

Olfaction Modulates Visual Perception in Binocular Rivalry

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Summary

Vision is widely accepted as the dominant sense in larger primates including humans, whereas olfaction is often considered a vestigial sense yielding only obscure object representations [1]. It is well documented that vision drives olfactory perception [2, 3], but there has been little indication that olfaction could modulate visual perception. Here we introduce smells to a well-established visual phenomenon termed binocular rivalry, perceptual alternations that occur when distinctively different images are separately presented to the two eyes [4]. We show that an odorant congruent to one of the competing images prolongs the time that image is visible and shortens its suppression time in a manner that is automatic, essentially independent of cognitive control, and partly subconscious. Our findings provide the first direct evidence that an olfactory cue biases the dynamic process of binocular rivalry, thereby demonstrating olfactory modulation of visual perception—an effect that has been hitherto unsuspected.

Results and Discussion

Whereas our perceptual world is interwoven with sensory inputs from various modalities, vision is commonly believed to dominate human perception—as the saying goes, “seeing is believing.” In comparison, human olfaction seems to be vague, fuzzy, and unreliable [2, 5]. It is thus not surprising that visual inputs strongly modulate olfactory perception. When visual and olfactory cues conflict with each other, olfaction is overridden by vision [2]. On the other hand, when visual cues and olfactory cues are congruent, visual cues facilitate olfactory detection, and such facilitation has been associated with enhanced neural activity in anterior hippocampus and rostromedial orbitofrontal cortex [3]. There has been little indication that the reverse could happen, i.e., that olfaction could modulate visual perception. Chemosensory emotional cues have been suggested to influence emotional perception subconsciously, but only when visual emotional cues are rendered extremely ambiguous [6]. To probe whether there is an active role of the sense of smell in the perceptual integrations of olfactory and visual cues (i.e., modulating visual perception rather than being modulated by vision), we introduced smells to a unique visual paradigm: binocular rivalry, which refers to the perceptual alternations that occur when

distinctively different images are separately presented to the two eyes [4].

In experiment 1, two odorants with the smell of rose (phenyl-ethyl alcohol, PEA, 0.5% v/v in propylene glycol) and marker pen (butanol, 0.25% v/v in propylene glycol) were introduced to address whether the dynamics of binocular rivalry could be influenced by olfactory cues. In each 60 s run, subjects viewed a composite rose/marker image through red/green anaglyph eyeglasses so that the rose and the marker images were dichoptically presented to the two eyes and engaged in rivalry. During this time, subjects indicated what they saw by pressing buttons every time perception switched while being exposed continuously to PEA or butanol (Figure 1A; see Supplemental Experimental Procedures available online for details). As compared with butanol, PEA was rated as much more like the smell of roses ($p = 0.008$), much less like the smell of marker pens ($p < 0.0001$), more pleasant ($p = 0.026$), and marginally less intense ($p = 0.06$). With dominance time (the average duration between button presses) as dependent variable, repeated-measures analysis of variance revealed a significant interaction between olfactory condition (PEA versus butanol) and visual image (rose versus marker) [$F(1,11) = 8.21$, $p = 0.015$; Figure 1B]. The dominance time of the rose image was significantly longer when the subjects smelled PEA as compared with butanol [$t(11) = 2.26$, $p = 0.045$]. Likewise, when the subjects smelled butanol as compared with PEA, the dominance time of the marker image was significantly longer [$t(11) = 3.19$, $p = 0.009$]. Although the two smells differed noticeably in pleasantness and marginally in intensity, these perceptual factors did not bias the subjects toward seeing one image versus the other ($p = 0.38$ and 0.35 for pleasantness and intensity, respectively, using mixed linear model analysis with olfactory condition as the factor and pleasantness and intensity ratings as the covariates). It could be argued that dominance time potentially includes instances of superimposed and piecemeal perceptions of the rival images, making the subjects prone to response biases. To address this possibility, we conducted a supplemental experiment (Figure S1) in which subjects' responses were based on exclusive visibility (meaning seeing only one of the rival images and not any part of the other), and here the main results of experiment 1 were replicated.

