Binaral Interactions in the Rat Piriform Cortex

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Wilson, Donald A. Binaral interactions in the rat piriform cortex. J. Neurophysiol. 78: 160–169, 1997. Single-unit recordings were made from layer II/III anterior piriform cortex (aPCX) neurons in adult Wistar rats to examine odor response patterns to unilaterally and bilaterally delivered stimuli. Isopropyl acetate odor stimulation was presented either unilaterally through tubes inserted into the external nares, or bilaterally during unilateral olfactory bulb lidocaine infusions. Olfactory bulb multiunit or slow-wave activity was recorded simultaneously bilaterally to monitor selectivity of unilateral odor stimulation. The results demonstrate that 1) commissural input to aPCX neurons is sufficient to drive odor responses, and 2) aPCX neurons can be classified on the basis of spatial receptive field type. These receptive fields include cells that respond 1) selectively to ipsilateral stimulation, 2) selectively to contralateral stimulation, 3) to either ipsilateral or contralateral stimulation, and 4) selectively to bilateral stimulation. The potential functions of binaral convergence in the piriform cortex are discussed, and may include enhancement of perceived odor intensity and bilateral access to olfactory memory.

INTRODUCTION

Convergence of inputs from bilateral receptive fields is a common feature of vertebrate sensory systems. This bilateral convergence allows for relative comparisons of spatially disparate inputs that can result in higher-order sensory processes such as depth perception in vision and stimulus localization in audition.

In the mammalian olfactory system, the stimulus enters two relatively isolated air passages through the external nares. Within each air passage is an olfactory receptor sheet, which in turn projects ipsilaterally to the main olfactory bulb (MOB). Mitral/tufted cells in the olfactory bulb project to the olfactory cortex, which is composed of several subregions including the anterior olfactory nucleus, the cortical nucleus of the amygdala, and the piriform cortex (Price 1987).

It has been demonstrated anatomically that bilateral, or binaral, convergence occurs at most central olfactory structures (Haberly and Price 1978; Luskin and Price 1983). These interhemispheric connections are carried through the anterior limb of the anterior commissure. For example, in the olfactory bulb, input from the ipsilateral naris reaches the apical dendrite of mitral/tufted cells, whereas the most direct input from the contralateral naris terminates on inhibitory interneurons called granule cells (Price and Powell 1970). In the piriform cortex, however, binaral convergence occurs within different subfields of the apical dendrites of layer II and III pyramidal neurons (Friedman and Price 1984). Fibers from the ipsilateral olfactory bulb (ipsilateral naris) compose the lateral olfactory tract (LOT) and terminate in the piriform cortex superficial layer Ia, whereas commissural fibers from the contralateral hemisphere (contralateral naris) terminate in the deeper layer Ib, along with intracortical association fibers (Haberly 1985; Haberly and Price 1978; Luskin and Price 1983). In the anterior piriform cortex (aPCX), the source of these commissural fibers is primarily the contralateral pars lateralis of the anterior olfactory nucleus, which receives direct input from the olfactory bulb (Luskin and Price 1983). Fibers in layers Ia and Ib form excitatory synaptic connections with pyramidal neurons (Haberly 1985; Haberly and Bower 1984).

These anatomic data suggest that single piriform cortex pyramidal neurons may have binaral response properties—that is, they may perform relative comparisons between activity in the two olfactory receptor sheets—similar to the binocular cells of the primary visual cortex. To date, there have been relatively few single-unit examinations of mammalian piriform cortex odor response patterns and all have relied on bilaterally presented odors (Duchamp-Viret et al. 1996; Giachetti and MacLeod 1975; Haberly 1969; Collum et al. 1991; Nemitz and Goldberg 1983; Schoenbaum and Eichenbaum 1995; Tanabe et al. 1975). These studies have found that piriform cortex units respond to odors with relatively short latencies and with a variety of temporal patterns.

