

POPULATION CODING STRATEGIES AND INVOLVEMENT OF THE SUPERIOR COLLICULUS IN THE TACTILE ORIENTING BEHAVIOR OF NAKED MOLE-RATS

S. D. CRISH,^{1*} C. M. DENGLER-CRISH¹
AND C. M. COMER

Laboratory of Integrative Neuroscience, and Department of Biological Sciences, University of Illinois at Chicago, 845 West Taylor Street, Chicago, IL 60607, USA

Abstract—Even simple behaviors of vertebrates are typically generated by the concerted action of large numbers of brain cells. However, the mechanisms by which groups of neurons work together as functional populations to guide behavior remain largely unknown. One of the major model systems for exploring these mechanisms has been mammalian visuomotor behavior. We describe here experiments that establish a new model system for analyzing the sensory control of behavior by neuronal populations using a mammalian somatosensory response: orientation to touch cues in a rodent. We found that the CNS mechanisms used to direct these orientation responses to touch can be delineated from behavioral experiments.

In this study we demonstrate that the superior colliculus, a component of the vertebrate midbrain most often thought of as a visual structure, is an essential component of the naked mole-rat's unique tactile orienting behavior. Furthermore, the information processing that underlies this behavior displays striking parallels with that used for visual orientation at anatomical and computational levels. © 2006 Published by Elsevier Ltd on behalf of IBRO.

Key words: sensorimotor integration, blind, tectum, somatosensory, orienting, saccade.

Mammalian visual orientation (saccadic eye movements, and/or head and body movements) depends fundamentally on the midbrain superior colliculus (SC). In most mammals, the superficial SC contains a topographic sensory map of the visual field (Cynader and Berman, 1972; Dräger and Hubel, 1975). In the deep layers of the SC, neurons discharge in association with visually triggered orienting movements and cells are “tuned” to fire preferentially for certain directions of movement. The representation of preferred directions for deep SC cells forms a motor map that is “in register” with the overlying visual sensory map (Robinson, 1972; Roucoux et al., 1980; Dean et al., 1986; Munoz and Guitton, 1991). Presumably the activity of superficial SC sensory neurons ultimately is translated into activity in premotor cells in deeper collicular layers (Huerta

and Harting, 1984; Sparks and Nelson, 1987). Thus, at one level of analysis, point-to-point mapping between sensory and motor regions of the CNS explains visuomotor orientation.

However, even a discrete visual stimulus activates a large proportion of collicular sensory neurons and a large corresponding population of deep premotor cells (McIlwain, 1975, 1991; Sparks et al., 1975). So, at a more realistic level, it is essential to know how neural activity is “read out” across large populations of naturally activated cells to elicit just a single movement of the eyes and/or head to a new and appropriate position in space. While the problem is easily posed in this visuomotor example, it is a problem common to guidance of orienting movements toward non-visual stimuli. Indeed, the tectum is well known to be a site of polymodal integration: within intermediate and deep laminae there are maps of auditory space and of the body surface and these are roughly “in register” with the spatiotopy of the visual map in a wide variety of mammals (Dräger and Hubel, 1976; Chalupa and Rhoades, 1977; Stein and Meredith, 1993). At present, there is little information on how non-visual information is translated into orienting motor output. We now provide evidence for the population coding strategies used to accomplish orientation to somatosensory cues by a mammal.

Naked mole-rats (*Heterocephalus glaber*) are eusocial rodents native to eastern Africa. They spend their entire lives in extensive underground burrow systems (Jarvis, 1981; Brett, 1991). Most likely because of adaptation to this unique environment, mole-rats are functionally blind and have poor sound localization abilities (Heffner and Heffner, 1993; Hetling et al., 2005). However, they exhibit a novel array of relatively large, heavily innervated sensory hairs along their body (Fig. 1). We have termed these hairs “somatic vibrissae” (Park et al., 2003). Stimulation of even one somatic vibrissa produces a turn of head or head and body that brings the snout to the approximate rostro-caudal location of the stimulus (Crish et al., 2003a; Fig. 2).

The topographic nature of this response, as well as the ease of its measurement, makes it an ideal model for studying somatosensory guidance of movements. We first tested the hypothesis that the naked mole-rat SC is involved in mediating tactile orienting behavior. This hypothesis was motivated by the known role of the SC in visual orientation, the similarity of orienting movements toward visual and touch cues at the level of motor performance, and the polymodal nature of the SC in most mammals.