Still, the above findings could be due to a semantic bias (i.e., a conceptual link between rose/marker smell and rose/marker image), or even to the possibility that subjects might have guessed the purpose of the experiment, rather than to the influence of olfactory cues. To investigate these alternative possibilities, we recruited an independent group of subjects in experiment 2, who performed the same task while being exposed to two bottles of purified water. The subjects were however told that one of the bottles contained a low concentration of rose smell and the other contained a low concentration of marker smell, and they were told which smell they were going to receive each time. Subjects rated the purified water as more pleasant ($p = 0.05$, one-tailed t test) and more like the smell of roses ($p = 0.05$, one-tailed t test) but similarly intense ($p = 0.25$) when the water was suggested as containing a rose smell as compared to a marker smell. However, despite

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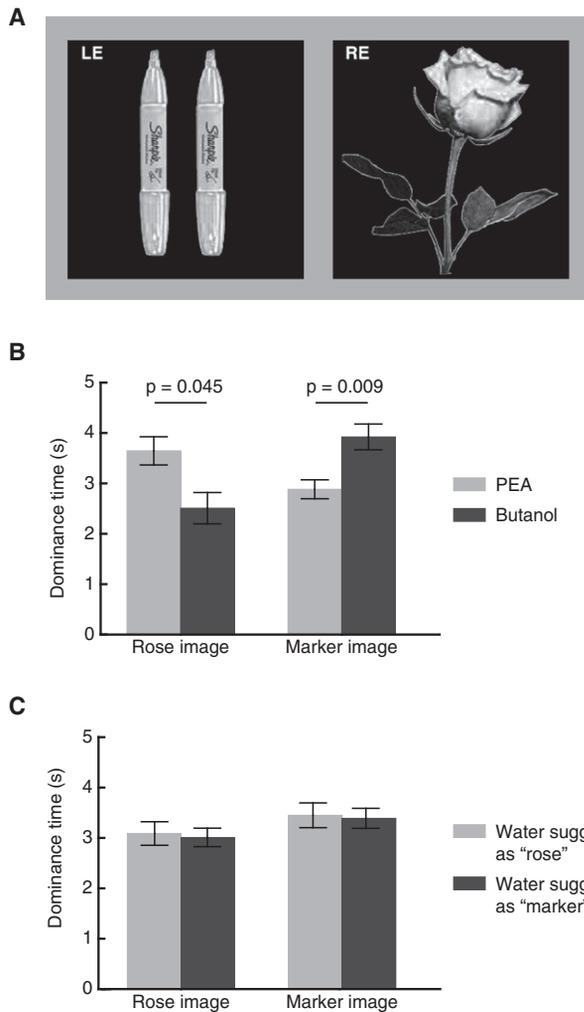


Figure 1. Olfactory Information Modulates the Dominance of Visual Percepts in Binocular Rivalry

(A) Visual stimuli used in experiments 1 and 2. Subjects viewed the stimuli through red/green anaglyph glasses; the rose image was projected to one eye while the marker image was projected to the other eye. Subjects indicated when their perception switched from seeing predominantly the rose or marker image to predominantly the marker or rose image by pressing one of two buttons.

(B) Olfactory cues influence visual processing. Compared with butanol, the dominance time of the rose image was longer and the dominance time of the marker image shorter when subjects smelled phenylethyl alcohol (PEA), and vice versa.

(C) Suggestion does not affect binocular rivalry. The dominance time of both the rose image and the marker image remained the same under the two conditions in which purified water was suggested as containing a rose or marker smell. Error bars in (B) and (C) represent standard errors of the mean, adjusted for individual differences.

being susceptible to suggestions when making olfactory judgments, subjects were not influenced by the suggested smell contents in perceiving one image versus the other in the binocular rivalry task. No interaction was found between olfactory condition (water suggested as containing rose smell versus water suggested as containing marker smell) and visual image (rose versus marker) [$F(1,11) = 0.004$, $p = 0.95$]. In other words, there was no difference in the dominance time of either the rose image [$t(11) = 0.27$, $p = 0.79$] or the marker image [$t(11) = 0.18$, $p = 0.86$] between the two olfactory

