

OSCILLATORY DYNAMICS OF OLFACTORY STRUCTURES IN RESPONSE TO PREDATOR AND NON-PREDATOR ODORS

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Neural activity in the mammalian olfactory system is characterized by oscillations. Examination of the functional roles of oscillatory activity in mammalian olfactory systems is necessary to understanding the processing of olfactory information. In 1950, Adrian described mass oscillatory activity in the mammalian olfactory bulb (OB) in both the absence and presence of odors (Adrian 1950). These oscillations of field potentials ranged from 1 to 100 Hz. Mechanisms of oscillation generation, conditions of elicitation, as well as the possible functional significance of these oscillations have all been explored by numerous studies over the past half-century. The gamma frequency (~30-100 Hz) in particular has been extensively examined over the years (Freeman 1978; Freeman and Schneider 1982; Bressler 1988; Kay 2003), though recently beta oscillations have begun to receive attention.

Vanderwolf and others have suggested that olfactory structures respond to predator odors with bursts of oscillatory activity in the beta frequency band (15-40Hz) (Heale and Vanderwolf 1994; Heale, Vanderwolf et al. 1994; Zibrowski and Vanderwolf 1997; Zibrowski, Hoh et al. 1998; Vanderwolf and Zibrowski 2001). However, those same oscillation bursts were seen in response to some non-predator odors. The predator odor used in the studies mentioned above was trimethylthiazoline (TMT), a synthetic compound initially isolated from fox feces. In this study we compare physiological and behavioral responses to TMT with a panel of other odorants to determine which elicit similar responses.

Odors were presented to the rats in an enclosed chamber made from modified polycarbonate rat cages. Odors were presented in a habituation paradigm of five 2-minute odor trials with 3-minute vent trials following each. All odor tests began with one 2-minute plain air trial followed by a 3-minute vent trial. Olfactory bulb (OB) local field potential (LFP) responses were recorded during odor exposure, and behavior was concurrently recorded by webcam. Theta (3-15 Hz), beta (15-40Hz), low gamma (35-60Hz), and high gamma (60-115Hz) oscillation patterns are examined in response to each

odor. Beta oscillation bursts have been seen in response to some odors, particularly toluene, when presented in short duration to awake (Chapman, Xu et al. 1998) and anesthetized rats (Neville and Haberly 2003), however no examination has previously been done on longer term exposures like the paradigm used here.

We compared responses to TMT with responses to fox urine, to measure the effectiveness of another predator odor in eliciting the bursts of beta oscillations. We compared these responses with those to raccoon urine, male rat urine and female rat urine (estrus, non-estrus, and mixed). As toluene has been found to elicit beta oscillations, we tested this odorant as well as other monomolecular odorants: amyl acetate, benzaldehyde, acetone, indole, vanillin. Additional comparisons were made with familiar food odors (Rat Chow, Froot Loops, tap water) and novel food odors (apple juice, peanut butter).

We find similarities between predator and non-predator odors across frequency bands, as well as some differences between the two predator odors tested. We find that the responses to the two predator odors, TMT and fox urine, differ from each other, particularly in the beta band. TMT shows a very different response pattern from some of the monomolecular chemicals and from other ethologically relevant odors.

In our examination of multiple odorants, we noted that isoamyl acetate (IAA) produced frequency responses different from all the other monomolecular odors tested. Our results indicate that amyl acetate produces a significantly different pattern of activation than the other odorants tested. There is a significant enhancement of higher frequencies of gamma over other odorants. Additionally, the power in the gamma band is much higher during odor presentation than during vent or plain air trials. This suggests that IAA, which is used as a control odor in many olfactory studies, may be inappropriate for this purpose.

In presenting each odor several times, we attempted to assess levels of habituation or sensitization in response to the various odors. The amount of beta activity has been shown to increase over trials (Vanderwolf and Zibrowski 2001; Ravel, Chabaud et al. 2003), and the frequency of beta oscillations has been shown to decrease over trials (Ravel, Chabaud et al. 2003). In this study beta fluctuations are seen within the two minutes of exposure, as well as across the five odor trials. Methodological differences from previous studies likely explain variations in results. We also examine changes in

gamma frequency and power across the testing and find that for many odorants there is an increase in gamma power over the first three trials followed by a decrease in the final two.

Theta oscillations in the OB are highly correlated with respiration rate in mammals. Recent research in our laboratory has found that oscillations in the high gamma range (>60 Hz) are correlated with the sniff cycle and that low gamma oscillations (<60 Hz) are not (Kay 2003). In this study, we replicate these results in the untrained condition. Respiration depth and frequency can be influenced by the odor type, and thus can influence the frequency of gamma responses. To demonstrate this, we correlate theta oscillatory activity with Types 1 and 2 gamma activity across several odors.

Odor-induced oscillatory activity has been shown to be related to perception and memory of an odorant and some significant correlations have been made between trained behavioral responses to familiar odors (Kay and Freeman 1998; Kay 2003; Ravel, Chabaud et al. 2003). Little work has been done, however, to correlate spontaneous behavioral odor responses with concurrent olfactory oscillations, perhaps due to the short duration of odor exposure in most olfactory studies. We find that behavioral responses, such as freezing and attentive sniffing, are strongly correlated with concurrent oscillatory activity. Our results suggest that variations in oscillatory patterns can be attributed primarily to behavioral variations.

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