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# Odor Tracking in Rats With Orbital Frontal Lesions

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Rats track self-, conspecific, and artificial odors to locate food. The orbital frontal cortex has been implicated in olfactory behavior, but whether it plays a role in a species-typical behavior, such as odor-guided navigation, has not been studied. Rats were trained to track 1 of 3 different odors deposited on a string. After rats were reliably tracking a scented string, they received a series of 2- and 3-odor discrimination tests. Next, all the rats received bilateral aspiration lesions of the orbital frontal cortex and experienced the same sequence of tasks. Rats learned to track and discriminate between different odors reliably. These results suggest that other areas of the brain mediate odor-guided navigation following damage to the orbital frontal cortex.

The orbital frontal cortex is thought to be the primary neocortical region involved in olfactory representations. It corresponds roughly to the region receiving projections from the central part of the dorsal medial nucleus (MD) of the thalamus and is roughly analogous to Brodmann's areas 11–14 in humans. In addition to impaired olfactory discrimination (Potter & Butters, 1980), damage to the orbital frontal cortex of humans results in impairments in taste (Small et al., 1999), reduced behavioral spontaneity (Jones-Gotman & Milner, 1977), perseverative behavior (Milner, 1964), loss of affective learning (Angrilli, Palomba, Cantagallo, Maietti, & Stegagno, 1999), and impaired social behavior (Blumer & Benson, 1975). Much of the work in humans reflects experiments examining olfactory deficits subsequent to resection of the orbital frontal cortex as a treatment for intractable epilepsy (Jones-Gotman & Zatorre, 1993; Zatorre & Jones-Gotman, 1991). Other work with humans involves the use of functional imaging of brain activity during tasks in which the subject is presented with a series of olfactory stimuli (Small et al., 1999; Zatorre & Jones-Gotman, 2000). Taken together, this work suggests that the orbital frontal cortex is involved in higher level behavioral processing in which information from different sensory modalities is combined, and, thus, that it might be especially involved in complex olfactory behavior.

Studies with rats suggest that the function of the orbital frontal cortex is largely conserved across species (e.g., Kolb, 1984). For example, unit activity in the orbital frontal cortex is related to the formation of cross-modal associations involving olfactory stimuli (Alvarez & Eichenbaum, 2002; Lipton, Alvarez, & Eichenbaum, 1999; Ramus & Eichenbaum, 2000; Ragozzino & Kesner, 1999; Schoenbaum, Chiba, & Gallagher, 1999). In addition, lesions of the orbital frontal cortex impair learning of various odor-guided tasks, including delayed nonmatching to sample (Otto & Eichenbaum, 1992) and tactile–olfactory configural learning (Whishaw, Tomie, & Kolb, 1992). Thus, both human and rat work, as well as studies with laboratory monkeys (e.g., Rolls, 1998), have led to the conclusion that the orbital frontal cortex plays an important role in complex olfactory-mediated behaviors.

Previously, we have demonstrated that rats can track strings scented with artificial odors, the odor of a conspecific, or their own odor (Wallace, Gorny, & Whishaw, 2002). This work also demonstrated that rats are able to discriminate among several different scented strings presented at the same time and use this information to reach a goal. This task is interesting because, at least from a conceptual view, odor tracking involves not only the association of the scent and tracking behavior and identification of the appropriate trail but also the possibility that the tracking animal maintains a representation of the target at the end of the trail. Thus, the complexity of the behavior suggests that it is a candidate behavior requiring the orbital frontal cortex. The purpose of the current experiments is to examine whether the orbital frontal cortex is involved in odor-guided navigation. The rats were trained to find a food pellet at the end of a scented string, with the scent being an artificial scent, the scent of another rat, or the rat's own scent. The rats received orbital frontal lesions and were given the same problems that they experienced prior to surgery.

## Method

### *Subjects*

Twelve adult female Long–Evans rats (University of Lethbridge vivarium), weighing 250–300 g, were housed in groups of 4 in wire mesh cages. The colony room was maintained at 20–21 °C and a 12:12 hr light–dark cycle.

### *Surgery*

Rats were deeply anesthetized with sodium pentobarbital (50 mg/kg ip). A trephine was made in the skull at the junction of the parietal suture and temporal ridge. While removing the overlying skull, we took care not to damage the blood vessel that runs along the rhinal fissure. We removed the orbital frontal cortex by aspirating the tissue. The lesion area was restricted to the dorsal and ventral components of the agranular insular cortex

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(Zilles's areas AID and AIV) and some of the adjacent lateral orbital cortex (Zilles's area LO; see Figure 1). Testing resumed 2 weeks after the surgery.

