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Report

Binaral Rivalry between the Nostrils and in the Cortex

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Summary

When two different images are presented to the two eyes, we perceive alternations between seeing one image and seeing the other. Termed binocular rivalry, this visual phenomenon has been known for over a century [1] and has been systematically studied in recent years at both the behavioral and neural levels [2]. A similar phenomenon has been documented in audition [3]. Here we report the discovery of alternating olfactory percepts when two different odorants are presented to the two nostrils. This binaral rivalry involves both cortical and peripheral (olfactory receptor) adaptations. Our discovery opens up new avenues to explore the workings of the olfactory system and olfactory awareness.

Results and Discussion

Most of our sensory organs come in pairs: eyes, ears, and nostrils. Typically, the two eyes form slightly different retinal images of the same object (binocular disparity). There are small differences in time and intensity between a sound arriving at one ear versus the other, as well as between a smell arriving at one nostril versus the other [4]. The two nostrils are asymmetrical in air flow, which switches every couple of hours [5], and in their sensitivity to odorants with different sorption rates [6]. Most of the time, our brain integrates these minor differences and generates stable, accurate representations of the environmental input (e.g., stereopsis, sound localization, and odor localization [4, 7, 8]). Binocular rivalry occurs when two distinctly different images are presented separately to the two eyes [1, 2]. Successive periods of dominance of the left-eye stimulus and the right-eye stimulus are described as unpredictable in duration, as if being generated by a stochastic process driven by an unstable time constant [9, 10]. Similarly, when alternating tones an octave apart are played out of phase to each ear, most listeners experience a single tone oscillating from ear to ear whose pitch also oscillates in synchrony with the localization shift [3]—a demonstration of rivalry between the two ears. Here we set out to test whether rivalry also exists in olfaction.

Binaral Rivalry

In experiment 1, phenylethyl alcohol (PEA, 0.5% in propylene glycol, 8 ml) and *n*-butanol (0.5% in propylene glycol, 8 ml), each contained in a narrow-mouth bottle fitted with a Teflon nosepiece, were simultaneously presented to a subject's two nostrils, so that one nostril was exposed to PEA while the other was exposed to *n*-butanol. Subjects sampled from the two bottles intermittently (see Supplemental Experimental Procedures available online) instead of continuously; this was done because olfaction is especially prone to adaptation (occurring within 30–40 s of odor presence) [11, 12]. The two odorants have differences in structure and smell. Both carry a hydroxide radical, but PEA has a benzene ring, whereas *n*-butanol has a chain structure (Figure 1A). PEA smells floral and is usually described as a "rose" smell, whereas *n*-butanol has the smell of a marker pen. Across 20 samplings, all 12 subjects experienced switches between smelling predominantly the rose smell and smelling predominantly the marker smell (Figure 1A; Table S1; see Figure 1B for an illustration of the visual analog scale used for olfactory similarity ratings). Some subjects experienced more frequent and drastic switches than others. On average, to the same individual, the percepts of the same two odorants altered from a maximum of 79.2% like "rose" to a maximum of 72.8% like "marker," which is comparable to the range of similarity ratings when subjects were exposed to PEA and *n*-butanol alone (78.9% like "rose" to 85.7% like "marker"; see Supplemental experiment 1 and Figure S1). This separation was even greater across the entire sample of 12 subjects, ranging from 94% like "rose" to 92% like "marker." Whereas how biased a subject was toward perceiving the "rose" smell or the "marker" smell, as reflected by the mean of his/her similarity ratings across the 20 samplings, followed a normal distribution with the mean at 53.9% similar to "marker" (Figure 1C), their similarity ratings formed a bimodal distribution, with the local maxima at 66% similar to "marker" and 65% similar to "rose" (Figure 1D). This shows that the observed fluctuations (Figure 1A) cannot result from large random sampling errors; rather, they reflect genuine switches in olfactory percepts within the subjects.

No predictable pattern of the switch was evident across subjects or within the same subject, in line with observations in binocular rivalry [9, 10]. Nine out of the twelve subjects perceived mostly "marker" at the beginning, possibly because *n*-butanol is a "stronger" stimulus than PEA. Although rated as equally familiar to the subjects [$F(1,11) = 0.048$, $p = 0.83$], *n*-butanol was perceived to be more intense [$F(1,11) = 12.13$, $p = 0.005$] and less pleasant [$F(1,11) = 31.29$, $p = 0.00016$] than PEA, independent of nostril (left, right, or both) tested [$F(2,22) = 1.26$, $p = 0.30$ for familiarity; $F(1.26,13.81) = 3.32$, $p = 0.083$ for intensity; $F(2,22) = 0.73$, $p = 0.49$ for pleasantness]. Such dominance of the "stronger" competitor is also well documented in binocular rivalry [13–15].

The intensity of the perceived smell decreased over the 20 samplings [$F(19,209) = 1.97$, $p = 0.011$], but its pleasantness was not affected by the number of times the odorants were sampled [$F(19,209) = 1.19$, $p = 0.27$]. Across the 12 subjects, there was significant correlation between the pleasantness and the similarity ratings (how similar the smell was to "rose" or "marker") of the perceived smell [bivariate Pearson correlations between pleasantness and similarity ratings, each obtained via a 100-unit visual analog scale as described in Supplemental Experimental Procedures; average $r = 0.40$, $SEM = 0.12$, $t(11) = 3.30$, $p = 0.007$], mirroring the pleasantness difference between PEA and *n*-butanol.