The present report examines aPCX single-unit responses to ipsilateral and contralateral olfactory bulb inputs. Two approaches were used. First, odors were delivered unilaterally through tubes inserted into the nares while olfactory bulb activity was simultaneously monitored bilaterally to confirm localization of the stimulus. The second method involved unilateral olfactory bulb lidocaine application to reversibly block ipsilateral or contralateral olfactory bulb activity during bilateral odor presentations. The results demonstrate that commissural input can drive aPCX unit responses to odors, and that, in addition to odor/molecular receptive fields, aPCX single units have spatially defined (ipsilateral/contralateral) receptive fields.

METHODS

Subjects

Eleven male Wistar rats (150–350 g) obtained from Charles River Labs were used as subjects. Animals were housed in polypropylene cages lined with wood chips. Food and water were available ad libitum. Lights were maintained on a 12:12 light:dark cycle with testing occurring during the light portion of the cycle.

Electrophysiology

Animals were anesthetized with urethan (1.5 g/kg) and placed in a stereotaxic apparatus. Both olfactory bulbs were exposed through
holes drilled in the dorsal surface of the skull and a third hole drilled over the aPCX, ~1 mm anterior to bregma. Recordings were made with tungsten microelectrodes (5–12 MΩ, A-M Systems).

Olfactory bulb activity was monitored with the use of simultaneous, bilateral multiunit or slow-wave recordings. Multiunit activity was recorded in the olfactory bulbs by lowering a tungsten microelectrode into the ventral mitral cell body layer, approximately in the middle of the anterior-posterior extent of the bulb. Multiunit activity was band-pass filtered (300 Hz–3 kHz) and passed through a window discriminator. Multiunit odor responses were monitored with peristimulus time histograms. In some animals, slow-wave activity was recorded in the ventral mitral cell body layer with tungsten microelectrodes, band-pass filtered (0.3 Hz–1 kHz), and sampled at 1 kHz. Slow-wave activity was quantified with fast Fourier transform (FFT) power spectrum analysis of 4-s time periods during odor stimulation with the Spike2 software package.

Single-unit activity was recorded in the aPCX. The tungsten recording electrode (5–12 MΩ) was lowered from the dorsal skull surface. Placement of the recording electrode in layer II/III of the piriform was confirmed histologically. After the recording session, the location of the electrode tip was determined to have responded to the stimulus if cumulative firing rate in any bin during the stimulus was above baseline variability. This measure, which has been used in the olfactory bulb (Wilson et al. 1985), was chosen because, as previously reported (McCol-lum et al. 1991) and as described below, aPCX single-unit odor responses were frequently very brief and habituated rapidly. Furthermore, predor spontaneous activity was often very slow or silent (especially in the lidocaine experiments), thus precluding statistical comparison of predor versus postodor firing rates. Because our objective was to describe the frequency of occurrence of ipsilaterally and contralaterally driven responses, the most im-

FIG. 1. Uninatural stimulation apparatus. Air was forced through odorant-saturated filter paper by computer-controlled activation of a syringe pump and simultaneous opening of a solenoid valve. Odor was delivered to a device inserted into the animal’s naris, and inhaled by normal respiration, as described in METHODS. Humidified clean air was directed over the open end of the delivery devices.
FIG. 2. Anterior piriform cortex (aPCX) single-unit response to isoamyl acetate delivered bilaterally and unilaterally through tubes inserted into the nares. A: bilateral odor presentation produced a robust aPCX excitatory response. B: unilateral odor presentation to ipsilateral naris selectively activated ipsilateral main olfactory bulb (MOB) as shown in histograms of multiunit activity recorded simultaneously in ipsilateral and contralateral MOB. aPCX single unit responded to this ipsilateral stimulation. C: unilateral odor presentation to contralateral naris selectively activated contralateral MOB. aPCX unit also responded to this contralaterally delivered odor stimulus. D: single-unit nature of this and all recordings was verified with autocorrelation analysis.
portant requirement was to apply a constant, sensitive criterion in all circumstances. This measure satisfies that requirement. Because of variability of responses, no attempt was made to quantify response magnitude for comparisons of relative effectiveness of ipsilateral versus contralateral inputs.

