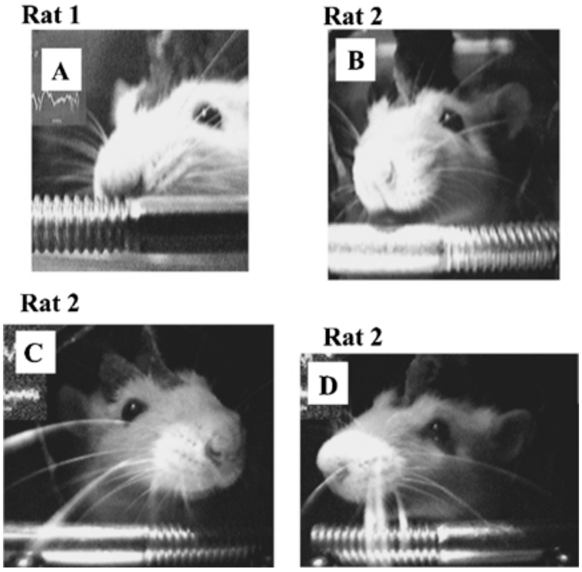

Figure 4. (A) Rat 1 felt the bar mostly with its snout and the small microvibrissae surrounding the snout. (B) Rat 2 often rubbed its upper lip over both the smooth and rough side of the bar. (C) and (D) In later stages of training, Rat 2 often tipped its head to one side and whisked over the bar.

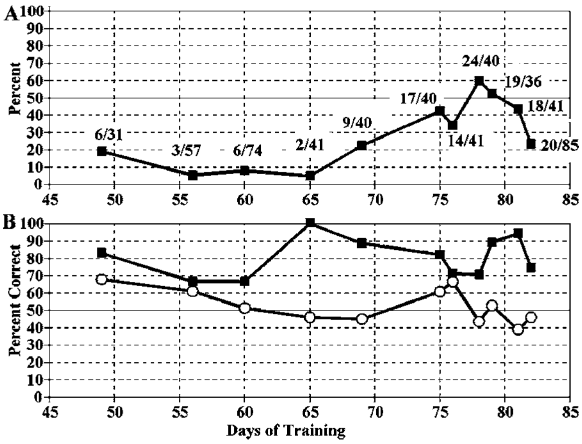

Figure 5. (A) The fraction of trials in which the rat employed the LB/WB strategy. Fractions indicate the total number of trials for which the rat used the LB/WB strategy over the total number of trials that day. (B) Performance when the rat used the LB/WB strategy (filled squares) compared to when it did not use this strategy (open circles).

In contrast, Rat 2's exploration generally involved much more extensive lip contact with the bar, as shown in Fig. 4(B). In addition, careful analysis of the video data indicated that Rat 2 introduced a new exploratory strategy on approximately day 49 of training. This new behavior involved the *sequential* use of both the lips and whiskers. Specifically, the rat would first rub its lip over the bar, as in Fig. 4(B), then remove its lip from the bar, tip its head to one side, and whisk over the bar, as illustrated in Fig. 4(C) and (D). In general, the whiskers clearly came in contact with both the rough and the smooth sides of the bar, but on some trials the whisks were limited to only one side of the bar (i.e., the rat moved its whiskers only over the rough *or* the smooth side.).

To better understand these changing trends in the Rat 2's exploratory strategy, we performed a more detailed analysis of the video data after day 49. For each day analyzed (about every fifth day, see Fig. 5) each trial was scored to determine whether the rat's lips touched the rough and/or the smooth side of the bar, and whether the rat whisked over the rough and/or smooth sides of the bar. This analysis broke the rat's exploratory behavior into a total of 16 possible combinations of lip and whisker movements: the lip could touch the smooth side, the rough side, both sides, or neither side, and the rat could whisk over the smooth side, the rough side, both sides, or neither side.

Of the 16 possible strategies, the only one that was correlated with an above-chance performance on the texture discrimination task was the one in which the rat placed its lip on both the textured and smooth surfaces, and also whisked over both surfaces (Lip-Both/Whisk-Both (LB/WB)). The LB/WB strategy was not present in the video records prior to day 49, and the rat gradually increased the use of this strategy from day 49 through 83. Figure 5(A) shows the fraction of the trials in which the rat employed the LB/WB strategy. Between days 49 and 65, the rat used the strategy on average about 8 percent of the time, but between days 75 and 83, the rat used the strategy on average on more than a third of the trials.

Importantly, on trials in which the rat employed the LB/WB strategy, its performance on the discrimination task improved dramatically. Figure 5(B) compares Rat 2's performance from day 49 onwards, when employing the LB/WB strategy (filled squares), with the performance when it did not use this strategy (open circles). The LB/WB strategy resulted in an average performance level of 78% correct, while other strategies resulted in the rat getting far fewer trials correct.

3.3. *Sampling with the Macro and Microvibrissae*

Finally, it was observed that when the rat placed its microvibrissae on the bolt, it did not do so "smoothly."