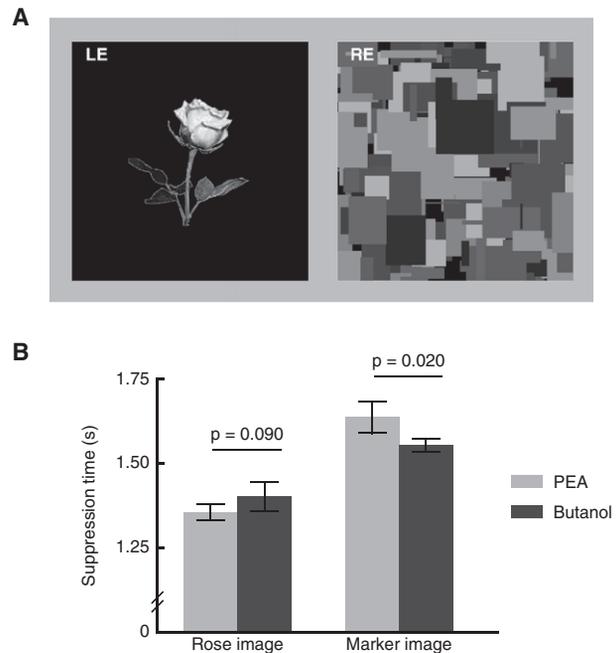


Figure 2. Olfactory Information Modulates the Suppression of Visual Percepts in Continuous Flash Suppression

(A) Visual stimuli in experiment 3. At the beginning of each trial, a standard dynamic noise pattern was presented to the subjects' dominant eye at full contrast, and the test figure (the rose image or the marker image) was presented to the nondominant eye at a random location along the midline within the region corresponding to the location of the noise pattern. The contrast of the test figure was ramped up gradually from 0 to full contrast within 1 s starting from the beginning of the trial and then remained constant until the subjects made a button press to indicate whether they saw the rose image or the marker image, whereas the contrast of the dynamic noise was ramped down gradually from full contrast to 0 within 2 s starting from 1 s after the test figure reached its full contrast.

(B) Olfactory cues modulate visual processing in the absence of visual awareness. Compared with butanol, when subjects smelled PEA, the suppression time of the rose image tended to be shorter and the suppression time of the marker image longer. Error bars represent standard errors of the mean, adjusted for individual differences.

conditions (water suggested as containing rose smell versus water suggested as containing marker smell) (Figure 1C).

We thus conclude that the change of the temporal dynamics of binocular rivalry, as observed in experiment 1, is not due to the intensity or pleasantness of the smells, to the semantically mediated conceptual bias, or to the cognitive control of the subjects who had guessed the purpose of the experiment. Instead, it results from the sensory congruency or incongruency between olfactory cues and visual inputs.

The olfactory cues could have exerted their modulation effect when they were congruent with the current dominant visual image, as is the case with the reported tactile modulation of binocular rivalry [7], or when they were congruent with the currently suppressed visual image. The latter would imply that olfactory modulation occurs unconsciously. To test this, in experiment 3 we measured the time needed for the two images (rose versus marker) to break from interocular continuous flash suppression [8, 9] under the two olfactory conditions (PEA versus butanol, respectively), a technique that targets the information processing while the stimuli remain invisible [10, 11] (Figure 2A; see Supplemental

Experimental Procedures for details). Again, a significant interaction was observed between olfactory condition (PEA versus butanol) and visual image (rose versus marker) [$F(1,13) = 52.50, p < 0.001$]. When the subjects were exposed to PEA as compared with butanol, the suppression time of the rose image tended to be shorter [$t(13) = -1.83, p = 0.09$] and the suppression time of the marker image was longer [$t(13) = 2.65, p = 0.02$] (Figure 2B), whereas accuracy was high (96.95% correct on average; see Supplemental Experimental Procedures) and equal [$F(1,13) = 0.275, p = 0.61$]. Because the subjects did not know whether they were presented with the rose image or the marker image before they responded (by the nature of interocular suppression), this result suggests that olfactory modulation of visual processing occurs in the absence of visual awareness.

The dynamic process of binocular rivalry is known to be influenced by visual factors like contrast [12], brightness [13], contour density [14], visual context [15], and to a certain extent visual attention [16, 17]. More recently, it has been demonstrated to be modulated by auditory [18] and tactile [7] cues. Here we provide the first empirical evidence that it can also be affected by olfactory inputs.

Animals range and forage using a combination of olfactory and visual cues [19]. Extensive neuroanatomical convergence has been identified between retinal and olfactory projections [20] and higher visual and olfactory regions [21], which likely contributes to the integration of olfactory and visual inputs and hence to the sensory modulation of vision by olfaction observed here. In binocular rivalry, the competition between the information from the two eyes potentially occurs at multiple stages of visual processing [4, 22] and has been suggested to be functionally accounted for in terms of predictive coding in a Bayesian framework [23]. Because the observed effects rely on the association between a visual object and its smell, olfactory information may influence visual processing at visual object representation stages: strengthening the representation of one object and/or weakening the other in a manner that is automatic, essentially independent of cognitive control, and partly subconscious.

