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# Changes in Odor Quality Discrimination following Recovery from Olfactory Nerve Transection

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## Abstract

Following recovery from olfactory nerve transection, animals regain their ability to discriminate between odors. Odor discrimination is restored after new neurons establish connections with the olfactory bulb. However, it is not known if the new connections alter odor quality perception. To address this question, 20 adult hamsters were first trained to discriminate between cinnamon and strawberry odors. After reaching criterion ( $\geq 90\%$  correct response), half of the animals received a bilateral nerve transection (BTX) and half a surgical sham procedure. Animals were not tested again until day 40, a point in recovery when connections are re-established with the bulb. When BTX animals were tested without food reinforcement, they could not perform the odor discrimination task. Sham animals, however, could discriminate, demonstrating that the behavioral response had not been extinguished during the 40 day period. When reinforcement was resumed, BTX animals were able to discriminate between cinnamon and strawberry after four test sessions. In addition, their ability to discriminate between these two familiar odors was no different than that of BTX and sham animals tested with two novel odors, baby powder and coffee. These findings suggest that, after recovery from nerve transection, there are alterations in sensory perception and that restoration of odor quality discrimination requires that the animal must again learn to associate individual odor sensations with a behavioral response.

## Introduction

Unlike other neurons in the central nervous system, olfactory sensory neurons are continuously replaced throughout life. Morphological studies suggest that olfactory neurons are replaced about every 30 days (Graziadei and Monti Graziadei, 1978, 1980), though a few studies report a longer life span (Hinds *et al.*, 1984; Mackay-Sim and Kittle, 1990). Replacement neurons also have a remarkable capacity to re-establish connections with the olfactory bulb following injury. After olfactory nerve transection, sensory neurons in the epithelium degenerate and there is an increase in differentiation of basal cells. This gives rise to a new population of olfactory neurons (Graziadei, 1973; Graziadei and DeHan, 1973; Simmons *et al.*, 1981; Costanzo, 1984). Axon fibers from replacement neurons reach the glomerular layer of the bulb within 20–30 days after lesion (Harding *et al.*, 1977; Graziadei and Monti Graziadei, 1978, 1980; Jennings *et al.*, 1995; Yee and Costanzo, 1995). Electrophysiological studies have shown that these new sensory neurons are functional. In the regenerated olfactory epithelium, extracellular recordings of receptor cell activity and electro-olfactograms (EOGs) have demonstrated that odor responses are similar to those obtained from controls (Simmons and Getchell, 1981a,b). Recordings from olfactory nerve fibers (Oley *et al.*, 1975) and second-order cells in

the olfactory bulb (Costanzo, 1985) provide additional evidence that the reconnected axons have the capacity to transmit olfactory information to the central nervous system.

Restoration of odor-mediated behavior following recovery from nerve transection has been demonstrated in the pigeon (Oley *et al.*, 1975; Walker *et al.*, 1981), mouse (Harding and Wright, 1979), goldfish (von Rekowski and Zippel, 1993) and hamster (Yee and Costanzo, 1995). Yee and Costanzo (1995) showed a direct correlation between the time course of olfactory nerve reinnervation and recovery of odor detection and discrimination. New axon fibers were first observed in the nerve layer 10 days after surgery and in the glomerular layer at ~20 days. As early as 19 days after nerve transection, animals began to detect and discriminate between odors. Their performance gradually returned to preoperative levels ( $\geq 90\%$  correct response) within a period of 40 days. These findings demonstrate that the reinnervated olfactory bulb has the capacity to detect odors, and to discriminate between different odors. However, the results do not address an important question: is odor quality perception changed in the reinnervated bulb?

In this study, we compared the behavioral recovery for BTX and sham animals after 40 days of recovery. No

training or reinforcement was given during this 40 day recovery period. On days 40 and 43, animals were tested without food reinforcement to determine if they could discriminate between the two previously learned odors. Reinforcement was again introduced on day 46, and animals were then tested to determine if additional training was required to perform the discrimination task. BTX animals required additional training sessions before they could perform the odor discrimination task. This suggests that, after recovery from nerve transection, there are alterations in sensory perception. A preliminary report of the results has been published in abstract form (Yee and Costanzo, 1996).

