Olfaction Modulates Early Neural Responses to Matching Visual Objects

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Abstract

■ Sensory information is initially registered within anatomically and functionally segregated brain networks but is also integrated across modalities in higher cortical areas. Although considerable research has focused on uncovering the neural correlates of multisensory integration for the modalities of vision, audition, and touch, much less attention has been devoted to understanding interactions between vision and olfaction in humans. In this study, we asked how odors affect neural activity evoked by images of familiar visual objects associated with characteristic smells. We employed scalp-recorded EEG to measure visual ERPs evoked by briefly presented pictures of familiar objects, such as an orange, mint leaves, or a rose. During presentation of each visual stimulus, participants inhaled either a matching odor, a nonmatching odor, or plain air. The N1 component of the visual ERP was significantly enhanced for matching odors in women, but not in men. This is consistent with evidence that women are superior in detecting, discriminating, and identifying odors and that they have a higher gray matter concentration in olfactory areas of the OFC. We conclude that early visual processing is influenced by olfactory cues because of associations between odors and the objects that emit them, and that these associations are stronger in women than in men. ■

INTRODUCTION

Multisensory integration is an obligatory feature of perception. Thus, for example, the sounds of spoken words are automatically bound to the lip movements that evoke them (Driver, 1996). Likewise, the sight of a prosthetic arm being stroked can influence the felt position of one's own arm when the latter is stroked concurrently but hidden from view (Botvinick & Cohen, 1998). Despite considerable research on multisensory integration, relatively little attention has been devoted to understanding the nature of olfactory–visual interactions. Olfaction and vision have anatomically distinct brain pathways, but they both subserve object identification functions (Gottfried, 2010). Specialized associations between the olfactory and visual features of objects are therefore a likely source for multisensory integration of visual stimuli and their characteristic odors.

It is well known that visual features such as color and shape can facilitate odor detection (Gottfried & Dolan, 2003) and identification (Dematte, Sanabria, & Spence, 2009), but olfaction can also influence visual perception. For example, odors can influence eye movements toward matching visual objects (Seigneuric, Durand, Jiang, Baudouin, & Schaal, 2010; Seo, Roidl, Muller, & Negoias, 2010). Likewise, during binocular rivalry, odors can increase the dominance time of matching images relative to nonmatching images (Zhou, Jiang, He, & Chen, 2010), and this effect is heightened when the same hemisphere processes the matching olfactory and visual objects (Zhou, Zhang, Chen, Wang, & Chen, 2012), suggesting that olfaction can influence relatively early cortical stages of visual processing. This is particularly interesting, given the mounting evidence to suggest that multisensory information is represented in "primary" sensory areas of the brain (Liang, Mouraux, Hu, & Iannetti, 2013; Meyer, Kaplan, Essex, Damasio, & Damasio, 2011; Meyer et al., 2010). Although the convergent olfactory pathways that would allow such an effect on visual perception are unknown, Jadauji, Djordjevic, Lundstrom, and Pack (2012) have suggested that the primary visual cortex (V1) might play a role in higher-order olfactory functioning. They found that repetitive TMS of V1 enhanced olfactory discrimination (Jadauji et al., 2012), indicating that olfactory and visual brain processes might be more closely coupled than previously thought.

Several investigations have noted a marked sexual dimorphism in human olfactory perception. Generally, women perform better on tasks of odor discrimination, detection, and memory than men (Doty & Cameron, 2009). Women have a greater concentration of gray matter in OFC than men (Garcia-Falgueras et al., 2006), an area implicated in higher-order olfactory perception (Savic, Gulyas, Larsson, & Roland, 2000) and olfactory–visual integration (Jadauji et al., 2012; Royet et al., 1999). It remains unclear whether olfactory sex differences translate to differences in multisensory processing, but it is possible that olfactory–visual interactions are expressed differently in women and men.

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In this study, we investigated the influence of olfaction on visual perception by measuring neural responses to familiar visual stimuli in the presence of matching and nonmatching odors. We used scalp-recorded EEG to determine the time course of olfactory–visual interactions. Previous ERP studies have shown that odors can influence a late, semantic stage of processing associated with the presentation of matching images (Grigor, Van Toller, Behan, & Richardson, 1999; Sarfarazi, Cave, Richardson, Behan, & Sedgwick, 1999). Our aim was to investigate whether early visual responses might also be affected by the presence of matching versus nonmatching odors and to determine whether any such olfactory–visual interactions differ between men and women. Because the color and shape of a visual stimulus can influence olfactory perception (Dematte et al., 2009), we also tested whether odors differentially affect the processing of color and shape in vision.

METHODS

Participants

This study was approved by the human ethics committee of The University of Queensland in accordance with the National Health and Medical Research Council's guidelines. Informed consent was obtained from all participants. Twenty-six participants (13 women, mean age = 24.46 years; 13 men, mean age = 25.15 years) were recruited from The University of Queensland. Before beginning the experiment, they were screened for their ability to distinguish between the test odors. They completed a questionnaire about factors relating to their sense of smell, such as whether they were allergic to odors or had ever had nasal surgery. The women were asked if they might be pregnant. All of the participants reported a normal sense of smell, had normal or corrected-to-normal vision, were nonsmokers, and had no known odor allergies. None of the women reported being pregnant.