RESULTS

A total of 70 single units was recorded from aPCX layers II/III in 10 animals. Of these, 32 cells were tested for responses to unilaterally delivered odors, and 38 cells were tested for spontaneous activity and/or odor responses during unilateral olfactory bulb lidocaine application. Simultaneously, olfactory bulb activity was recorded bilaterally in all animals to monitor and confirm the unilateral nature of odor stimulation and lidocaine actions. Olfactory bulb multiunit responses to odor were characterized by robust excitation. Olfactory bulb slow-wave responses to odors were characterized by large-amplitude waves in phase with respiration, as previously reported (Adrian 1950). Both of these measures were reliable and sensitive indicators of odor stimulation. aPCX single units responded to odor stimulation most frequently with excitation, and very rarely with suppression in our sample. This excitation generally did not last through the entire 4-s odor stimulus (e.g., Figs. 3 and 7).

Unilateral odor presentation

Figure 2 is a representative example of an aPCX single-unit response to odor stimulation of either the ipsilateral or contralateral naris. The same aPCX unit is shown for each stimulus. Bilateral odor stimulation (Fig. 2A), produced a rapid increase in this cell’s activity. Similar excitatory responses were observed to unilateral odor stimulation delivered to either naris. For example, odor presented to the ipsilateral naris (Fig. 2B) selectively activated the ipsilateral olfactory bulb and excited the aPCX unit. Odor presented to the contralateral naris (Fig. 2C) selectively activated the contralateral olfactory bulb and also excited the aPCX unit. Figure 2 thus is an example of a binaral aPCX unit with bilateral receptive fields.

Unilateral odor presentation could, however, result in “cross talk” between nasal passages, where a stimulus presented to one naris excited both olfactory bulbs. In these cases, stimulus rates were adjusted within each animal to eliminate cross talk. Figure 2 shows simultaneous bilateral multiunit recordings of MOB activity and single-unit recording of aPCX activity in response to odor presented to the naris ipsilateral to the aPCX recording. When the odor was presented at a high rate/concentration (25 ml/min; Fig. 3, top), leakage occurred between nasal passages, possibly through the septal window, such that both olfactory bulbs responded. At lower stimulus rates/concentrations (10 ml/min; Fig. 3, bottom) no detectable leakage occurred between hemispheres. Note the aPCX unit responded to odor in both conditions.

FIG. 3. Unilateral odor presentation could result in “cross talk” between nasal passages. Stimulus rates were adjusted within animals to eliminate cross talk. This figure shows simultaneous bilateral multiunit recording of MOB activity and single-unit recording of aPCX activity in response to odor presented to the naris ipsilateral to the aPCX recording (stimulus presentation marked by horizontal bar). Top: when the odor was presented at a high rate (25 ml/min), leakage occurred between nasal passages, possibly through the septal window, such that both MOBs responded. Bottom: at lower stimulus rates (10 ml/min) no leakage occurred between hemispheres. Note aPCX unit responded to odor in both conditions.

aPCX units matching some or all of these response patterns were observed within each animal. For example, in three of the five animals tested, both cells responding selectively to the ipsilateral naris and cells responding selectively to the contralateral naris were observed. In one animal, cells representative of all four response groups were observed. In addition, MOB odor response magnitude did not dramatically vary over the course of single recording sessions, suggesting that nasal latency did not vary markedly within sessions. Finally, in at least one animal, a unit responding selectively to the ipsilateral naris was recorded simultaneously (with template matching) with a unit responding selectively to the contralateral naris. These observations suggest that unilateral response patterns are not due to lateralized differ-
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in the peak of the lidocaine effect; Fig. 5, A top). Importantly, lidocaine applied to the contralateral olfactory bulb (Fig. 5, A middle) also resulted in a significant decrease in spontaneous aPCX unit activity of nearly 50% (1-sample t-test vs. hypothesized mean change of 0%; ipsilateral lidocaine, t(20) = -92.9, P < 0.001; contralateral lidocaine, t(20) = -54.5, P < 0.001; Fig. 5B).