## Materials and methods

### Subjects

Ten female and 10 male hamsters (*Mesocricetus auratus*), ranging in age from 6 to 9 months, were purchased from Charles River (Wilmington, MA). Animals were individually housed in standard plastic cages and kept in a 12 h light:dark cycle. Animals were placed on a limited food schedule of 10–12 g/day with water *ad libitum* 3 days prior to preoperative training. The animals were checked every other day to make sure that they did not lose >15% of their body wt. If an animal dropped below this level, preoperative training was discontinued and an *ad libitum* feeding schedule was introduced. After preoperative training, BTX surgery was performed and all animals were placed on the *ad libitum* feeding schedule. Postoperative testing began after a recovery period of 40 days with animals remaining on the *ad libitum* feeding schedule throughout testing. Behavioral protocols and surgical procedures were reviewed by the Institutional Animal Care and Use Committee (IACUC) to assure compliance with Federal, State and Virginia Commonwealth University regulations.

### Test apparatus and odor stimuli

Animals were trained and tested in a Plexiglas apparatus designed to fit into a standard hamster cage (Yee and Costanzo, 1995). It consisted of two chambers, a holding chamber (21 × 25 × 15 cm) and a test chamber (10 × 10 × 15 cm), separated by a sliding partition. Plastic beads impregnated with odors (PolyIFF, International Flavors and Fragrances, New York) served as odor stimuli. The odors (cinnamon, strawberry, baby powder and coffee) were selected because they are not normally encountered in the hamster's environment. The intensity of the odors were evaluated and matched by human observers to a series of standard 1/3 log step dilutions of butanol (Cain *et al.*, 1983). The intensity of each of the four odor stimuli was most frequently matched to the 0.14% butanol concentration and all the intensity judgements were within 1/3 of a log unit of this concentration. Human observers did not report any irritation or unpleasant sensations associated

with the odors. Odor beads were placed in polystyrene containers and inserted through an opening in the back wall of the test chamber that served as the odor delivery port. Odor containers were checked by sniffing for odor intensity on each test day and were replaced every two weeks. Air from a compressed air source was used to flush air from the test chamber after each trial. The entire behavioral apparatus was cleaned with 95% alcohol and air-dried after every session.

### Odor discrimination training and testing

A discrete trial go/no go paradigm was used to train animals to discriminate between cinnamon and strawberry. Details of this procedure have been described in a previous paper (Yee and Costanzo, 1995). Prior to training, animals were randomly assigned cinnamon or strawberry as the S+ odor. Animals were trained to give a correct response (i.e. scratching or biting at the odor container and/or odor port) during S+ trials by reward with a small food pellet. They received a light puff of air as punishment when they gave the same response during S- trials (false positives). A correct response was assigned to S- trials if the animal did not scratch or bite at the odor container. Neither air puff nor food reward was given if it failed to give the correct response on S+ or S- trials. After each trial, the animal was guided back into the holding chambers and the sliding partition was closed. Air puffs were discontinued after animals reached a performance level of 70% correct response. A daily test session consisted of 10 S+ trials and 10 S- trials presented randomly, with no more than three of the same odor stimulus trials occurring in succession. Animals were considered trained if correct responses were recorded on 18/20 trials.

After at least six consecutive sessions at or above this 90% criterion, animals received three more sessions with reinforcement given on only half of the S+ trials. This partial reinforcement was used to prepare the animal for postoperative extinction by strengthening the association between the behavioral response and the odor. After the last test session (day 0) animals received either a bilateral olfactory nerve transection (BTX) or a surgical sham procedure. Animals were allowed to recover (days 0–40) without further testing. On days 40 and 43, animals were tested without reinforcement to determine if they could still discriminate cinnamon from strawberry. Retesting was initiated on day 40 because a previous study demonstrated that the reinnervated bulb can support odor discrimination at this stage of recovery (Yee and Costanzo, 1995). On day 46, animals were randomly assigned to one of two groups. Group A was tested with the same preoperative odor pair: cinnamon and strawberry. Group B was tested with a pair of novel odors: baby powder and coffee. Food reinforcement was resumed and, on the first S+ trial, animals received a food reward whether or not they gave a response. This was done to pair the S+ odor with food reinforcement. For the

remaining 19 trials, animals were required to emit a scratching or biting response on S+ trials to receive food reinforcement. No punishment was administered if the animal gave an incorrect response or failed to respond during postoperative testing. Animals were tested every third day until day 61, when the study ended.