The intermittent nature of samplings prevented us from adequately characterizing the temporal dynamics of olfactory rivalry, because the interval between two adjacent samplings

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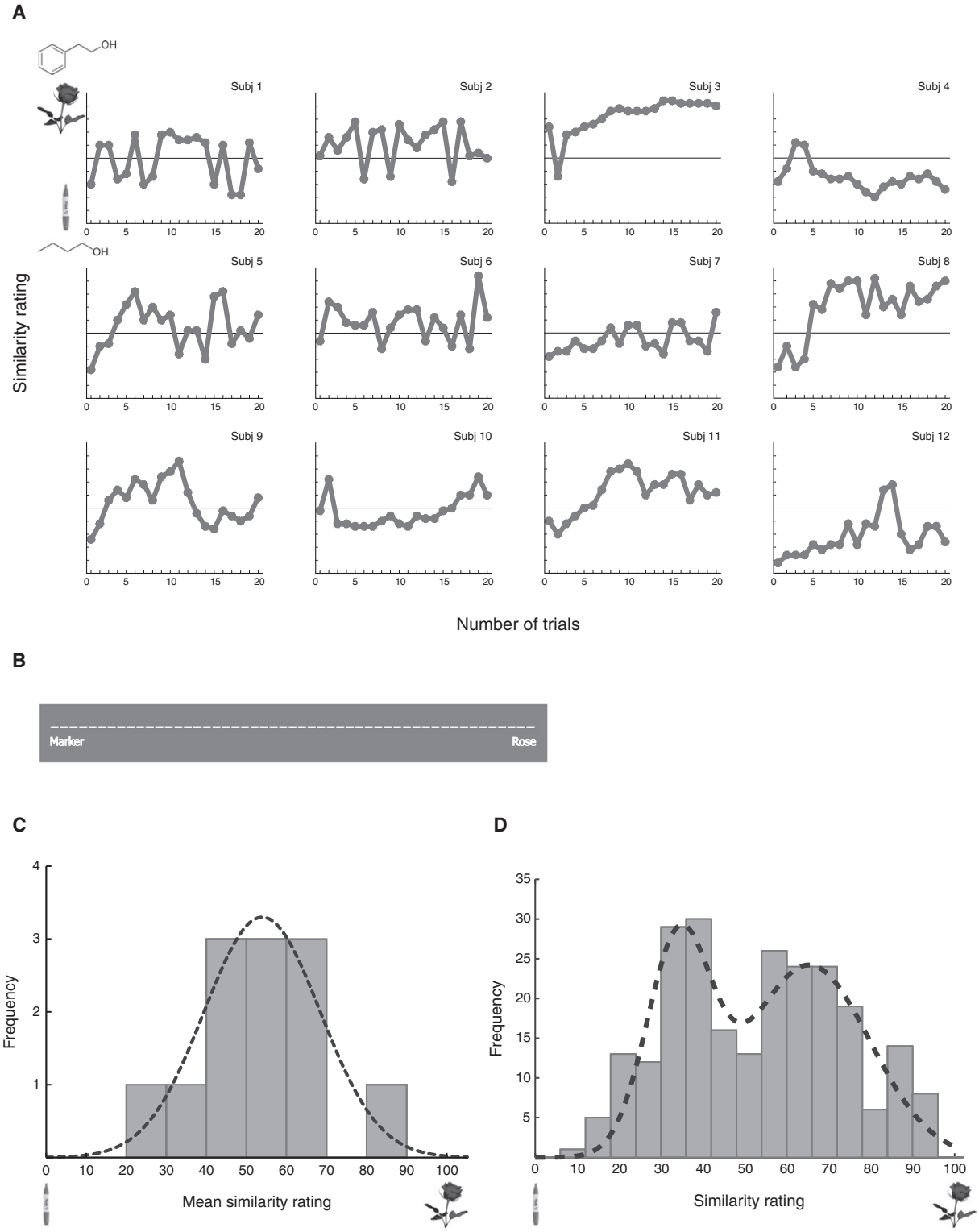

Figure 1. Binaral Rivalry

(A) All 12 subjects tested experienced switches between perceiving predominantly "rose" and predominantly "marker" (y axis indicates similarity rating to "rose" or "marker" on a 100-unit visual analog scale as shown in B) over 20 intermittent samplings (x axis) of phenylethyl alcohol (PEA) and *n*-butanol, one odor presented to each nostril. Dots above the middle line indicate an olfactory percept of predominantly "rose"; dots below the middle line indicate an olfactory percept of predominantly "marker."

(B) Illustration of the visual analog scale used for olfactory similarity ratings.

(C) Histogram of the mean similarity ratings across the 20 samplings from the 12 subjects. How biased a subject was toward perceiving "rose" or "marker," as reflected by his/her mean similarity rating, follows a normal distribution, with the mean at 53.9% similar to "marker."

was typically around 20–30 s, including the time during which the subjects recorded the similarity, intensity, and pleasantness ratings. Nevertheless, the dispersion in the bimodal distribution of the similarity ratings (Figure 1D) suggests that the transitions between the two olfactory percepts were likely marked by mixed percepts. This is analogous to observations in visual rivalry [16], although such an analogy should be viewed with some caution because of the differences in the nature of stimulus delivery: whereas intermittent stimulus presentation, chosen here to reduce olfactory adaptation, is also used in visual rivalry, the majority of studies on the latter have adopted continuous stimulus exposure.