In summary, by introducing olfactory cues to the binocular rivalry paradigm, we have shown for the first time that the dynamic process of binocular rivalry can be influenced by olfactory cues. Our discovery adds to the sensory integration literature [24–26] and demonstrates that olfaction can modulate visual processing. In other words, the eyes are inclined to see what the nose smells.

Supplemental Information

Supplemental Information includes Supplemental Results, one figure, and Supplemental Experimental Procedures and can be found with this article online at doi:10.1016/j.cub.2010.05.059.

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References

1. Ackerman, D. (1991). *A Natural History of the Senses* (London: Vintage).
2. Morrot, G., Brochet, F., and Dubourdiou, D. (2001). The color of odors. *Brain Lang.* 79, 309–320.
3. Gottfried, J.A., and Dolan, R.J. (2003). The nose smells what the eye sees: Crossmodal visual facilitation of human olfactory perception. *Neuron* 39, 375–386.
4. Blake, R., and Logothetis, N.K. (2002). Visual competition. *Nat. Rev. Neurosci.* 3, 13–21.
5. Cain, W.S. (1979). To know with the nose: Keys to odor identification. *Science* 203, 467–470.
6. Zhou, W., and Chen, D. (2009). Fear-related chemosignals modulate recognition of fear in ambiguous facial expressions. *Psychol. Sci.* 20, 177–183.
7. Lunghi, C., Binda, P., and Morrone, M.C. (2010). Touch disambiguates rivalrous perception at early stages of visual analysis. *Curr. Biol.* 20, R143–R144.
8. Tsuchiya, N., and Koch, C. (2005). Continuous flash suppression reduces negative afterimages. *Nat. Neurosci.* 8, 1096–1101.
9. Fang, F., and He, S. (2005). Cortical responses to invisible objects in the human dorsal and ventral pathways. *Nat. Neurosci.* 8, 1380–1385.
10. Jiang, Y., Costello, P., and He, S. (2007). Processing of invisible stimuli: Advantage of upright faces and recognizable words in overcoming interocular suppression. *Psychol. Sci.* 18, 349–355.
11. Yang, E., Zald, D.H., and Blake, R. (2007). Fearful expressions gain preferential access to awareness during continuous flash suppression. *Emotion* 7, 882–886.
12. Mueller, T.J., and Blake, R. (1989). A fresh look at the temporal dynamics of binocular rivalry. *Biol. Cybern.* 61, 223–232.
13. Kaplan, I.T., and Metlay, W. (1964). Light intensity and binocular rivalry. *J. Exp. Psychol.* 67, 22–26.
14. Fahle, M. (1982). Binocular rivalry: Suppression depends on orientation and spatial frequency. *Vision Res.* 22, 787–800.
15. Alais, D., and Blake, R. (1999). Grouping visual features during binocular rivalry. *Vision Res.* 39, 4341–4353.
16. Meng, M., and Tong, F. (2004). Can attention selectively bias bistable perception? Differences between binocular rivalry and ambiguous figures. *J. Vis.* 4, 539–551.
17. Chong, S.C., Tadin, D., and Blake, R. (2005). Endogenous attention prolongs dominance durations in binocular rivalry. *J. Vis.* 5, 1004–1012.
18. van Ee, R., van Boxtel, J.J., Parker, A.L., and Alais, D. (2009). Multisensory congruency as a mechanism for attentional control over perceptual selection. *J. Neurosci.* 29, 11641–11649.
19. Wyatt, T.D. (2003). *Pheromones and Animal Behavior: Communication by Smell and Taste* (London: Cambridge University Press).
20. Cooper, H.M., Parvopassu, F., Herbin, M., and Magnin, M. (1994). Neuroanatomical pathways linking vision and olfaction in mammals. *Psychoneuroendocrinology* 19, 623–639.
21. Gottfried, J.A. (2006). Smell: Central nervous processing. *Adv. Otorhinolaryngol.* 63, 44–69.
22. Tong, F., Meng, M., and Blake, R. (2006). Neural bases of binocular rivalry. *Trends Cogn. Sci.* 10, 502–511.
23. Hohwy, J., Roepstorff, A., and Friston, K. (2008). Predictive coding explains binocular rivalry: An epistemological review. *Cognition* 108, 687–701.
24. McGurk, H., and MacDonald, J. (1976). Hearing lips and seeing voices. *Nature* 264, 746–748.
25. Blake, R., Sobel, K.V., and James, T.W. (2004). Neural synergy between kinetic vision and touch. *Psychol. Sci.* 15, 397–402.
26. Beauchamp, M.S. (2005). See me, hear me, touch me: Multisensory integration in lateral occipital-temporal cortex. *Curr. Opin. Neurobiol.* 15, 145–153.