### Surgical Procedures

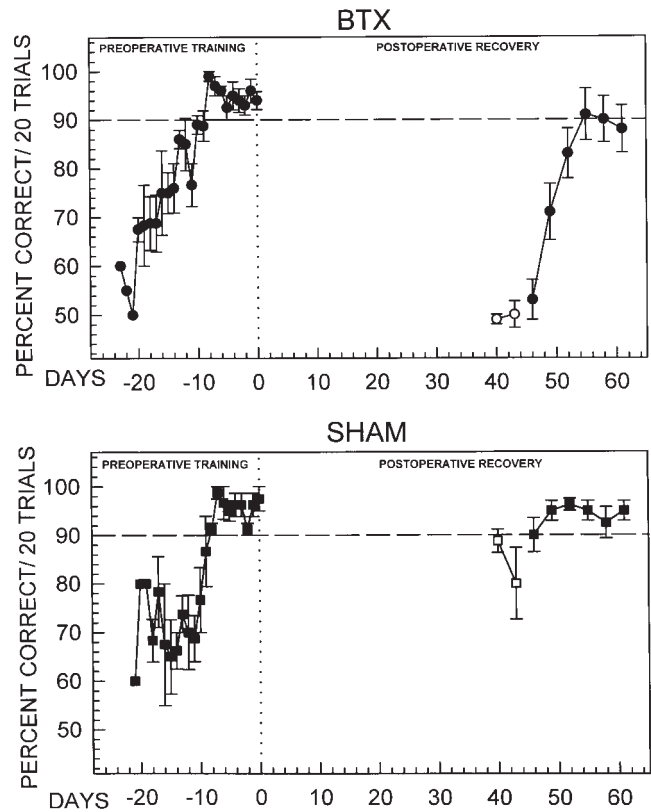
Animals ( $n = 10$ ) receiving the bilateral nerve transection were first sedated with halothane and then anesthetized with sodium pentobarbital (80 mg/kg, i.p.). The frontal bones overlying the olfactory bulbs were removed and the dura was cut and retracted to expose the olfactory bulbs. A flexible Teflon blade was inserted between the cribriform plate and each olfactory bulb, and then manipulated under and around each bulb. This procedure resulted in transection of all olfactory axons that project through the plate to the bulb. Following transections, the skin incision was sutured closed and animals were returned to their home cages. Sham animals ( $n = 10$ ) received identical surgical exposure of the olfactory bulbs but the olfactory nerves were not transected. Details of the olfactory nerve transection procedure have been described previously (Yee and Costanzo, 1995).

## Results

### Group A

Figure 1 depicts the training and recovery for BTX and sham animals in group A. These animals were trained to discriminate between cinnamon and strawberry and then tested postoperatively to determine if they retained the ability to discriminate between these two odors. Within 2 weeks of training animals typically reached criterion levels ( $\geq 90\%$  correct). On days 40 and 43, BTX animals were tested (without food reinforcement) and none of them was able to discriminate between the two odors. Animals were observed entering the test chamber at the beginning of every S+ and S- trial and sniffing at the odor container, but failed to give a correct response on the S+ trials. Therefore, their score was near the 50% level based solely on the number of correct responses assigned to S- trials. On day 46, food reward was resumed. After the animals received a food pellet on the first S+ trial to reassociate the S+ odor with reward, they subsequently gave an excessive number of false positive responses (i.e. scratching at or biting the S- odor container) during the remainder of the day 46 test session. With additional testing, animals were able to learn to avoid responding on S- trials and reached a criterion level of performance by the fourth session (day 55). There was no difference in performance levels between those animals assigned cinnamon and those assigned strawberry as the S+ odor, or between male and female animals.

