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Review article

Tactile learning in rodents: Neurobiology and neuropharmacology

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ABSTRACT

Animal models of learning and memory have been the subject of considerable research. Rodents such as mice and rats are nocturnal animals with poor vision, and their survival depends on their sense of touch. Recent reports have shown that whisker somatosensation is the main channel through which rodents collect and process environmental information. This review describes tactile learning in rodents from a neurobiological and neuropharmacological perspective, and how this is involved in memory-related processes.

Contents

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1. Introduction

Learning and memory begin with the reception of olfactory, auditory, visual or tactile information related to a particular situation or experience [47]. Memory processing subsequently occurs in different brain regions in a well-defined temporal series of physiologically based stages and biochemical cascades. To discriminate the different features of an object, primates actively move their palms and fingers across its surface to activate receptors in a spatiotemporal pattern, with the resultant information being transmitted to higher brain regions [26,45]. Mice and rats are nocturnal animals that live underground in tunnels. Therefore, they need to be able to explore their environment without being reliant on visual information. Previous studies have shown that these species primarily use their whiskers to acquire information about their immediate surroundings. The whiskers also play an important role in social interaction as whiskerless rats are unable to avoid facial bites during fighting [14]. Moreover, it has been reported that lack of tactile contact with other rats leads to tail manipulation and self-biting behaviors in isolated rats [60]. On the other hand, in humans, similar to rodents, touch is a very important factor in communication and learning as it can change our emotional and physical health. This is more crucial for blind people who in the absence of vision rely more on touch especially for reading and learning. Consequently, for expansion of our knowledge on tactile learning and its underlying mechanisms we have to study other species especially rodents, for whom contact is the main means of social interaction and learning. Accordingly, in the present article we reviewed the latest findings regarding the neurobiology and neuropharmacology of tactile learning in rodents.

2. The role of vibrissae in tactile learning

Whiskers or vibrissae are a type of hair that have large size, large and well-innervated hair follicle and have an identifiable representation in the somatosensory cortex. As noted above, mice and rats are nocturnal animals that are dependent on sensory inputs from the periphery to obtain information about their surrounding environment. For rats, the facial whiskers comprise the primary tactile organ [118]. These animals actively sweep their whiskers through space and across objects during an exploratory whisking cycle (forward and backward motion). These movements, which occur at frequencies ranging from 6 to 15 Hz, allow rats to collect information on object position, texture, aperture size and distance [27]. Guic-Roblès et al. were the first to demonstrate the ability of rats to discriminate between rough and smooth textures based on whisker movements [52]. Interestingly, the results of another study showed that rats can also discriminate object orientation using their whiskers [88]. Other experimental studies have demonstrated that rats require more training and more contact time per trial to master more difficult tasks (for example, exploring similar textures) [122]. However, after several practice sessions, they are able to perform discriminations that are difficult even for humans, such as selecting between a smooth surface and one with grooves that are 50 mm deep and spaced at 90 mm [33] or sandpaper texture discrimination from rough P150 to smoother P180, P280, and P400 (100, 82, 52, and 35 μm mean grit sizes, respectively) [79]. In contrast, rats whose whiskers were trimmed soon after the birth, failed to perform a difficult discrimination task and whisked at frequencies below the normal range [72,123]. For more information on the role of whiskers in touch perception and the neuroanatomy of tactile learning please see the following review articles [34,70].

3. The role of different brain regions in tactile learning

3.1. Neocortex

A study by Smith in 1939 was one of the first to investigate different features of tactile learning. The author trained rats to choose between rough or smooth textures in a Y-maze, after which he induced lesions in different regions of the neocortex. This resulted in little or no behavioral impairment except when the somatosensory cortex was lesioned. However, the involvement of the whiskers, hind and/or forepaws was not mentioned in this report [102]. Later, Zubek used brain lesions to demonstrate that the primary somatosensory cortex, particularly the region encompassing the forelimbs, is involved in tactile discrimination [122]. It was also demonstrated that pre-trained rats with either frontal or somatic cortex lesions showed noticeable postoperative impairments when tested for reversal learning, whereas animals with occipital cortex lesions did not differ significantly from controls [44]. Similarly, it seems that associative pairing of tactile stimulation could affect somatosensory cortical responses. Godde et al. measured cortical neuron receptive fields using a protocol of associative (Hebbian) pairing of tactile stimulation. They reported a selective enlargement of the receptive fields of cortical neurons representing the stimulated regions of skin [48].

3.2. Barrel-field cortex

Hurwitz et al., in an interesting study trained rats to perform a motor response consequent to the detection of vibrissal cues derived from either active exploration or from passive detection. Then they induced thrombotic infarction of the vibrissal cortical barrel-fields of the primary somatosensory cortex. The results demonstrated that unilateral and bilateral infarction resulted in a reliable performance deficit in both active and passive sensory tasks [61].

The role of the posterior medial barrel subfield (PMBSF) within the primary somatosensory cortex has also been investigated in relation to vibrissa-based roughness discriminations. Removal of the PMBSF resulted in severe deficits, although, the rats were able to perform the task when they were allowed to explore the stimuli with their forepaws [53].

3.3. Forebrain

Previous studies have shown that other cortical regions are also involved in tactile learning [39,44,119]. For example, bilateral administration of N-methyl-D-aspartate (NMDA) in the basal forebrain, which produces degeneration of basal forebrain cholinergic neurons in rats, induced a severe impairment of tactile discrimination learning [119]. Furthermore, Peterson et al. showed that deletion of NMDA receptors from the forebrain results in a less clearly defined barrel field [86].