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Supplemental Information

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Supplemental Results

Compared to phenyl ethyl alcohol (PEA), isoamyl acetate (IA) was rated as much more like the smell of bananas ($p < 0.001$) and much less like the smell of roses ($p < 0.001$). As shown below in Figure S1b, olfactory cues significantly modulated the mean duration over which each of the rivalry images was exclusively in view (indicated by the mean duration of the key presses for seeing exclusively one of the rivalry images) [significant interaction between olfactory condition (PEA vs. IA) and visual image (rose vs. banana), $F(1, 23) = 12.38$, $p = 0.002$]. The mean dominance time of the rose image was significantly longer when the subjects smelled PEA as compared with IA [$t(23) = 4.37$, $p < 0.001$]. Correspondingly, the mean dominance time of the banana image was significantly longer [$t(23) = 2.34$, $p = 0.029$] when the subjects smelled IA as compared with PEA. A similar pattern was observed with the total duration that one of the rivalry images exclusively dominated the other (indicated by the total duration of the key presses for seeing exclusively one of the rivalry images) [$F(1, 23) = 14.34$, $p = 0.001$]. Olfactory cues did not influence how frequent (indicated by the number of key presses) the subjects exclusively saw the rose image versus the banana image (no significant interaction between olfactory conditions and visual images, $F(1, 23) = 0.116$, $p = 0.737$).

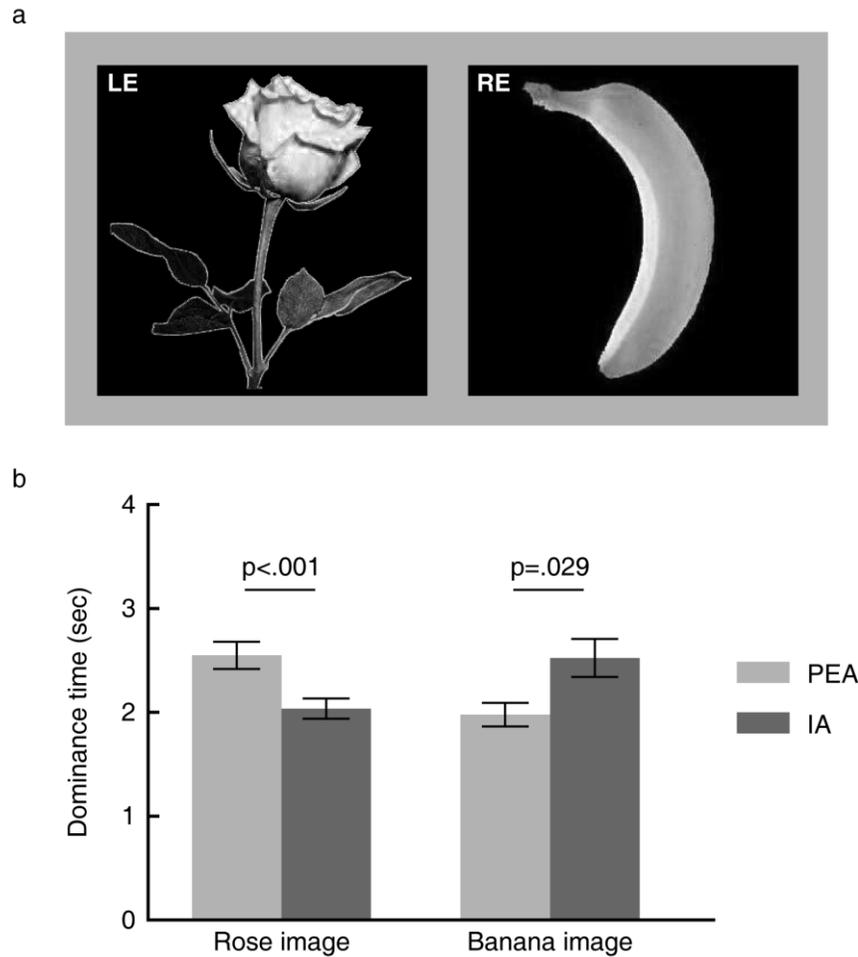


Figure S1.