### *Feeding*

At the beginning of the experiment, feeding was restricted to maintain the animals at 85% of their free-feeding weight. Large food pellets (750 mg; Bio-Serv, Frenchtown, NJ) were used as reward during testing. Rats reliably carry these pellets to a refuge for eating (Whishaw, Coles, & Bellerive, 1995). After testing each day, the rats were fed with LabDiet Laboratory Rodent Pellets (Canadian Lab Diet, Leduc, Alberta, Canada) in their home cages to supplement the food obtained on the table.

### *Apparatus*

The open field was a 204-cm-diameter circular wooden table painted white. The table was elevated 75 cm above the floor. Eight 11.5-cm-diameter holes were arrayed around the perimeter of the table (Wallace et al., 2002). The table was constructed such that a cage could be affixed beneath any of the holes from which the rat could exit. The apparatus was located in a large room that could be made completely dark. A camera equipped to record under both light and dark conditions (with infrared wavelengths) was positioned perpendicular to the apparatus. The experimenter used an infrared spotter to monitor the rat's behavior during dark testing.

The strings used in this study were 100% cotton butcher twine approximately 2 mm in diameter. Overhand knots were tied at each end of the string so that thumbtacks could hold the string in position on the table. Vanilla and rat odors were used as olfactory stimuli during the course of this experiment. Vanilla odor was placed on strings as they were dipped in pure vanilla extract; the excess fluid was wiped off. A string was scented with rat odor by being rubbed gently on a rat's body and tail for 15–30 s. Neutral strings were placed on the table without any odors added to them. Each string was kept in a different jar and handled with a new pair of rubber gloves each time, which minimized odor contamination between strings. In addition, the strings were frequently replaced.

### *Procedure*

Prior to training and testing, rats were habituated to the table for 6 days; rats could leave the home base and retrieve five food pellets located randomly around the table. After habituation, rats were randomly assigned to one of three groups. Each group was required to track a different odor. The *own group* tracked a string scented with each rat's own odor. The *other group* was required to track a string scented with another rat's odor. The *vanilla group* tracked a string scented with vanilla. A trial was counted as correct if (a) the rat left the home base, (b) followed the target string to the end, and (c) obtained the food pellet. If the rat followed one of the other strings present on the table, the trial was recorded as an error, and the rat was allowed to explore the table until it obtained the food pellet. Rats were given three trials per day across all training and testing conditions. During training and testing, string locations were changed randomly from trial to trial and across days, which thereby eliminated positional cues and made distal spatial cues irrelevant for task performance. The table was rotated between rats and wiped down with Windex cleaner every day after testing. The following sections detail the training and testing used during the experiment.

*Habituation and training.* Throughout training, the string to be tracked plus two neutral strings were placed on the table such that they radiated in straight lines from the rat's home base. Training proceeded in three phases. The first phase (10 days) required rats to track a 50-cm string under light conditions. The second phase (5 days) extended the length of the strings to 100 cm. The third and final phase (8 days) of training required each group to track a 100-cm string under infrared light, a wavelength in which rats cannot see (Deegan & Jacobs, 1993).

*Two-odor string tracking.* The first phase of discrimination testing examined the rat's ability to discriminate among two scented strings and an unscented string. Each group was exposed to a set of strings three times a day under dark conditions. A set of strings included the string that the rat was trained to track, a string that one of the other groups was trained to track, and a neutral string. For example, a rat trained to track vanilla would be exposed to (a) a vanilla-scented string, an other-rat-scented string, and a neutral string; or (b) a vanilla-scented string, an own-scented string, and a neutral string. This phase of discrimination testing required 2 days to pair each group's training scented string with the other two groups' training scented strings. Rats received a total of 6 days on the two-scented string discrimination test, resulting in 3 days per testing pair.

*Three-odor string tracking.* The second phase of discrimination testing examined the rat's ability to discriminate among three scented strings. Each group was exposed to their training string and the other two groups' training strings. Rats were presented with the three scented strings three times per day for 8 days under dark conditions.