Cortical and Peripheral Olfactory Adaptations

Similar to binocular rivalry [17], the binaral competition observed here is related to adaption. In experiment 2, when one nostril was adapted for 2 min to PEA and the same nostril was then presented again with PEA while the other nostril was presented with *n*-butanol, subjects (n = 4) reported smelling the "marker" smell. Conversely, when one nostril was preadapted to *n*-butanol and the same nostril was then presented again with *n*-butanol while the other nostril was presented with PEA, the same subjects reported smelling the "rose" smell. Nevertheless, experiment 2 did not tell us whether the contribution of adaptation is a result of central (adaptation occurring in the cortex) or peripheral (adaptation occurring at the peripheral receptor neurons) components.

As a preparatory step toward addressing this issue, we examined the effect of adaptation on the perceived intensity of the odorants in experiment 3. Subjects were adapted for 2 min to an odorant in one nostril and then rated the perceived intensity of the same adapting odorant or a different odorant in either the same or the other nostril. As would be expected from adaptation, when either PEA or *n*-butanol was presented to the nostril that had been preadapted to it, it was rated as much less intense [t(11) = −4.64, p = 0.001] than before the adaptation (Figure 2). One interesting question is whether such adaptation is purely peripheral, i.e., whether it results from only the fatigue of the peripheral olfactory receptor neurons over prolonged exposure to the odorant. We found this not to be the case. When the same odorant was presented to the other nostril, which had not been adapted to it, there was also a significant drop in its intensity rating [t(11) = −3.57, p = 0.004], although the effect was less drastic as compared to when it was presented to the preadapted nostril [t(11) = −2.66, p = 0.022]. Hence, both cortical and peripheral mechanisms are involved, as demonstrated previously by Cain [18]. This adaption is odorant specific. The intensity rating of the odorant (*n*-butanol or PEA) that had not been adapted to was not affected [t(11) = −0.74 and −1.63, p = 0.47 and 0.13, respectively, for the two nostrils] (Figure 2).

Subsequently, in experiments 4 and 5, we set forth to assess whether both cortical adaptation and adaptation of the olfactory receptors contributed to the alternations in olfactory percepts observed in experiment 1. We hypothesized that if cortical adaptation is an important component of binaral rivalry, alternating olfactory percepts would be experienced independent of adaptation in the olfactory epithelium (mononaral

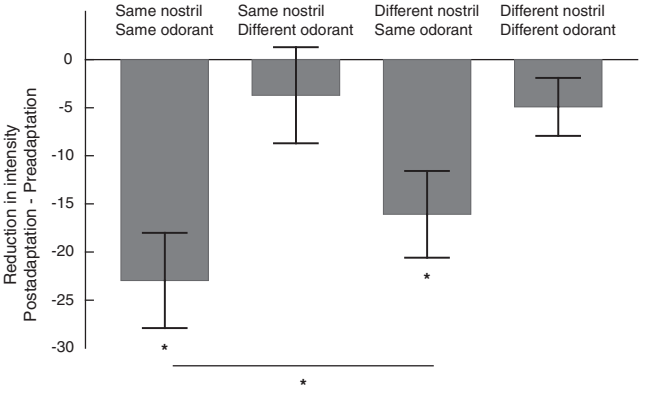

Figure 2. Olfactory Adaptation Consists of Both Cortical and Peripheral Components

Because there was no significant effect of adapting side [F(1,11) = 0.40, p = 0.54], adapting odorant [F(1,11) = 0.55, p = 0.47], testing side [F(1,11) = 0.004, p = 0.95], or testing odorant [F(1,11) = 0.27, p = 0.61], the 16 combinations of adapting side, adapting odorant, testing side, and testing odorant (see Supplemental Experimental Procedures for details) are collapsed into four categories: same nostril/same odorant, same nostril/different odorant, different nostril/same odorant, and different nostril/different odorant. Same or different is with respect to the adapting nostril and adapting odorant—e.g., same nostril/same odorant means that the same nostril that had been preadapted to an odorant (PEA/*n*-butanol) was presented with the same odorant (PEA/*n*-butanol). The y axis depicts the difference in the intensity ratings obtained after versus before the adaptation on a 100-unit visual analog scale. Error bars represent standard errors of the mean. Asterisks indicate significant difference from zero or between conditions, p < 0.05.

rivalry) (experiment 4), as in monocular rivalry [19]. Indeed, 10 of the 12 subjects (83%) experienced switches between smelling predominantly "rose" and smelling predominantly "marker" when they sampled intermittently from two bottles, each containing a 1:1 mixture (8 ml) of PEA (0.5% in propylene glycol, 4 ml) and *n*-butanol (0.5% in propylene glycol, 4 ml) (Figure 3; Table S1). On average, for the same individual, the percepts altered from a maximum of 70% like "rose" to a maximum of 78.7% like "marker." Across the 12 subjects, the similarity ratings ranged from 90% like "rose" to 92% like "marker." Similar to the aforementioned binaral rivalry situation, subjects experienced a decrease in the intensity of the perceived smell [F(19,209) = 2.19, p = 0.004] over time. Their pleasantness ratings again correlated significantly with the similarity ratings across subjects [average r = 0.44, SEM = 0.11, t(11) = 3.94, p = 0.002] and were not affected by the number of times the odorants were sampled [F(19,209) = 1.11, p = 0.35].