Like BTX animals, sham animals learned to discriminate between cinnamon and strawberry after 2 weeks of pre-

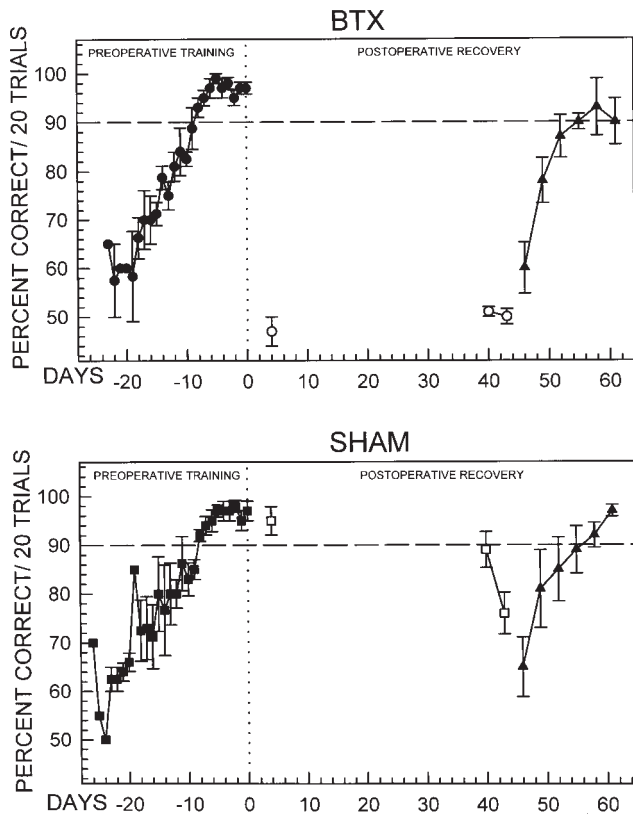


**Figure 1** Training and recovery curves for BTX and sham animals in group A. The BTX animals ( $n = 5$ ) were tested with cinnamon and strawberry odors (●). The sham animals ( $n = 4$ ) were also tested with cinnamon and strawberry odors (■). Filled symbols represent testing with food reinforcement. Open symbols represent testing without reinforcement. Criterion was set at 90% correct response. Surgery was performed on day 0. Data points represent the mean  $\pm$  SEM.

operative training. One of the sham animals died during recovery (on day 30) and is not included in Figure 1. On postoperative day 40 sham animals were tested to determine if they could perform the discrimination task. In contrast to the BTX animals, sham animals performed at criterion levels demonstrating that the behavioral response had not been extinguished after the 40 day period without testing. However, on day 43 additional testing without food reinforcement led to a decrease in performance level. When food reward was reintroduced again on day 46, sham animals immediately returned to criterion. The difference in mean performance level on day 46 for BTX ( $53 \pm 4.06$ ) and sham animals ( $90 \pm 3.54$ ) was statistically significant ( $P < 0.001$ ). The average number of sessions required for BTX animals to reach criterion ( $3.80 \pm 0.37$ ) was significantly greater ( $P < 0.01$ ) than that for sham animals ( $1.25 \pm 0.25$ ).

### Group B

Figure 2 gives the training and recovery curves for BTX and sham animals in group B. This group of animals was trained preoperatively with cinnamon and strawberry and then



**Figure 2** Training and recovery curves for the BTX and sham animals in group B. The BTX animals ( $n = 5$ ) were tested with cinnamon and strawberry odors (●). The sham animals ( $n = 5$ ) were tested with the same odors (■). On days 46–61, animals were tested with new odors (baby powder and coffee) (▲). Filled symbols represent testing with food reinforcement. Open symbols represent testing without food reinforcement. Criterion was set at 90% correct response. Surgery was performed on day 0. Data points represent the mean  $\pm$  SEM.