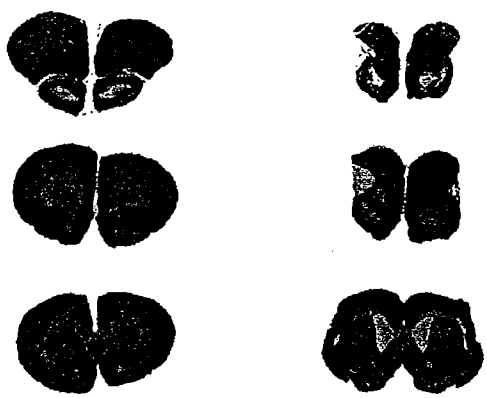

*Figure 1.* Representative Cresyl violet-stained sections from a control brain (left) and an orbital frontal lesion brain (right).

## Results

Groups were not found to be significantly different in their abilities to track the different odors (Wallace et al., 2002). Group membership was excluded as a factor in the current set of analyses; therefore, within-subject analyses of variance (ANOVAs) were used to examine the effects of days, lesion, and the Days × Lesion interaction. For analyses in which the assumptions of sphericity were violated, we used the Greenhouse–Geisser method for adjusting degrees of freedom.

### *Histology*

The lesions were intentionally large to ensure that the entire orbital frontal region was removed. As can be seen in Figure 1, rats that received aspiration lesions had most of the agranular insular cortex, all of the lateral orbital cortex, and the posterior part of the ventrolateral orbital cortex removed, with some additional damage to the adjacent parietal and motor regions. Examination of the thalamus showed mild degeneration in the medial region of MD and in the lateral nuclei.

### *Training*

Figure 2 presents pre- and postsurgery mean percentage correct for each phase of training. It is clear from the figure that the animals showed minimal savings from the preoperative training,

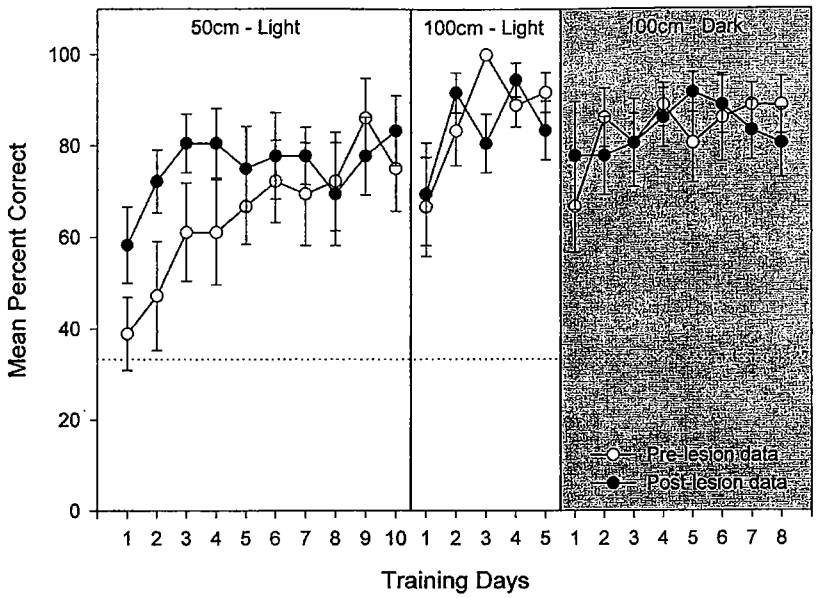


*Figure 2.* The left panel presents percent correct responding before and after the orbital frontal lesions on the first phase of training, with a 50-cm string under light conditions. The middle panel presents percent correct responding before and after the orbital frontal lesions on the second phase of training, with a 100-cm string under light conditions. The right panel presents percent correct responding before and after the orbital frontal lesions on the last phase of training, with a 100-cm string under dark conditions. Data are means (± *SEM*).

although they were capable of relearning the discrimination. The ANOVA conducted on mean percentage correct for the first phase of training (50-cm strings under light conditions) revealed a significant effect of day, $F(9, 99) = 4.084$, $p < .05$, which reflects the improved performance over days in both pre- and postoperative training. The effect of lesion and the Lesion × Day interaction were not significant, thus confirming that there was no significant savings from the preoperative training. The ANOVAs conducted on the mean percentage correct for the second phase of training (100-cm strings under light conditions) and the final phase of training did not result in a significant effect of lesion, day, or Lesion × Day interaction.

### *Two-Odor String Tracking*

The left panel of Figure 3 presents group mean percentage correct on the two-odor discrimination problems pre- and postlesion. One should recall that rats had to discriminate among three strings: the string presented during training, a string scented with an odor used during training by one of the other groups, and a neutral string. During testing, none of the rats tracked the neutral string. Although both prelesion, $t(11) = 10.975$, $p < .05$, and postlesion, $t(11) = 4.494$, $p < .05$, percentage correct responding were significantly higher than chance, there was no significant effect of lesion.