Concerning the peripheral adaptation at the olfactory epithelium, we hypothesized that if it also plays a significant role in binaral rivalry, a swap of the sides of the two olfactory stimuli would render the previously suppressed smell perceivable again (in parallel to observations in binocular rivalry [20, 21]). To test this idea, in experiment 5, we instructed subjects to simultaneously and continuously sniff from two bottles, one containing PEA (0.5% in propylene glycol, 8 ml) and the other containing *n*-butanol (0.5% in propylene glycol, 8 ml), until they

(D) Histogram of the similarity ratings (240 ratings from 12 subjects, each with 20 samplings). The distribution can be modeled with the sum of two normal distributions (dotted curve): $y = h_1 e^{-(x-\mu_1)^2/2\sigma_1^2} + h_2 e^{-(x-\mu_2)^2/2\sigma_2^2}$, where h_1, μ_1, and σ_1 are the height, mean, and standard deviation, respectively, of the first normal distribution and h_2, μ_2, and σ_2 are the height, mean, and standard deviation, respectively, of the second normal distribution. Here, μ_1 corresponds to 66% similar to "marker" and μ_2 corresponds to 65% similar to "rose."

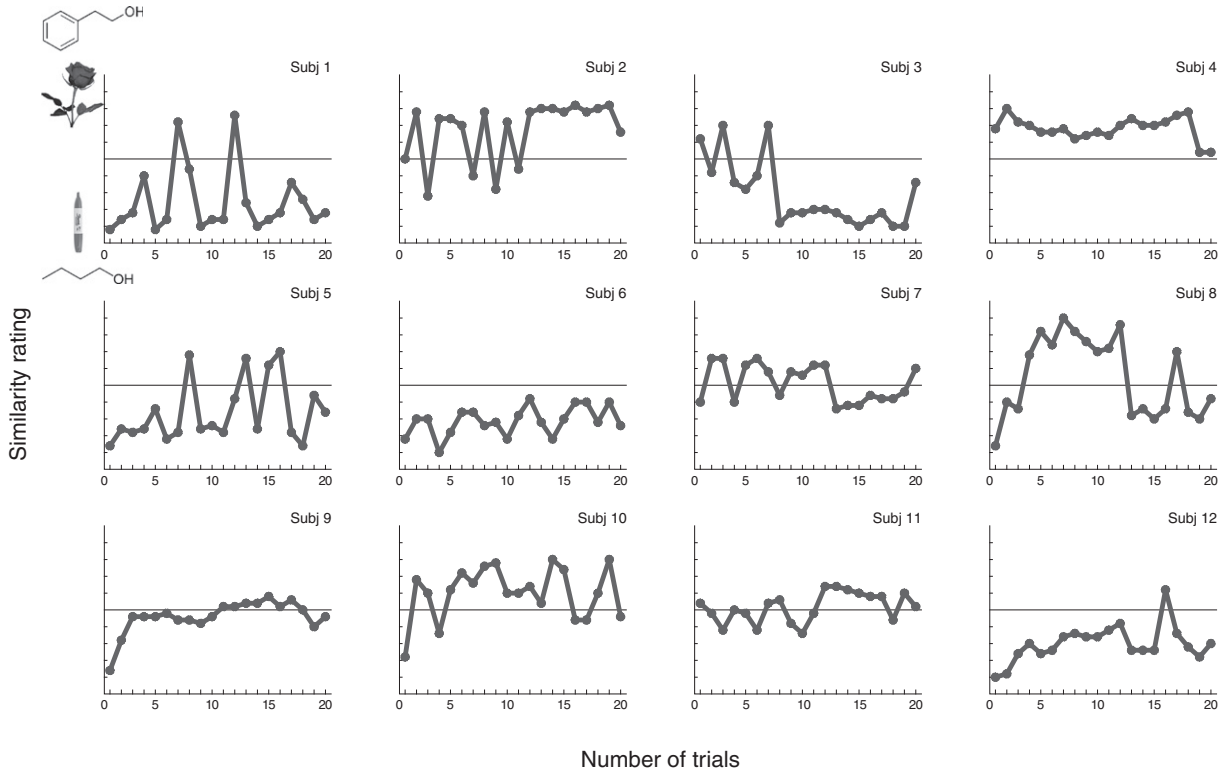

Figure 3. Mononaral Rivalry

Ten of the twelve subjects tested experienced switches between perceiving predominantly "rose" and predominantly "marker" (y axis indicates similarity rating to "rose" or "marker" on a 100-unit visual analog scale) over 20 intermittent samplings (x axis) of a 1:1 mixture of PEA and *n*-butanol. Dots above the middle line indicate an olfactory percept of predominantly "rose"; dots below the middle line indicate an olfactory percept of predominantly "marker."

could no longer detect whichever smell they had detected first (e.g., if a subject first smelled "marker," he was instructed to keep sniffing until he no longer smelled the "marker" smell). Then, unbeknownst to the subjects, the two bottles were either quickly swapped or not swapped and re-presented to the two nostrils. Consistent with our hypothesis, 10 of the 12 subjects tested (83%) reported smelling the same smell again (e.g., marker) when the bottles were swapped, but not when the bottles were not swapped.

