# Report

# 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 (phenylethyl 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



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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