### *Three-Odor String Tracking*

Each group's mean percentage correct on the three-odor discrimination test is presented in the right panel of Figure 3. An ANOVA conducted on daily mean percentage correct revealed a significant effect of days, $F(7, 77) = 6.173$, $p < .05$. The effect of lesion and the Days × Lesion interaction were not found to be significant. Post hoc analysis of the days effect revealed a significant linear trend, $F(1, 11) = 37.043$, $p < .05$, across the three-odor discrimination testing sessions.

## Discussion

This study shows that rats with orbital frontal lesions are able to locate food by tracking a scented string, whether it has an artificial odor, the odor of a conspecific, or self odor. In addition, the rats were able to discriminate the reinforced odor from competing odors. Orbital frontal lesions did produce impairments in trained rats, but the ability of the rats to relearn suggests that tracking can be performed with relatively low-level associations dependent on other olfactory areas of the central nervous system.

The ability of orbital frontal lesion rats to perform the tracking task is surprising. Odor-guided navigation requires an animal to organize its behavior through time. For example, an animal has to sample the scented strings, choose one, and follow it to the end to make the correct response. In addition, these behaviors have to occur in a fixed sequence without the animal getting distracted by other odor cues or spatial cues from the previous trials. One of the hallmarks of the frontal syndrome is an inability to order behaviors through time (e.g., Kolb & Whishaw, 2003). This impairment may reflect (a) an inability to plan or use information in a prospective way, (b) an inability to maintain attention on a task or filter out distracting information, or (c) an inability to encode recently completed tasks or use information in a retrospective way. The learning observed subsequent to orbital frontal lesions indicates that the orbital frontal subjects retain strategies that are sufficient to organize their behavior serially to complete the task.

The ability of the orbital frontal lesion rats to track is also surprising with respect to other theories of orbital frontal cortex

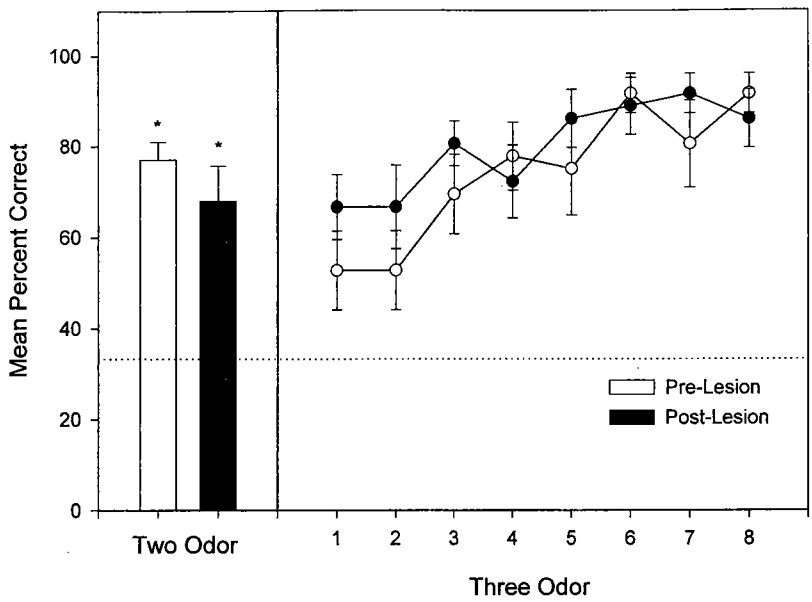


*Figure 3.* The left panel presents the performance on two-odor probes before and after the orbital frontal lesions. The right panel presents the performance for the three-odor discrimination training before and after the orbital frontal lesions. Data are means (± *SEM*). * $p < .05$.

function. Some researchers have suggested that the orbital frontal cortex may be involved in the formation of cross-modal associations (Rolls, 1998; Zatorre & Jones-Gotman, 2000). In rats, explicit examination of the role of the orbital frontal cortex in cross-modal associations has produced data that support this suggestion. Whishaw et al. (1992) demonstrated that orbital frontal lesions disrupt previous learning and subsequent acquisition of a tactile–odor configural task. In addition, Lipton et al. (1999) have shown that cells in the orbital frontal cortex fire preferentially during a spatial–odor configural task. It is possible that the rats originally learned our task by encoding a cross-modal association present during tracking.