Instead, it used a "sampling strategy" similar to that described for free exploration. Video analysis revealed the rat rhythmically bumped its lip up and down on the two sides of the bar, usually between 5 and 8 Hz, but also sometimes at lower frequencies, between 1 and 5 Hz. This sampling usually involved iterations of lip placement on and removal from the discriminandum, but sometimes reflected periods when the lip was in constant contact with the discriminandum and pressed downwards with more and less force.

4. Discussion

4.1. Synchronized Sampling by Micro and Macrovibrissae

The simultaneous, and temporally synchronized, use of the micro and macrovibrissae (Fig. 3(A)) strongly suggests that these two systems should not be studied in isolation. Using its two sets of whiskers, the rat must acquire information about 3D object properties, integrate information from multiple receptor types (sensor fusion), and somehow perceptually "stabilize" the incoming sensory data, given that the explorer itself, and possibly the object being explored, is/are moving.

The current work has shown that an essential feature of rat exploratory behavior, and one that is almost certainly related to how the rat solves these problems, is that both sets of whiskers take discrete, synchronized tactual "samples" of the environment. (Fig. 3(B); c.f. Welker, 1964). Interestingly, the frequency of this peripheral sampling is similar to the frequency of oscillations that occur in groups of neurons at various levels of the rat sensorimotor system (Nicolelis et al., 1995; Semba and Komisaruk, 1984; Hartmann and Bower, 1998). This suggests that both peripheral and central oscillations may directly reflect a mechanism for the temporal segmentation of incoming sensory data, and that the relationship between peripheral and central (neural) sampling warrants further study.

This periodic sampling strategy might subserve at least two possible functions. First, sampling the environment with the microvibrissae could ensure the stabilization of incoming sensory data. In other words, the discrete microvibrissal placements could serve as a "zero-point" for referencing the data acquired by the macrovibrissae. Head movements of the rat would thus have two consequences: they place the array of microvibrissae, resulting in tactile input, and they reposition and reset the reference point for the array of macrovibrissae. This would permit the rat to construct stable spatial representations of the environment even though its head is moving during exploration. Second, a periodic sampling strategy could help to ensure that the rat perceives object qualities in a way that is independent of the temporal characteristics of the movements executed to extract them. To achieve this, the animal must either cancel out the temporal characteristics of the movement (e.g., via an efference copy), or ensure that information is "parsed" the same way regardless of the speed of the movement. A periodic sampling strategy—implemented either through peripheral movements and/or through neural oscillations—could accomplish this second mechanism.

4.2. Exploratory Sequences and Adaptive Rhythmic Movements

Figures 4 and 5 of this study provide some of the first evidence that, like humans, rats' exploration consists of a series of movement sequences in which increasingly refined information is gathered about an object (c.f. Klatzky and Lederman, 1992). When the rat did not use the LB/WB strategy, its performance on the texture discrimination task was greatly degraded. This means that the rat must determine which portions of incoming data are relevant to the current behavioral task, and must select and refine its movements to optimally acquire the relevant data.

It seems likely that Rat 1, and possibly Rat 2, used visual cues in addition to tactile cues to perform the texture discrimination task. Future experiments might examine how visual inspection is incorporated in the exploratory movement sequences. Performing such experiments in infrared light would disentangle the relative roles of vision and touch. However, the current work clearly demonstrates the tremendous importance of the vibrissae in the intact animal, in the presence of other modalities.

If rat exploratory behavior consists of definable sequences of movements, then future studies might use the whisker system as a model for studying two computational problems that will be faced by any artificial active sensing system. First, how can exploratory movements be modulated in real-time by the (increasingly accurate) somatosensory information acquired? More specifically, how can the system ensure the most efficient acquisition of the information most salient to a particular task? Second, how can the system choose from among a variety of possible execution (e.g., movement) paths based upon an evaluation of the current state of the environment? Investigating this type of action selection is one approach towards examining the origins of autonomous behaviors.

4.3. Potential Hardware Applications

In addition to serving as a model system for studying exploratory behaviors, whisker sensors might directly complement visual and auditory sensors on remote rovers. Whiskers could explore the near-field environment when vision is limited (in the fog, or in darkness), and are not limited by reflections or glare. They are effective in acoustically and visually noisy environments, and do not need to emit sound or light. Whiskers are mechanically flexible, difficult to break, and compress to allow the animal/rover to get through narrow openings.

One can certainly imagine planetary rovers greatly aided by whisking devices. Such a system mounted on a rover could provide a small, cheap, independent information-extracting system that would operate efficiently under a wide variety of environmental conditions.

Acknowledgments

This research was performed in the laboratory of Dr. Jim Bower at Caltech. I am grateful to Carolyn Chan and Angela Poole, who performed much of the behavioral training, and to Drs. Christine Chee-Ruiter, Chris Assad, and Jim Bower for valuable discussions.

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