Despite the lidocaine-induced elimination of multiunit activity, and/or dramatic reductions in slow-wave activity in the ipsilateral olfactory bulb, some aPCX units maintained odor responsiveness to bilaterally presented odors, suggesting a contralateral source of activation (Figs. 6 and 7). These responses were generally expressed against a greatly reduced background firing rate. For example, Fig. 6 shows multiunit olfactory bulb activity recorded ipsilaterally to aPCX single-unit activity before (top) and after (bottom)

Unilateral olfactory bulb lidocaine application

A total of 38 aPCX single units in five animals was tested for the effects of unilateral olfactory lidocaine application on spontaneous activity (ipsilateral lidocaine, n = 21; contralateral lidocaine, n = 21; 3 cells were tested in both conditions). Lidocaine application on the dorsal surface of the olfactory bulb significantly reduced olfactory bulb activity as determined by complete cessation of multiunit activity (e.g., Fig. 6) or drastic reduction in odor-evoked slow-wave activity recorded in the ventral mitral cell layer (e.g., Fig. 7). Maintenance of some slow-wave activity during lidocaine application might be expected because of the contribution of remaining subthreshold synaptic activity to this measure. The bilateral bulb recordings demonstrated that lidocaine application produced selective unilateral effects on bulb activity (e.g., Figs. 7 and 8).

Lidocaine application on the olfactory bulb ipsilateral to the aPCX recording resulted in a 92% decrease in spontaneous aPCX unit activity (sampled during a 100-s period at

Figures 4 and 5 illustrate the effects of unilateral and bilateral olfactory bulb lidocaine application on aPCX unit activity.

Fig. 4. aPCX single-unit odor response patterns to bilateral and unilateral stimulation through naris tubes. Selective response patterns including cells that responded to ipsilateral stimulation but not contralateral stimulation, that responded to contralateral stimulation but not ipsilateral stimulation, that responded to either ipsilateral or contralateral stimulation, and that responded only to bilateral stimulation. Values are means ± SE.

Fig. 5. aPCX single-unit spontaneous activity following unilateral lidocaine surface application onto either ipsilateral or contralateral MOB. Ipsilateral application resulted in a nearly complete cessation of aPCX activity, whereas contralateral applications resulted in a 50% decrease in spontaneous activity.
olfactory bulb lidocaine application. Despite complete elimination of ipsilateral olfactory bulb multiunit activity by the lidocaine, the aPCX unit continued to respond to the bilaterally presented odor (Fig. 6, bottom right). Recall that olfactory bulb recordings were made from the ventral mitral cell body layer and lidocaine applications were made on the dorsal bulb surface. Thus these recordings are most probably indicative of suppression throughout the bulb.

Another example of maintained aPCX unit odor responses during ipsilateral olfactory bulb lidocaine is shown in Fig. 7. In this example, bilateral olfactory bulb slow-wave recordings showed typical, large-amplitude slow-wave oscillations during bilateral odor stimulation, and the simultaneous aPCX single-unit recording showed an excitatory response to the odor (Fig. 7, top). After lidocaine application to the ipsilateral olfactory bulb (Fig. 7, middle), the ipsilateral bulb slow-wave response was dramatically reduced, yet the aPCX unit response, although diminished, remained. FFT analysis of olfactory bulb activity before and after lidocaine application (Fig. 7, bottom) demonstrated that the lidocaine selectively depressed the olfactory bulb ipsilateral to the aPCX recording.

In other aPCX units, ipsilateral olfactory bulb lidocaine blocked odor responsiveness, suggesting that these units were either not responsive to contralateral activation or were so depressed that contralateral inputs were insufficient to produce detectable responses. For example, as shown in Fig. 8, top, bilateral odor exposure produced bilateral olfactory bulb slow-wave responses and an excitatory response in the simultaneously recorded aPCX unit. Lidocaine application on the olfactory bulb ipsilateral to the aPCX recording (Fig. 8, middle) eliminated both the ipsilateral bulb response and the aPCX unit response to odor. After recovery from the lidocaine suppression of bulb activity (Fig. 8, bottom), the aPCX unit odor response recovered. Furthermore, bilateral lidocaine application eliminated all odor responses, suggesting that the aPCX unit responses reflect odor responsiveness and are not trigeminally mediated.