tested postoperatively with baby powder and coffee in order to determine how long it would take to learn to discriminate between two novel odors. On day 4, all five BTX animals in group B were tested to determine the effectiveness of the nerve transection. They failed to give the correct response on almost all S+ and S– trials, demonstrating that the bilateral nerve transection was complete. This control was included because behavioral studies have reported that only a few intact olfactory nerve connections are required for animals to make odor discriminations (Walker *et al.*, 1981; Lu and Slotnick, 1994). Data from the sham animals also served as a control to demonstrate that the surgical exposure of the bulbs alone did not affect performance levels on the discrimination task. On days 40 and 43, BTX animals could not perform the discrimination task. At the beginning of each S+ and S– trial, animals entered the test chamber and sniffed at the odor container. The BTX animals failed to respond correctly on almost all S+ trials, whereas sham animals retained their ability to discriminate between the two odors. On day 46, food reward was resumed and animals were then tested with the two new odors, baby

powder and coffee. Both BTX and sham animals were able to learn to discriminate between the two new odors and achieved a criterion level of 90% correct by day 55. There was no difference between the BTX and sham animals in the performance levels or the number of sessions needed to reach criterion.

### Comparison of groups A and B

Figure 3 compares the recovery curves for BTX animals in groups A and B. Both groups reached a criterion level of performance after the same number of sessions (4 sessions, 9 days). A statistical comparison (ANOVA) revealed no differences in performance levels between the two groups. These results suggest that, after sensory connections are re-established with the bulb in BTX animals, learning to discriminate between the two familiar preoperative test odors was no different than that for the two novel odors. Sham animals retained the ability to discriminate between the two familiar odors after recovery for 40 days. However, like the BTX animals, they also required four sessions to learn to discriminate between the two novel odors. Thus a ‘familiar’ odor is no longer perceived as familiar by a BTX animal after it receives new connections to the olfactory bulb.

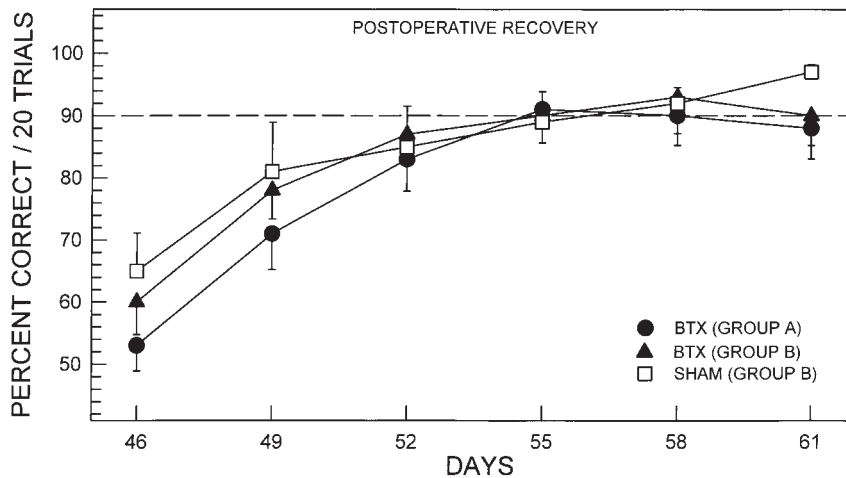
### Discussion

In a previous study, we found that animals reacquired the ability to discriminate between odors after recovery from nerve transection. However, since the animals were tested throughout the postoperative recovery period and received food reinforcement, it was not possible to determine if odor quality perception was altered or remained the same. In this study, animals did not receive testing or food reward during the first 40 days of recovery. The results demonstrate that BTX animals were not able to perform the odor discrimination task at 40 days of recovery, while sham animals retained a criterion performance level. With subsequent training, however, BTX animals reacquired the ability to discriminate between the two test odors. These findings suggest that odor quality perception changed after recovery, and that the ability to discriminate between previously learned odors requires the reassociation of the test odors with the correct behavioral response.

### Parameters effecting odor perception

We considered several behavioral and morphological parameters that might account for the observed findings. After 40 days without testing, it is conceivable that animals would be less motivated or that they would forget how to perform the behavioral task. To strengthen the association between odors and the correct response, animals were trained with partial reinforcement prior to surgery. When retested at 40 days after surgery without reinforcement, both BTX and sham animals were observed entering the test





**Figure 3** Comparison of postoperative recovery curves. ●, The performance of BTX animals in group A; ▲, the performance of the BTX animals in group B; □, the performance of the sham animals in group B. Data points represent the mean  $\pm$  SEM.

chamber and sniffing at the odors. This level of activity suggests that they retained motivation and did not forget the behavioral task.