It is worth noting that although the mononaral rivalry (experiment 4) resembles binaral rivalry (experiment 1) in perceptual experience (Figure 1A; Figure 3), the two phenomena recruit different mechanisms. Whereas mononaral rivalry is independent of adaptation in the olfactory epithelia located in the two nostrils (experiment 4), there is a significant peripheral component in binaral rivalry, as shown in experiment 5. These results are consistent with what has been observed in visual rivalry [22, 23].

In the visual system, inhibitory interactions could take place among both monocular neurons (binocular/interocular competition) and binocular pattern-selective neurons (monocular/pattern competition), and the persisting neural signals could be passed on to higher stages of processing, where visual competition can continue [2]. Anatomical parallels exist between the olfactory system and the visual system. Olfactory system is largely ipsilateral [24]. Odorants entering one nostril are detected by the olfactory epithelium, from which the olfactory information is conducted to the ipsilateral olfactory bulb. Axons of the mitral and tufted cells of each bulb coalesce and form the olfactory tract, one on each side, which conveys olfactory information ipsilaterally to the primary olfactory cortex (anterior olfactory nucleus, olfactory tubercle, anterior and posterior piriform cortex, amygdala, and rostral entorhinal cortex). There is inhibitory interaction between the two olfactory bulbs [25]. In addition, there is inhibitory interaction among olfactory bulb glomeruli [26], which receive olfactory inputs from different types of odorant receptors [27]. The two olfactory tracts are nevertheless connected to each other via the anterior olfactory nuclei and the anterior commissure [28, 29]. Such anatomical substrates possibly contribute to the binaral and mononaral rivalries observed here, yet the neural mechanisms of olfactory rivalry remain to be elucidated.

Conclusions

We have shown alternating odor percepts when two different odorants are presented to the two nostrils, thereby demonstrating, for the first time, perceptual rivalry in the olfactory system. Binaral rivalry involves adaptations at the peripheral sensory neurons and in the cortex. Our work sets the stage for future studies of this phenomenon, which will further characterize its perceptual properties, delineate the neural correlates of cortical and peripheral adaptation, and elucidate the mechanisms of olfactory awareness [30].

Supplemental Data

Supplemental Data include Supplemental Experimental Procedures, one table, and two figures and can be found with this article online at http://www.cell.com/current-biology/supplemental/S0960-9822(09)01478-X.

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References

1. Alais, D., and Blake, R. (2004). Binocular Rivalry (Cambridge, MA: MIT Press).
2. Tong, F., Meng, M., and Blake, R. (2006). Neural bases of binocular rivalry. Trends Cogn. Sci. *10*, 502–511.
3. Deutsch, D. (1974). An auditory illusion. Nature *251*, 307–309.
4. von Békésy, G. (1964). Olfactory analogue to directional hearing. J. Appl. Physiol. *19*, 369–373.
5. Bojsen-Moller, F., and Fahrenkrug, J. (1971). Nasal swell-bodies and cyclic changes in the air passage of the rat and rabbit nose. J. Anat. *110*, 25–37.
6. Sobel, N., Khan, R.M., Saltman, A., Sullivan, E.V., and Gabrieli, J.D. (1999). The world smells different to each nostril. Nature *402*, 35.
7. Rajan, R., Clement, J.P., and Bhalla, U.S. (2006). Rats smell in stereo. Science *311*, 666–670.
8. Porter, J., Anand, T., Johnson, B., Khan, R.M., and Sobel, N. (2005). Brain mechanisms for extracting spatial information from smell. Neuron *47*, 581–592.
9. Fox, R., and Herrmann, J. (1967). Stochastic properties of binocular rivalry alternations. Percept. Psychophys. *2*, 432–436.
10. Lehky, S.R. (1995). Binocular rivalry is not chaotic. Proc. Biol. Sci. *259*, 71–76.
11. Poellinger, A., Thomas, R., Lio, P., Lee, A., Makris, N., Rosen, B.R., and Kwong, K.K. (2001). Activation and habituation in olfaction–an fMRI study. Neuroimage *13*, 547–560.
12. Sobel, N., Prabhakaran, V., Zhao, Z., Desmond, J.E., Glover, G.H., Sullivan, E.V., and Gabrieli, J.D. (2000). Time course of odorant-induced activation in the human primary olfactory cortex. J. Neurophysiol. *83*, 537–551.
13. Levelt, W.J.M. (1965). On Binocular Rivalry (Soesterberg, The Netherlands: Institute for Perception RVO-TNO).
14. Kaplan, I.T., and Metlay, W. (1964). Light intensity and binocular rivalry. J. Exp. Psychol. *67*, 22–26.
15. Fahle, M. (1982). Binocular rivalry: Suppression depends on orientation and spatial frequency. Vision Res. *22*, 787–800.
16. Blake, R., O'Shea, R.P., and Mueller, T.J. (1992). Spatial zones of binocular rivalry in central and peripheral vision. Vis. Neurosci. *8*, 469–478.
17. Blake, R. (1989). A neural theory of binocular rivalry. Psychol. Rev. *96*, 145–167.
18. Cain, W.S. (1977). Bilateral interaction in olfaction. Nature *268*, 50–52.
19. Campbell, F.W., Gilinsky, A.S., Howell, E.R., Riggs, L.A., and Atkinson, J. (1973). The dependence of monocular rivalry on orientation. Perception *2*, 123–125.
20. Blake, R., Westendorf, D.H., and Overton, R. (1980). What is suppressed during binocular rivalry? Perception *9*, 223–231.
21. Arnold, D.H., Law, P., and Wallis, T.S. (2008). Binocular switch suppression: A new method for persistently rendering the visible 'invisible'. Vision Res. *48*, 994–1001.
22. Logothetis, N.K., Leopold, D.A., and Sheinberg, D.L. (1996). What is rivalling during binocular rivalry? Nature *380*, 621–624.
23. Haynes, J.D., Deichmann, R., and Rees, G. (2005). Eye-specific effects of binocular rivalry in the human lateral geniculate nucleus. Nature *438*, 496–499.
24. Gottfried, J.A. (2006). Smell: Central nervous processing. Adv. Otorhinolaryngol. *63*, 44–69.
25. Bennett, M.H. (1968). The role of the anterior limb of the anterior commissure in olfaction. Physiol. Behav. *3*, 507–515.
26. Aungst, J.L., Heyward, P.M., Puche, A.C., Karnup, S.V., Hayar, A., Szabo, G., and Shipley, M.T. (2003). Centre-surround inhibition among olfactory bulb glomeruli. Nature *426*, 623–629.
27. Mori, K., Nagao, H., and Yoshihara, Y. (1999). The olfactory bulb: Coding and processing of odor molecule information. Science *286*, 711–715.
28. Powell, T.P., Cowan, W.M., and Raisman, G. (1965). The central olfactory connexions. J. Anat. *99*, 791–813.
29. Kikuta, S., Kashiwadani, H., and Mori, K. (2008). Compensatory rapid switching of binasal inputs in the olfactory cortex. J. Neurosci. *28*, 11989–11997.
30. Jiang, Y., and He, S. (2006). Cortical responses to invisible faces: Dissociating subsystems for facial-information processing. Curr. Biol. *16*, 2023–2029.