As shown in Fig. 9, a mean of 52% of the aPCX cells in this sample (21 cells, 5 animals) responded to bilaterally presented odor. After ipsilateral olfactory bulb lidocaine application, 21% of the cells continued to respond to the odor, presumably via direct commissural activation.

As a final test of the contralateral nature of odor driven responses, in a single animal the olfactory bulb ipsilateral to the aPCX recording site was aspirated. Within 2 h postaspiration, multiunit aPCX responses to bilaterally presented odors were observed (not shown). Subsequent histological analyses showed complete tissue removal and damage extending caudal to the accessory olfactory bulb. Furthermore, the ipsilateral olfactory epithelium was damaged, as evidenced by minor bleeding from the ipsilateral naris. The odor responses, in the absence of an ipsilateral olfactory bulb, are further evidence of contralaterally driven odor input to the aPCX.

**DISCUSSION**

The present results demonstrate that aPCX layer II/III single units can respond to unilateral odor stimulation of the contralateral naris. Furthermore, these results suggest that, similar to monocular and binocular receptive fields of mammalian visual cortical neurons, aPCX neurons have monocular and binaral receptive fields.
FIG. 7. aPCX single-unit and simultaneous MOB slow-wave response to bilateral odor presentation before and after lidocaine application on ipsilateral MOB. Ipsilateral lidocaine dramatically reduced aPCX spontaneous activity, but did not block the aPCX odor response despite dramatically reducing ipsilateral MOB slow-wave activity. Fast Fourier transform (FFT) analysis showed that contralateral MOB slow-wave activity was not reduced by lidocaine infusion.
FIG. 8. aPCX single-unit and simultaneous MOB slow-wave response to bilateral odor presentation before and after lidocaine application on ipsilateral MOB. In this example, the aPCX single-unit spontaneous activity and odor response were blocked by ipsilateral MOB lidocaine infusion. Responses returned as lidocaine effect diminished.

aPCX responsiveness to contralateral naris stimulation could be mediated by 1) odor leakage through the septal window, 2) interbulbar interactions such that the contralateral bulb somehow activated the ipsilateral bulb to in turn excite the aPCX, or 3) direct commissural input to the aPCX from the contralateral hemisphere. First, although odor leakage can occur (Fig. 3), the bilateral olfactory bulb recordings showed selective unilateral bulb activation to unilaterally presented odors, and thus no detectable cross talk between passages. Furthermore, aPCX units continued to respond to odors despite verified lidocaine suppression of the ipsilateral bulb.

The second potential mechanism, interbulbar interaction, does occur but cannot account for the present results. Interolfactory bulb interaction is primarily inhibitory to mitral/ tufted cells in the rat (Price and Powell 1970; von Baumgarten et al. 1962). In the present study, evidence of this interbulbar inhibition was seen in the lidocaine experiments. In several cases, unilateral olfactory bulb blockade with lidocaine enhanced the magnitude of contralateral bulb odor responses, as seen quantitatively in the FFT analysis in Fig. 7 and qualitatively in the slow-wave amplitude of olfactory bulbs contralateral to lidocaine-suppressed bulbs (Figs. 7 and 8). Thus, if the interbulbar interaction influenced aPCX activity, it might be expected to reduce the probability of observing aPCX unit odor responses. Instead, we observed
hibitory interneurons, which could produce a relative weak-
formation coding in the olfactory system, as well as serve as
than LOT fiber terminals. In addition, LOT fibers, but not The ®nding of binaral receptive ®elds in aPCX should
pared with LOT fiber density in the rat aPCX ( Friedman for humans ) . The observation here that aPCX neurons have
tralaterally driven mononaral aPCX neurons was surprising of, or access to, olfactory memories acquired unilaterally in
response ( Fig. 4 ) supports this hypothesis. Second, the ante-
Potential anatomic substrates of spatial receptive ®elds
These results suggest, therefore, that aPCX responses to
contralateral naris stimulation are mediated by direct com-
Missual input to the aPCX, rather than indirectly through internasal cross talk or interbulbar connections. Further evidence for a direct, functionally significant commissural input to the aPCX comes from the olfactory bulb lidocaine effects on spontaneous aPCX activity. Blockade of contralateral ol-
factory bulb activity produced a 50% decrease in aPCX spontaneous activity (Fig. 5). Although the magnitude of this effect was significantly less than that observed for ipsilateral bulb suppression, it suggests a relatively strong, tonic excitatory input to the aPCX mediated by commissural fi-
bers. The primary route for these fibers involves the MOB projection to the anterior olfactory nucleus pars lateralis, which in turn projects via the anterior commissure to aPCX layer Ib (Luskin and Price 1983).