We recognized that differences in odor intensity could provide cues and possibly assist animals in identifying the S+ or S- odor. The odor concentration levels released from the odor beads used in this study were determined by diffusion and could not be adjusted. However, when the intensity of the odor beads were matched to a set of standard odor concentrations by human subjects, they were found to be quite similar (within 1/3 of a log unit). This suggests that the discrimination of odors was most likely based on differences in odor quality and not intensity. If BTX animals had been using odor intensity as a cue, then they should have been able to discriminate between cinnamon and strawberry on days 40 and 43. This was not the case. Changes in odor sensitivity after recovery from nerve transection could also occur. A separate study to test for differences in odor sensitivity following recovery from nerve transection is currently underway.

Another parameter that could explain changes in odor perception would be a decrease in the amount of sensory information reaching BTX bulbs after recovery. A reduction in sensory information would make it more difficult to perform any odor-mediated behavioral task. The nerve transection procedure can lead to damage to the olfactory bulbs and the formation of scar tissue, both of which might impede fibers from reaching their appropriate targets in the olfactory bulb. Several studies have demonstrated that olfactory discrimination is retained even with incomplete reinnervation of the olfactory bulb. Harding *et al.* (1978) were the first to report that animals were able to perform a buried food task with only 10% carnosine synthetase activity, suggesting that only 10% of reinnervated neurons can support odor mediated behavior. Lu and Slotnick (1994) also demonstrated that only a very small area of bulb is

required for odor discrimination. Walker *et al.* (1981) studied recovery in the pigeon and showed that odor sensitivity was related to the amount of neural reinnervation. They found an increase in odor sensitivity in animals with longer recovery times. Although in a previous study we demonstrated recovery of olfactory discrimination function within 40 days, it is possible that longer recovery periods are needed for a complete restoration of normal odor perception.

It has been proposed that odor receptor subtypes project onto the olfactory bulb so as to create specific 'odor maps' and that these 'odor maps' are used to discriminate between odors (Kauer, 1991; Scott *et al.*, 1993; Ressler *et al.*, 1994; Shepherd, 1994; Mori and Yoshihara, 1995; Sullivan *et al.*, 1995; Buck, 1996; Sullivan and Dryer, 1996). In recovery from nerve transection it is likely that the regenerated nerves could project to new or different glomeruli, changing the projection patterns or odor maps, and thus lead to changes in odor perception. Only a few studies have examined whether nerve fiber projection patterns are replicated after sensory deafferentation in mammals. Using 2-deoxyglucose (2-DG), Guthrie *et al.* (1995) showed that new areas of uptake in the bulb were observed after specific loci in the medial aspect of the bulb known to elicit high 2-DG activity levels to propionic acid. Recently, Mombaerts *et al.* (1996) developed a genetically altered strain of mice in which olfactory neurons expressing the P2 receptor genes could be visualized using X-gal staining. Using these P2 mice and the nerve transection procedure used in this study, Costanzo (1997) has shown that P2 receptor axons established multiple convergence sites in the glomerular layer after reinnervation. This raises the possibility that new olfactory nerves may find their way back to the same general area of the bulb but that they are often likely to connect to different glomerular targets. Hence alterations in nerve fiber projections could explain changes in odor perception.

This study provides evidence that there is a change in odor quality perception following recovery from nerve transection and that animals must be retrained to discriminate between odors, even familiar ones, before they can reacquire the ability to perform an odor discrimination task. Although there are several behavioral and morphological parameters that could account for the observed findings, we hypothesize that there are changes in odor perception due to alterations in the nerve fiber projections to the olfactory bulb and that resulting changes in spatial activity patterns alter the way the brain interprets odors. Future studies are planned to further examine changes in projection patterns that occur following recovery from nerve transection. Such changes could have important functional implications for odor quality perception and how the brain interprets odors.

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