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Supplemental Data

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Supplemental Experimental Procedures

Participants

Subjects were healthy non-smokers (aged 18-35 yrs) who reported having a normal sense of smell and no respiratory allergy or upper respiratory infection at the time of testing. They were blind to the purpose of the study and to the side of the nostril a smell was presented. Subjects were blindfolded in experiments 3 and 5. All gave informed consent for participation.

Olfactory Stimuli

The olfactory stimuli consisted of phenyl ethyl alcohol (PEA, 0.5% in propylene glycol) and n-butanol (0.5% in propylene glycol) in experiments 1 and 5, PEA (0.5% in propylene glycol), n-butanol (0.5% in propylene glycol), and purified water in experiments 2 and 3, and 1:1 mixture of PEA (0.5% in propylene glycol) and n-butanol (0.5% in propylene glycol) in experiment 4. They were presented in narrow-mouth glass bottles, each containing 8 ml clear liquid and fitted with a Teflon nosepiece. PEA (0.5% in propylene glycol) and n-butanol (0.5% in propylene glycol) were supra-threshold stimuli for all subjects.

Procedure

Experiments 1 and 4 were carried out in the same session separated by 10 min. Twelve subjects (5 males, 7 females; mean age = 21.8, SEM = 1.4) sampled either the PEA bottle (0.5% in propylene glycol) or the n-butanol bottle (0.5% in propylene glycol) with either the left nostril, or the right nostril, or both nostrils, and then rated the familiarity, intensity, and pleasantness of the smell on a 100-unit visual analog scale. The order of the samplings was randomized, with a 2-minute break in between the samplings. After all ratings were made, subjects were told the labels of the two odorants, i.e. “rose” and “marker.” Half of the subjects then performed the binaral rivalry task (experiment 1, where PEA and n-butanol were presented simultaneously, one to each nostril), followed by the mononaral rivalry task (experiment 4, where two bottles each containing 1:1 mixture of PEA and n-butanol were simultaneously presented to the two nostrils). The other half performed the binaral and mononaral rivalry tasks in the reverse order. The binaral rivalry task consisted a total of 20 trials, each started with two low beeps followed by a high beep (SOA = 1s). At the high beep, the subjects took a single sniff of the PEA bottle and the n-butanol bottle simultaneously, and indicated if he/she smelled anything. If a smell was detected, they went on and rated how similar the smell was to “rose” or “marker” on a 100-unit visual analog scale with “rose” at one end, “marker” at the other end, and both smells or neither smell in the center (Figure 1B); the use of such bipolar scales is standard in assessing perceptions of

binary odor mixtures (e.g. [1]) and provides essentially the same information as two separate similarity scales (see Supplemental experiment 2 and Figure S2). They then rated the intensity and pleasantness, respectively, of the perceived smell, on a 100-unit visual analog scale. The next trial began immediately after they made the similarity, intensity, and pleasantness ratings. If no smell was detected, one was prompted to take another sniff. The sides of the bottles (left nostril vs. right nostril) were counterbalanced across subjects. In the mononaral rivalry task, two bottles both containing a 1:1 mixture of PEA (0.5% in propylene glycol, 4 ml) and n-butanol (0.5% in propylene glycol, 4 ml) were used. The task was otherwise identical to the binaral rivalry task.