(a) Visual stimuli used in Supplemental Experiment. When viewed through red-green anaglyph glasses, the rose image was projected to the subjects' one eye whereas the banana image was projected to the other eye. Subjects indicated when they saw exclusively the rose image or exclusively the banana image by holding down one of two buttons. They released both buttons during instances of superimposed and piecemeal perception of the rivalry images.

(b) Olfactory cues influenced visual processing. Compared with IA, the mean duration that the rose image was exclusively in view was longer and the mean duration that the banana image was exclusively in view was shorter when the subjects smelled PEA, and vice versa. Error bars represent standard errors of the mean, adjusted for individual differences.

Supplemental Experimental Procedures

Participants

38 healthy non-smokers participated in the main study (Experiments 1-3). 12 (4 males, 8 females, mean age = 19.0 yrs, SEM = 0.21) participated in Experiment 1, 12 (5 males, 7 females, mean age = 19.1 yrs, SEM = 0.26) in Experiment 2, and 14 (8 males, 6 females, mean age = 20.1 yrs, SEM = 0.75) in Experiment 3. An additional 24 healthy non-smokers (11 males, 13 females, mean age = 22.6 yrs, SEM = 0.33) participated in the supplemental experiment. All of the participants reported to have normal or corrected-to-normal vision, normal sense of smell, and no respiratory allergy or upper respiratory infection at the time of testing. They were naïve to the purpose of the experiments. All gave informed consent for participation.

Olfactory Stimuli

Smells were presented in identical 280 ml glass bottles. Each bottle contained 10ml clear liquid and was connected with two Teflon nosepieces via a Y-structure. The olfactory stimuli in Experiments 1 and 3 consisted of phenyl ethyl alcohol (PEA, 0.5% v/v in propylene glycol) and n-butanol (0.25% v/v in propylene glycol); both were supra-threshold to all subjects. Two bottles of purified water were used in Experiment 2, which served as a control experiment for Experiment 1. The olfactory stimuli in the supplemental experiment consisted of phenyl ethyl alcohol (PEA, 0.5% v/v in propylene glycol) and isoamyl acetate (IA, 0.0625% v/v in propylene glycol), both also supra-threshold to all subjects.

Visual Stimuli

All visual stimuli were viewed through red-green anaglyph eye-glasses. We individually adjusted which eye viewed which image in Experiments 1, 2, and the supplemental experiment to produce a more balanced rivalry between the two competing images in the absence of olfactory cues. In Experiments 1 and 2, a static image of a rose was presented to the subjects' one eye, meanwhile, a static image of two markers was presented to the other eye (Figure 1), both with a visual angle of about $6.0^\circ \times 7.6^\circ$. Experiment 3 employed continuous flash suppression, a variation of the binocular rivalry paradigm. At the beginning of each trial, a standard dynamic noise pattern was presented to the subjects' dominant eye at full contrast, and the test figure, which was either the rose image or the marker image, was presented to the subjects' non-dominant eye at a random location along the midline within the region corresponding to the location of the noise pattern. The contrast of the test figure was ramped up gradually from 0 to full contrast within 1 s starting from the beginning of the trial and then remained constant until the subjects made a button-press response to indicate whether they saw the rose image or the marker image, whereas the contrast of the dynamic noise was ramped down gradually from full contrast to 0 within 2s starting from 1s after the test figure reached its full contrast (Figure 2). The visual angle was about 11.3° both horizontally and vertically for the dynamic noise pattern, and about $3.6^\circ \times 4.6^\circ$ for the test figures. In the supplemental experiment, a static image of a rose was presented to the subjects' one eye whereas a static image of a banana was presented to the other eye (Figure S1a), both with a visual angle of about $3.0^\circ \times 4.1^\circ$.