Researchers have suggested that the orbital frontal cortex is critical for learning the strategies, or rules, that are necessary for solving a set of problems (Meunier, Bachevalier, & Mishkin, 1997; Otto & Eichenbaum, 1992). For example, Otto and Eichenbaum (1992) developed an olfactory-guided delayed-nonmatching-to-sample task for rats. They found that damage to the orbital frontal cortex resulted in impaired acquisition of this task. The authors concluded that the impaired acquisition was related to difficulties in learning the nonmatching rule inherent in the delayed-nonmatching-to-sample task. Considering that olfactory tracking and discriminating do not require rule induction to relate successive stimuli to the correct responses, our pattern of results suggests that although the orbital frontal cortex is sufficient for odor-guided behaviors, it is not necessary. The impaired acquisition of the delayed-nonmatching-to-sample task observed by Otto and Eichenbaum (1992) may reflect a difficulty in encoding the stimulus attributes that differentiate the odors used in their study rather than a difficulty encoding the nonmatching rule. That is, control rats may be able to use qualitative attributes of odors to control responding, whereas orbital frontal rats use relative intensity judgments to control responding. The difference in the stimulus attribute used to control responding by control versus orbital frontal rats may have mediated the differential learning rates observed between groups.

Studies examining a patient's ability to process olfactory information after resection of the orbital frontal cortex report that discriminations among odors are impaired (Zatorre & Jones-Gottman, 1991). This work, in combination with functional imaging of brain activity (Zatorre & Jones-Gottman, 2000), has led researchers to claim that the orbital frontal cortex plays a specialized role in odor processing. Our work demonstrates that the relearning observed after the orbital frontal lesions is consistent with other brain structures mediating olfactory learning.

From the current data set, it is not possible to determine whether different stimulus properties of the odor-guided navigational task mediated initial learning versus relearning observed after lesions. For example, initial learning may have been controlled by qualitative differences in odors, whereas subsequent relearning may have been controlled by relative differences in odor intensity. Patients with damage to the orbital frontal cortex demonstrate impaired odor discrimination, but odor intensity judgments are intact (Zatorre & Jones-Gotman, 1991). Therefore, it is entirely possible that the stimulus characteristics of odor-guided navigation are rich enough to permit encoding by multiple brain regions.

Although researchers have demonstrated the importance of diencephalic nuclei for olfactory behaviors, damage to these structures also produces impairments in other, nonolfactory-based tasks. For example, Koger and Mair (1994) demonstrated that thalamic lesions, although they spared simple olfactory discriminations, disrupted performance on an olfactory delayed-nonmatching-to-sample task. In contrast, the authors reported that damage to the orbital frontal cortex produced transient deficits in the delayed-nonmatching-to-sample task. More recently, thalamic lesions restricted to the intralaminar nuclei produced a deficit in a spatial version of the delayed-nonmatching-to-sample task (Mair, Burk, & Porter, 1998). Although it is clear that areas other than the

orbital frontal cortex contribute to the processing of olfactory information, an understanding of what each area contributes during an olfactory task remains an active area for investigation.

It is important to note that the rats in the present study were pretrained on the assumption that the task would be difficult to learn postoperatively. It was surprising that the rats reacquired the task at about the same rate as initially learned. It is unlikely that the absence of savings is due to the 2-week recovery period because, during the training, the running of animals was frequently interrupted for weekends and holidays with no discernable decrement in performance. In addition, it is not unusual for animals with cortical lesions to reacquire tasks without savings (Lashley, 1932). If future studies use the present paradigm, then it would be necessary to make a more comprehensive analysis of the cues used than was done in the present study. For example, in studies on visual discrimination, initial learning is mediated by pattern discrimination; however, subsequent relearning is controlled by flux discrimination (Cooper, Blochert, Gillespie, & Miller, 1972).

In summary, extensive work has suggested that the orbital frontal cortex is important for processing olfactory information. Here, we report that rats have a natural proclivity for tracking artificial, self-generated, and conspecific-generated odors, and they are able to do so with orbital frontal lesions. Although on the surface it appears that tracking is a relatively high-level task, the present results suggest that it can be performed without the olfactory neocortex. Given that in the present experiments the rats were pretrained and apparently displayed no savings relative to their prelesion acquisition performance, the extent that performance observed after the orbital frontal lesions is mediated by stimulus characteristics different from those used during initial learning requires further empirical evaluation.

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