Four out of the twelve subjects (2 males, 2 females) were recruited back for experiment 2, conducted at the same time of the day as the above session (experiments 1 and 4). They firstly inhaled through a pair of bottles, one containing either PEA or n-butanol, the other containing purified water (8 ml), for 2 min. Subsequently, and unknown to the subjects, the nostril that was adapted to PEA or n-butanol was presented with the adapting odorant (PEA or n-butanol) again, while the other nostril was presented with the non-adapting odorant (n-butanol or PEA). The subjects reported whether they perceived predominantly "marker" or "rose." The adapting odorant (PEA vs. n-butanol) as well as the adapting nostril (left vs. right) were counterbalanced across the four subjects.

In experiment 3, twelve subjects (5 males, 7 females; mean age = 23.4, SEM = 1.3) were tested for the effect of adaptation on the perceived intensity of the odorants. They firstly sampled either the PEA bottle or the n-butanol bottle with either the left nostril or the right nostril and rated the intensity of the smell on a 100-unit visual analog scale. The order of the samplings was randomized, with a 2-minute break in between. They subsequently inhaled through a pair of bottles, one containing either PEA or n-butanol, the other containing purified water, for 2 min. Immediately after that, the subjects sampled either the PEA bottle or the n-butanol bottle with either the left nostril or the right nostril, and rated its intensity again. For each subject, the adaptation-testing procedure was repeated 16 times [adapting nostril (left vs. right) × adapting odorant (PEA vs. n-butanol) × testing nostril (left vs. right) × testing odorant (PEA vs. n-butanol)] in a randomized manner, each time with a different combination of adapting nostril, adapting odorant, testing nostril, and testing odorant. There was a 3 min break in between the repetitions.

In experiment 5, twelve subjects (3 males, 9 females; mean age = 24.8, SEM = 1.4) were recruited to assess the role of olfactory receptor adaptation in binaral rivalry. They firstly were presented with PEA and n-butanol, respectively, and were told the labels ("rose" vs. "marker") of the odorants. After that, the subjects simultaneously smelled from the PEA bottle and the n-butanol bottle. They were instructed to keep sniffing until they did not perceive the smell they initially smelled from the pair of bottles. Immediately after that, unknown to the subjects, the two bottles were quickly swapped for half of the subjects, each of whom sampled from the bottles and reported what he/she perceived. Then, still unknown to the subjects, the two bottles were quickly swapped back and re-presented to the two nostrils. The subjects reported again what he/she perceived, and were asked to compare its strength to that of the previously perceived smell. For the other half of the subjects, the two bottles were not swapped the first time but were the second time.

In line with [2], the subjects were instructed to inhale through the nose but exhale via the mouth for all the experiments to prevent retronasal backflow, as retronasal olfaction occurs during breathing out through the nose [3]. Each went through a practice session to ensure that there was no airflow from their nose (i.e. the surface of the liquid was still) during exhalation.

Supplemental References

1. Sobel, N., Khan, R.M., Saltman, A., Sullivan, E.V., and Gabrieli, J.D. (1999). The world smells different to each nostril. Nature *402*, 35.
2. Cain, W.S. (1977). Bilateral interaction in olfaction. Nature *268*, 50-52.
3. Shepherd, G.M. (2006). Smell images and the flavour system in the human brain. Nature *444*, 316-321.

Table S1. The Magnitudes of Perceptual Changes for Each Subject in the Binaral and Mononaral Settings

Subject	Binaral Setting		Mononaral Setting	
	max similarity to "rose"(min similarity to "marker")	max similarity to "marker"(min similarity to "rose")	max similarity to "rose"(min similarity to "marker")	max similarity to "marker"(min similarity to "rose")
1	70% (30%)	78% (22%)	76% (24%)	92% (8%)
2	78% (22%)	68% (32%)	82% (18%)	72% (28%)
3	94% (6%)	64% (36%)	70% (30%)	90% (10%)
4	62% (38%)	80% (20%)	80% (20%)	46% (54%)
5	82% (18%)	78% (22%)	70% (30%)	86% (14%)
6	94% (6%)	62% (38%)	42% (58%)	90% (10%)
7	66% (34%)	68% (32%)	66% (34%)	64% (36%)
8	92% (8%)	76% (24%)	90% (10%)	86% (14%)
9	86% (14%)	74% (26%)	58% (42%)	86% (14%)
10	74% (26%)	64% (36%)	80% (20%)	78% (22%)
11	84% (16%)	70% (30%)	64% (36%)	64% (36%)
12	68% (32%)	92% (8%)	62% (38%)	90% (10%)
mean	*79.17% (20.83%)*	*72.83% (27.17%)*	*70.00% (30.00%)*	*78.67% (21.33%)*

