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Whisker-based discrimination of object orientation determined with a rapid training paradigm

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Abstract

Rats use their large facial whiskers to discriminate the spatial features of objects. Despite numerous electrophysiological recording studies in the central trigeminal whisker representations that document neurons tuned to the direction of whisker deflection, there is no behavioral evidence to date that rats can use their whiskers to discriminate between object orientations. In the present study, we characterized whisker-dependent orientation discrimination using a one-trial learning procedure. Sprague–Dawley rats were trained and tested in a three-arm 'Y-maze' that was outfitted with 180 independently moveable bars that protruded into the arms of the maze to contact the whiskers. On the first day, the maze was configured to have two arms with only horizontal bars and a third arm with only vertical bars and rats were allowed to freely explore all arms. On the second day, rats were isolated in one arm that contained only vertical bars as a conditioned stimulus (CS) and administered three mild foot shocks. On the third day, the maze was configured identically to the first day and rats were once again allowed to freely explore the maze. We measured the percentage of time spent in each arm of the maze and found that most rats spent significantly less time in the arm containing the CS after training compared to before training. Subsequent control experiments determined that the conditioned avoidance was attributable to orientation cues, was caused by the association of the conditioned and unconditioned stimulus and was whisker-dependent. Avoidance behavior was significantly reduced when the difference between the conditioned and non-conditioned orientation difference was reduced to 45°. Thus, rats can discriminate object orientation with their whiskers and an estimate of their discrimination thresholds can be rapidly acquired through the application of a one-trial learning paradigm.

Keywords: Vibrissa; Pavlovian; Barrel; Somatosensory; Orientation; Behavior; Fear conditioning; Whisker; Discrimination; Classical conditioning; Direction

1. Introduction

Rats detect and discriminate haptic features of the external world with their mystacial vibrissae, an exquisite sensory organ used in a wide variety of tactile behaviors (Vincent, 1912). The mystacial vibrissae are comprised of large lateral facial whiskers called macrovibrissae that are organized in a highly conserved matrix of five rows and seven arcs (Brecht, Preilowski, & Merzenich, 1997; Welker, 1971; Woolsey & Van der Loos, 1970) and the smaller and more numerous micovibrissae that are clustered around the nose and mouth. It has been suggested that the rat uses the macrovibrissae and microvibrissae for distinct functional roles: the macrovibrissae being essential for spatial object localization and

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microvibrissae for fine-grained object recognition (Brecht et al., 1997). Indeed, many studies have shown that the large facial whiskers are involved in spatial tasks such as gap detection (Harris, Petersen, & Diamond, 1999; Hutson & Masterton, 1986; Sachdev, Egli, Stonecypher, Wiley, & Ebner, 2000), texture discrimination (Carvell & Simons, 1990, 1995, 1996; Cybulska-Klosowicz & Kossut, 2001; Guic-Robles, Valdivieso, & Guajardo, 1989), distance discrimination (Krupa, Mattel, Brisben, Oliveira, & Nicolelis, 2001), and aperture width discrimination (Shuler, Krupa, & Nicolelis, 2002).

Neurophysiological recordings in central trigeminal nuclei have repeatedly shown that neuronal responses are often 'tuned' to the angle of whisker deflection. Directionally tuned responses have been documented in the trigeminal ganglion (Jones, Depireux, Simons, & Keller, 2004; Jones, Lee, Trageser, Simons, & Keller, 2004; Lichtenstein, Carvell, & Simons, 1990; Shoykhet, Shetty, Minnery, & Simons, 2003; Szwed, Bagdasarian, & Ahissar, 2003), principal trigeminal brainstem nucleus (Minnery, Bruno, & Simons, 2003; Minnery & Simons, 2003), ventroposteromedial (Ito, 1988; Simons & Carvell, 1989; Timofeeva, Merette, Emond, Lavallee, & Deschenes, 2003) and reticular (Hartings, Temereanca, & Simons, 2000) nuclei of the thalamus and the primary somatosensory cortex (Brecht & Sakmann, 2002; Bruno, Khatri, Land, & Simons, 2003; Lee & Simons, 2004; Simons & Carvell, 1989). Directionally selective neurons could serve as a neural correlate for the perception of object orientation, yet there is no behavioral evidence to date that rats can discriminate between the orientation of objects with their whiskers. Therefore, we chose to study orientation discrimination behavior in the rat whisker system based on several behavioral studies that describe the rat whisker array as a spatial feature discriminator and numerous neurophysiological studies that describe directional sensitivity amongst neurons in the central whisker representations.

Sensory discrimination is typically assayed through repeated presentation of sensory stimuli and behavioral reinforcement. While this method has been shown to be an effective means to establish the precise discrimination thresholds, it often requires hundreds of trials to shape the animal's responses and hundreds more to establish the exact discrimination threshold. This is disadvantageous for studies that seek to relate behavioral discrimination thresholds to the functional organization of the corresponding central sensory representation for two reasons: first, repeated pairings of a stimuli and reinforcement can induce pronounced changes in both behavioral thresholds and central sensory representations, a process known as perceptual learning (for review see Gibson, 1953; Gilbert, Sigman, & Crist, 2001; Recanzone, 2000). Second, the functional representation of the whisker array is dynamically maintained. For example, the area of primary somatosensory cortex activated by a single whisker can change dramatically following removal of the surrounding whiskers (Glazewski, Chen, Silva, & Fox, 1996; Lebedev, Mirabella, Erchova, & Diamond, 2000; Polley, Chen-Bee, & Frostig, 1999), an increase in whisker-related activity (Polley, Kvasnak, & Frostig, 2004; Welker, Rao, Dorfl, Melzer, & van der Loos, 1992), or even in the absence of any overt manipulation (Masino & Frostig, 1996). For both of these reasons, if the central representation of a sensory stimulus is to be compared to behavioral discrimination, it is advantageous to devise a behavioral method that is rapid and presents a minimal number of stimulus/reinforcement pairings.

The method of one-trial learning is widely used to study the neural basis and consolidation of fearful memories (for review see McIntyre, Power, Roozendaal, & McGaugh, 2003; Morris, 2001; Vianna et al., 2000). In these types of experiments learning is assayed through measuring the expression of defensive responses, such as freezing or avoidance, that are triggered by the recognition of the sensory cues present during the presentation of the unconditioned stimulus (US). This type of procedure potentially circumvents the problems associated with conventional methods for assaying discrimination thresholds because it is rapid and presents a single reinforcement trial. The major difficulty with the application of this one-trial learning procedure towards assessment of behavioral discrimination is that there is uncertainty in determining which sensory cues are associated with the US. In the present study, we describe a new application of the one-trial learning procedure in which tactile cues of object orientation are emphasized in the sensory discrimination task. By quantifying learned avoidance to the conditioned orientation, we show that rats can discriminate object orientation with their whiskers and we provide an estimate of their discrimination threshold.

These data have previously been presented in abstract form (Polley, Rickert, & Frostig, 2001).

2. Methods

2.1. Behavioral training apparatus

The discrimination task was conducted in a modified Y-maze (Fig. 1) containing a central start zone connected to three trough-shaped arms of equal length (0.5 m), width (6.35, 14.61, and 22.86 cm without bars at bottom, middle, and top, respectively), and height (18 cm) separated by 120°. Each arm was fitted with 60 independently moveable bars ($5.0 \times 1.75 \times 0.75$ cm; $L \times W \times H$). The dimensions of the maze were designed such that the rat could not pass through an arm without displacing its whisker arrays on the protuberant bars, yet the bars would not necessarily contact other skin surfaces. The bars could be turned to any radial position,