Procedure

In Experiment 1, twelve subjects were first told the labels of the two smells, i.e., “rose” and “marker.” They then inhaled each smell and rated on a 100-unit visual analog scale its intensity,

pleasantness, and similarities to the smells of rose and marker. There was a one minute break between the samplings. After that, the subjects completed a practice session so that they were comfortable with viewing the composite rose/marker image through red-green anaglyph glasses and maintaining their fixation while inhaling through the nose pieces fitted to a bottle. The subjects were instructed to inhale through the nose and exhale through their mouth for the duration of the image. They pressed one of two buttons when they saw predominantly “rose”, and pressed the other button when it switched to predominantly “marker.” The button presses marked the time points of perceptual switches. Each subject completed the actual binocular rivalry task twice. Each time the composite rose/marker image was presented for 60s and the subjects indicated what they saw through button pressing while being exposed continuously to PEA or butanol. Half of the subjects smelled PEA in the first run, butanol in the second run. The other half did the reverse. The two runs were separated by a 5 min break to avoid possible interference.

Experiment 2 followed the same procedure as Experiment 1, except that two bottles containing purified water were used. The subjects were however instructed that one of the bottles contained a low concentration of rose smell and the other bottle contained a low concentration of marker smell, and were told which smell they were going to receive each time.

In Experiment 3, fourteen subjects were similarly told the labels of the two odorants and were trained in a practice session to inhale through the nose pieces and exhale through their mouth while fixating on the visual displays. They were instructed to press one of two buttons as quickly as they could to indicate if they saw a rose image or a marker image. In the actual experiment, each subject completed four runs of the continuous flash suppression task, with a 5 minute break in between the runs. Each run consisted of 24 trials in random order. The rose image served as the test figure in half of the trials, and the marker image served as the test figure in the other half. The order of odorant presentations (twice PEA, twice butanol) was counterbalanced across the subjects.

The supplemental experiment was a replication and an extension of Experiment 1, in which we measured exclusive visibility and used two odorants (PEA and IA) with direct perceptual linkages to the competing images (rose and banana, respectively). The subjects firstly rated on a 100-unit visual analog scale how similar each smell was to the smells of rose and banana, respectively. Then after a practice session, they completed 4 runs of the actual binocular rivalry experiment. In each run, the composite rose/banana image was presented for 60s, and the subjects held down one of two buttons when they saw exclusively the rose image and the other button when they saw exclusively the banana image. They were instructed to release both buttons during instances of superimposed and piecemeal perception of the rivalry images. The order of odorant presentations (twice PEA, twice IA) was counterbalanced across the subjects. The procedure was otherwise identical to that of Experiment 1.

Analyses

In Experiments 1-2, the dependent measure was the mean duration that one image predominated the other, in other words, the averaged duration between pressing one button for beginning to see predominantly one of the rivalry images and pressing the other button for beginning to see predominantly the other rivalry image. In Experiment 3, the dependent measure was the mean duration for each test image to break from suppression. In the supplemental experiment, we aimed to measure the duration that one image exclusively dominated the other. The dependent

measures included the mean duration, the total duration, as well as the number of all key presses for each rivalry image.

The data were analyzed with repeated measures ANOVA, using olfactory condition (2 levels, PEA vs. butanol in Experiments 1 and 3, purified water instructed as having rose smell vs. purified water instructed as having marker smell in Experiment 2, PEA vs. IA in Supplemental Experiment) and visual image (2 levels, rose vs. marker in Experiments 1-3, rose vs. banana in Supplemental Experiment) as the within subject factors. Paired sample t tests were performed to further compare the dominance (Experiments 1, 2, and Supplemental Experiment) /suppression (Experiment 3) time for each image (rose vs. marker in Experiments 1-3, rose vs. banana in Supplemental Experiment) between the olfactory conditions (PEA vs. butanol in Experiments 1 and 3; purified water instructed as having rose smell vs. purified water instructed as having marker smell in Experiment 2, PEA vs. IA in Supplemental Experiment). In addition, to examine whether intensity and pleasantness contributed to the dominance of one image versus the other in Experiment 1, a mixed linear model was built with olfactory condition (PEA vs. butanol) as the factor and intensity and pleasantness ratings as the covariates. When analyzing response time data in Experiment 3, incorrect responses (occurred in less than 3% of the trials), as well as responses made in less than 500ms or more than 4s from the beginning of a trial (0.07% of the trials), were excluded beforehand.