Field potential response changes in the rabbit olfactory bulb accompany behavioral habituation during the repeated presentation of unreinforced odors

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Summary. Experiments were performed on waking rabbits to investigate the changes in both sniffing behavior and local field potential responses in the olfactory bulb during repeated exposure to unreinforced odors. Six rabbits were each implanted with 2 pairs of electrodes for differential recording of the bulbar extracellular field potential. Each animal was given 3 sequential sessions to each of 2 separate odors on 6 consecutive days, while monitoring the bulbar field potential activity and sniffing behavior. Behavioral sniffing responses exhibited rapid within-session decrement in amplitude and long term decrement across sessions. The within-session decrement showed spontaneous recovery between sessions. Both decremental changes in sniffing behavior were accompanied by changes in the bulbar field potential responses. The responses to novel odors were characterized by a reduction in amplitude of high frequency activity (40-80 Hz) and a corresponding increase in amplitude of low frequency activity (15-25 Hz). The high frequency component of the responses showed an initial increase in frequency to a novel odor on the first 3 presentations followed by a rapid decrease in frequency on subsequent trials in the first session which stabilized thereafter. No change in frequency or relative amplitude was observed for the low frequency component. The absolute difference between the odor evoked activity and the preceding control activity measured on each trial showed a significant decrement across sessions with no evidence for spontaneous recovery. The results demonstrate that olfactory bulb responses to novel unreinforced odors show both rapid and long-term changes which parallel changes in sniffing behavior. These changes, which have been predicted by a theoretical model of the olfactory bulb (Freeman 1979a, b), are postulated to reduce the spatial specificity of the response pattern to unreinforced odors.

Key words: Olfactory bulb – Field potential – Habituation – Rabbit

Introduction

Adrian (1950) originally proposed that the representation of odor quality in the vertebrate olfactory system may be encoded in unique spatial patterns of neuronal activity evoked by each discriminable odor. Support for this hypothesis has recently been obtained from investigations in both the olfactory epithelium (Mackay-Sim and Kubie 1981; Mackay-Sim et al. 1982; Mackay-Sim and Shamon 1984) and the olfactory bulb (Jourdan et al. 1980a, b; Jourdan 1982; Lancet et al. 1982; Freeman 1987; Freeman and Vianna Di Prisco 1986). Recent evidence from studies of the rabbit olfactory bulb suggest, however, that the expression of odor-specific patterns of activity in the bulb are controlled by a learning-dependent mechanism (Vianna Di Prisco and Freeman 1985; Freeman and Vianna Di Prisco 1986; Freeman 1987). Odor-specific patterns of high frequency (40-80 Hz) field potential activity were detected only after the acquisition of discrimination in a conditioning paradigm and only when a correct behavioral response was performed by the animals (Freeman 1987; Freeman and Vianna Di Prisco 1986). No significant odor-specific patterns of activity were observed for odors presented without reinforcement (Freeman 1978; Freeman and Schneider 1982; Grajski and Freeman 1987). In order to account for the latter findings it was proposed that the repeated exposure to an unreinforced odor results in rapid changes of...
Fig. 1. Changes in the magnitude of sniffing responses to repeated presentation of an unreinforced odor. Shown on the left are the pneumograph traces (6 s in duration) obtained during the 10 trials on the third session to Clove Oil. The left vertical line indicates the start of the test period. The vertical line just to the right indicates the calibrated arrival time of the odor in the nose-cone. The graph on the right displays the result of the respiratory response algorithm used to calculate response magnitude.

the bulbar response which manifest habituation (Gray et al. 1986; Freeman 1987). The process of habituation was postulated to concomitantly reduce the spatial specificity of the response pattern (Gray et al. 1986); a process which has subsequently been confirmed experimentally (Grajski and Freeman 1987).

Thus, taken together the data suggest that under the conditions of behavioral motivation the response of the olfactory bulb to a particular odor gradually changes until a unique spatial pattern of activity is evoked each time the odor is presented (Freeman and Vianna Di Prisco 1986). In the absence of behavioral arousal the pattern of the response also changes, but in such a way that the odor-specificity of the response is reduced (Freeman and Skarda 1985). A change of this sort could provide one possible explanation for the failure to detect odor-specific patterns of activity in response to unreinforced odors (Freeman 1978; Freeman and Schneider 1982; Grajski and Freeman 1987).

Evidence in support of this hypothesis comes from both single and multunit recording studies in mammals and fish. In these experiments as few as 1–10 presentations of an unreinforced odor were sufficient to produce long lasting changes in the response properties of recorded mitral cells (Freeman 1975; Potter and Chorover 1976; Scott 1977; Chaput and Panhuber 1982; Chaput and Holley 1985; Schild 1985). Therefore, we sought to determine if similar changes could be observed in the field potential responses of the rabbit olfactory bulb and if these changes were paralleled by changes in the animals' olfactory sniffing behavior. In the present study we quantitatively investigated the temporal sequence of changes in the responses of the bulbar field potential to the repeated presentation of unreinforced odors. Simultaneous measurements of sniffing behavior were also made to enable a comparison between the electrophysiological and behavioral response changes. We have developed a technique to examine, on a trial by trial basis, the changes in response of both the bulbar field potential and the animals' sniffing behavior to repeated odor stimulation. The results demonstrate that, 1) repeated exposure to unreinforced odors results in rapid and long-term changes in the responses of both the bulbar field potential and sniffing behavior, and 2) these changes differ from those observed under reinforcement (Freeman 1987).

These results have been presented previously in abstract form at the American Neuroscience Society conference held in Washington in 1986 (Skinner and Gray 1986).

Methods

Subjects

Experiments were performed on 6 adult male New Zealand White rabbits weighing 3–4 kgs. Each animal was surgically anesthetized with Ketamine (25 mg/kg) and Xylazine (10 mg/kg) and placed in a stereotaxic apparatus. After exposing the left dorsal bulbar surface 2 pairs of recording electrodes (stainless steel, 40 µm) were implanted across the bulbar dipole field for differential recording of the extracellular field potential activity. Two electrode pairs were utilized to improve the chances of recording stable responses. The wound openings were sealed with sterile agar saline and the entire assembly was fixed to the skull with dental acrylic. The animals were allowed 1 week to recover.

Training procedure

After recovery from surgery each animal was lightly restrained and placed in a sound resistant chamber. A pneumograph was placed around the abdomen for monitoring respiration. The recording connectors were mated and a nose-cone was fitted over the animals' muzzle. A steady stream of charcoal purified air was delivered into the nose-cone at a rate of 6–8 l/min through a 3-channel dilution olfactometer. The animal was left in this position for 30–60 min and then returned to its' home cage. The procedure was repeated 3–5 times on successive days until the animal became adapted to the restraint.

Following the familiarization procedure habituation training was carried out for each of 2 odors, clove oil and amyl acetate, diluted in water 1:100 and 1:1000, respectively. Methyl Salicylate (oil of wintergreen) was introduced on selected trials as a dishabituating stimulus. Each animal was given 3 sessions for each odor separately. Sessions were given on consecutive days and consisted of 10 trials of the odor interspersed at random with 10