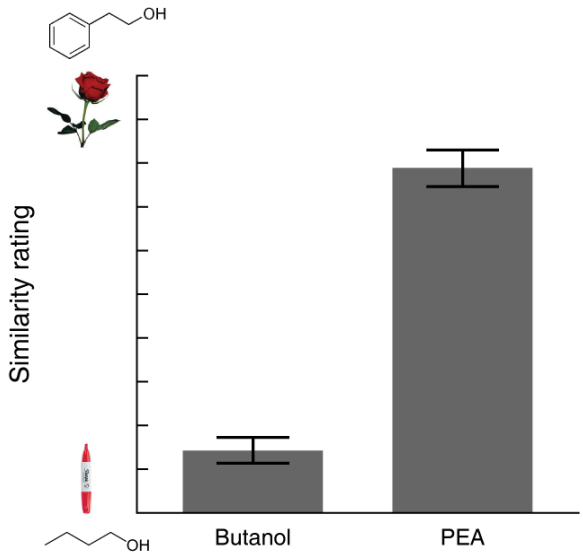

Figure S1.
Similarity ratings to "rose" and "marker" when the subjects in Supplemental experiment 1 were exposed to PEA and n-butanol, respectively. Error bars represent standard errors of the mean.

Supplemental Experiment 1
Seven healthy non-smokers (aged 19-23 yrs, 5 females) who reported having a normal sense of smell and no respiratory allergy or upper respiratory infection at the time of testing gave informed consent for participation. They were blindfolded during smell presentations. The apparatus and procedure were identical to that of experiment 1 (binaral rivalry) and experiment 4 (mononaral rivalry) except that only similarity ratings were collected and the subjects were given PEA (rose smell, presented with a pair of bottles, one containing 8 ml 0.5% PEA in propylene glycol, the other containing 8 ml purified water) in half of the trials and n-butanol (marker smell, presented with a pair of bottles, one containing 8 ml 0.5% n-butanol in propylene glycol, the other containing 8 ml purified water) in the other half trials in a randomized manner. Before the testing, they smelled PEA and butanol respectively, and were told their labels, i.e. "rose" and "marker." During the testing, these subjects on average rated PEA to be at most 78.9% like "rose," and butanol to be at most 85.7% like "marker," instead of 100% like "rose" or 100% like "marker" as one would predict with visual stimuli (Figure S1). Such range is comparable to those observed in experiment 1 (binaral rivalry, 79.2% like "rose" to 72.8% like "marker") and experiment 4 (mononaral rivalry, 70.0% like "rose" to 78.7% like "marker").

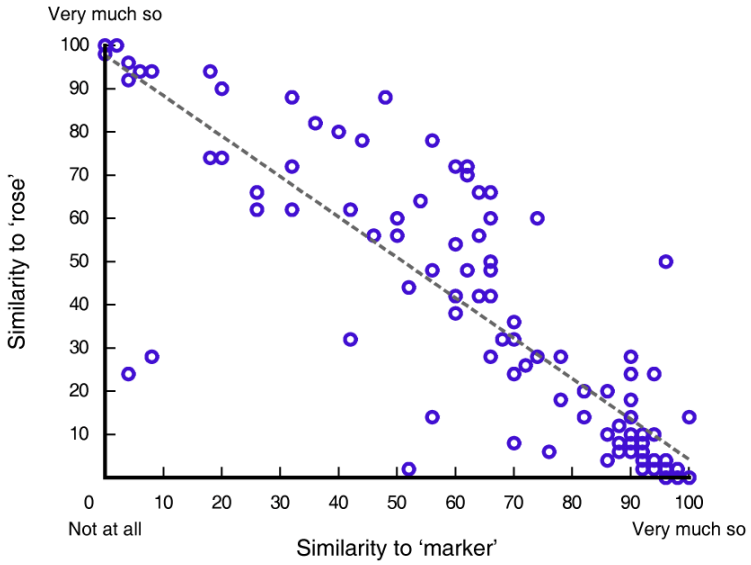

Figure S2.
Similarity ratings to "rose" and "marker" on two separate 100-unit visual analog scales when the subjects in Supplemental experiment 2 simultaneously sampled PEA and n-butanol, one to each nostril.

Supplemental Experiment 2

Another three healthy non-smokers (2 females and 1 male, all aged 19 and reported having a normal sense of smell and no respiratory allergy or upper respiratory infection at the time of testing) gave informed consent for participation in Supplemental experiment 2, which aims to verify whether the bipolar similarity scale with "rose" on one end and "marker" on the other end (Figure 1B, used in experiments 1 and 4, as well as Supplemental experiment 1) provides the same information as two separate scales assessing the similarities to "rose" and "marker" respectively. The three subjects simultaneously sampled n-butanol (0.5% in propylene glycol, 8 ml) and PEA (0.5% in propylene glycol, 8 ml), one to each nostril, over 40 trials. After each sampling, they rated how similar the perceived smell was to "rose" or "marker," respectively, on a 100-unit visual analog scale. The apparatus and procedure were otherwise identical to that of experiment 1 (binaral rivalry). Figure S2 shows a scatter plot of the 120 resulting pairs of similarity ratings. The x-axis and y-axis represent the similarity to "marker" and "rose," respectively. The two ratings show significantly negative correlation with each other ($r = -0.35$, -0.73, and -0.96, for the three subjects respectively, $ps < 0.028$; across the 120 data points, $r = -0.875$, $p < 0.0001$), thus justifying the use of bipolar similarity scales. Critically, this further supports rivalry behavior, instead of a simple fluctuation of the strength of the olfactory percepts.