Potential anatomic substrates of spatial receptive fields
The relatively similar proportion of ipsilaterally and con-
tralaterally driven excitation of aPCX units. Furthermore, as shown above, aPCX units continued to respond to odors despite lidocaine suppression of the ipsilateral bulb.
These results suggest, therefore, that aPCX responses to
ccontralateral naris stimulation are mediated by direct com-
issural input to the aPCX, rather than indirectly through

Lidocaine application to ipsilateral OB

FIG. 9. Percent of aPCX single units responding to bilateral odor stimuli before and after lidocaine application to ipsilateral OB. Despite elimination of detectable ipsilateral olfactory bulb activity, 21% of cells maintained odor responses.

drites have very few spines within layer Ib and dense, large spines within layer Ia (Haberly 1983; Heimer and Kalil 1978). Thus semilunar cells might be expected to receive strong input from the ipsilateral LOT and limited input from associational/commissural fibers. In fact, bullectomy results in a selective, rapid die-off of semilunar cells in the ipsilateral aPCX (Heimer and Kalil 1978). As another example, although most layer II/III pyramidal neurons have apical dendrites extending through both layers Ib and Ia, a subclass of layer III pyramidal cells has apical dendrites that end in profuse branching at the layer Ib/Ia border (Haberly 1983). Thus these cells might be expected to receive primarily asso-
association/commissural input and very limited ipsilateral LOT input.

Another potential anatomic substrate of, or factor contrib-
ting to, spatial receptive fields is the variation in density and thickness of layer Ia over the rostral/caudal and dorsal/ventral extent of the piriform cortex. Layer Ia is thickest near the LOT, and progressively thins in more lateral and caudal areas of the cortex (Schwob and Price 1984). Thus the relative proportion of the four described spatial receptive fields as shown in Fig. 4 might be expected to vary with location within the piriform cortex.

Functional role of spatial receptive fields
The functional role of commissural connections and bi-
naral receptive fields in olfactory coding is unknown. Al-
though commissural connections are important in other sen-
sory systems for stimulus localization, in humans simultane-
ous binaral comparisons do not appear suf®cient to allow odorant source localization (in the absence of concomitant trigeminal activation) (Kobal et al. 1989). However, lesion studies of olfactory guided behavior have suggested that the anterior commissure may be involved in at least two specific aspects of olfaction. First, lesions of the anterior commissure increase odor detection thresholds in rats (Bennett 1968). These results were interpreted as suggesting that intact commissural connections increase perceived odor intensity, perhaps through an additive effect of bilateral stimulation on higher structures. The present finding that 10% of aPCX neurons required bilateral stimulation to produce a detectable response (Fig. 4) supports this hypothesis. Second, the ante-
rior commissure appears to be critically involved in transfer of, or access to, olfactory memories acquired unilaterally in rats (Kucharski and Hall 1987; cf. Olsson and Cain 1996 for humans). The observation here that aPCX neurons have binaral receptive fields may help account for this apparent information transfer. Unilateral olfactory training may modify both ipsilateral and contralateral aPCXs.

The finding of binaral receptive fields in aPCX should have important implications for our understanding of inform-
ation coding in the olfactory system, as well as serve as an important paradigm for future work. For example, current research in our laboratory using this paradigm is addressing the following questions. 1) What is the role of experience in shaping binaral receptive fields (Wilson and Sullivan 1996)? 2) Do binaral aPCX units have similar odor receptive fields on both sides (i.e., do they respond to the same set of odors ipsilaterally and contralaterally)? 3) Does habituation
of aPCX unit responses to ipsilateral odors produce habituation to contralateral odors and vice versa?

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