The second aim of this study was to uncover population coding strategies used to produce orientation to tactile

¹ Present address: Department of Biological Sciences, Vanderbilt University, Laboratory 8270 MRB III, 465 21st Avenue South, Nashville, TN 37232, USA.

*Corresponding author. Tel: +1-615-343-4593; fax: +1-615-343-6707. E-mail address: sam.crish@vanderbilt.edu (S. D. Crish).

Abbreviation: SC, superior colliculus.



Fig. 1. Photograph of the naked mole-rat. Note the small eye, small external ear, and large somatic vibrissae.

cues. We used behavioral experiments to examine how the mole-rat brain integrates various combinations of tactile stimuli to produce a unitary orienting response.

EXPERIMENTAL PROCEDURES

Subjects

All naked mole-rats used in this and previous studies were non-breeding adults between 20 and 40 g in weight selected from colonies maintained at the University of Illinois at Chicago. Animals were housed in standard laboratory rodent cages connected with polycarbonate tubing in a climate-controlled room kept at 28 °C and 50–60% relative humidity. Animals had *ad libitum* access to a diet consisting of fresh sweet potatoes, corn, apples, and other fruit along with protein rich cereal (Pro-Nutra; Bokoma, South Africa). For further details of mole-rat care see [Artwohl et al. \(2002\)](#). All procedures were conducted in accordance with the National Institutes of Health Guide for Care and Use of Laboratory Animals. These experiments were approved by the University of Illinois at Chicago Animal Care and Use Committee. All efforts were made to reduce the number of animals and their suffering.

Lesions

To produce midbrain lesions, animals were anesthetized with i.p. injections of 100 mg/kg ketamine HCl and 2 mg/kg xylazine. Additional injections of 25 mg/kg ketamine HCl were given as needed to maintain anesthesia. A craniotomy was made in the skull above the SC. In four cases (SC1–4) the cortex was reflected forward and the needle of the aspirator was inserted between cerebrum and cerebellum to access SC unilaterally. To control for specificity of lesion site, in two cases the occipital cortex overlying the SC was aspirated unilaterally (CTX1, 2). As a surgical control two animals had a craniotomy performed but no tissue was removed (Sham1, 2).

Behavior testing: collicular involvement

For behavioral analysis of the animals that received surgical ablations, the subjects were allowed to recover for 1 week and then each was placed in a testing arena and allowed to acclimate for 2 h. Then a block of 25 orientation trials was performed. Each consisted of manual deflection of a single vibrissa with a wooden probe. Trials were separated by at least 1 min to prevent habituation of the response.

Responses were videotaped from directly overhead using a high-speed system (Xybion, SVC-10 B/W camera, Sony VO-5600 tape deck). Responses were played back frame-by-frame with a resolution of 60 frames per second. For the purposes of this study a response consisted of head displacement toward (or away from) the side of stimulation within 300 ms of stimulation. Negative responses occurred if no head displacement occurred within 300 ms of stimulation. After testing, the animal was anesthetized with 100 mg/kg Nembutal and perfused. After histological preparation, 40 μ m sections were taken on a freezing microtome. The sections were stained with Cresyl Violet.

Behavior testing: population coding

To assess how inputs from the array of somatic vibrissae are processed, we used an electromagnetic system that allowed reproducible stimulation of individual hairs—and pairs of hairs—in free-ranging animals ([Melzer et al., 1985](#)). Briefly, animals were placed in a circular plastic arena (17 cm diameter) that was surrounded by coils of wire that produced a magnetic field when AC current was applied to the coils. A fine strand of ferrous metal (~0.001 g) was cemented to the shaft of a hair (or hairs) with cyanoacrylate glue to make the hair capable of being deflected by the imposed magnetic field. If no hair was bonded with a metal strand, animals did not display responses to the transiently applied magnetic field. Responses were recorded as previously described. We observed no quantitative differences in turn metrics when hairs were stimulated manually versus being stimulated magnetically. For each trial, we documented the point of stimulation on the body, and the alignment of the longitudinal axis of the body and the head at the time of stimulation, we then noted the position of the head at the completion of any movement. The difference (in degrees) between initial and final positions was taken as the turning angle.

Statistics

Data were analyzed using Student *t*-tests in the ablation studies or a within subjects analysis of variance (ANOVA) in the population coding studies.

RESULTS

Surgical ablation of the SC

Unilateral ablation of the SC selectively abolished a mole-rat's orienting behavior for stimulation of vibrissae

Download English Version:

<https://daneshyari.com/en/article/4341751>

Download Persian Version:

<https://daneshyari.com/article/4341751>

[Daneshyari.com](https://daneshyari.com)