Stimuli

Participants were presented with familiar images and odors that were either related or unrelated to the images (congruent and incongruent conditions, respectively). The image shown on any given trial was either an object with a characteristic odor (odor-related objects), such as a rose or an orange, or an object without a characteristic odor (non-odor-related objects), such as a hat or box (Figure 1A). Odor-related objects were depicted either in grayscale or their natural color, that is, rose = red, mint = green, and orange = orange. Non-odor-related objects were depicted in grayscale and the same colors as those of the odor-related objects (i.e., red, green or orange, with equal frequency). There were seven exemplar images of each object, which were photographs of the same object taken from angles of 0°, 30°, 60°, 90°, 120°, 150°, and 180°. Importantly for the task, an outline shape was superimposed over each image and acted as a border around the object. The border was either a square or a diamond and presented in white or black in equal combinations for each image. Images were shown on

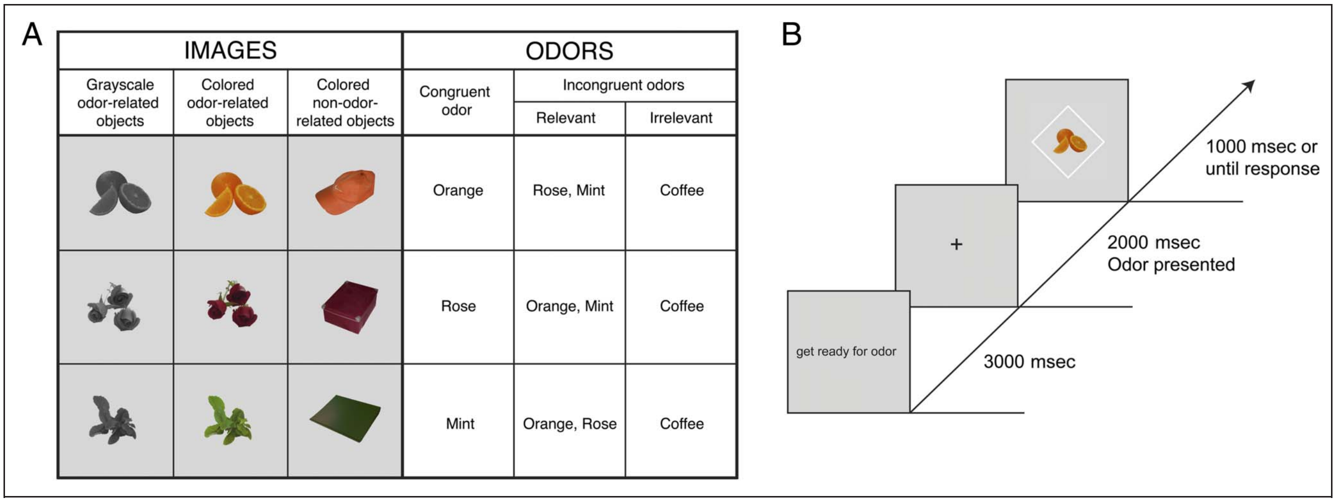

Figure 1. Example stimuli and schematic of sequence of olfactory and visual events in a single trial of the experiment. (A) In each trial, participants were presented with one odor and one image. The images were odor-related objects (orange, rose, and mint) and non-odor-related objects (cap, box, and folder) presented in color and grayscale. Only the three critical image conditions are shown. For each image condition, there were three associated odor conditions: congruent, incongruent-relevant, or incongruent-irrelevant (see text for details). (B) Timeline of events in a typical trial. Participants were instructed to get ready, and then an auditory cue directed participants to inhale. The odor stream was presented for 2000 msec, after which one of the visual objects appeared at fixation, surrounded by a white diamond or square. Participants had to indicate the shape of the border surrounding the object. The visual display remained on the screen for 1000 msec or until a manual response was made. ERPs were measured from 100 msec before to 1000 msec after the onset of the visual display.

a 22-in. Dell LCD monitor on a uniform light gray background. Participants placed their chin on a chin rest located 60 cm from the monitor.

The Cogent toolbox in Matlab (The MathWorks; Natick, MA) was used to present both the visual and olfactory stimuli. The odors presented were congruent or incongruent with respect to the images. The odors were orange and mint (Oil Garden essential oils), rose (Jurlique rosewater mist), and coffee (Queen Fine Foods Ltd. Flavoring Essence). Plain air was also delivered for "no odor" trials, which were intermingled with the critical odor trials. No-odor trials were included as an independent measure of visual ERPs to choose time windows and electrodes for the analysis, rather than as a critical condition of the experiment. An eight-channel liquid dilution olfactometer (Knosys Olfactometers, www.knosysknosys.com) was used to deliver the odors to participants by running a clean air stream (1.5 L/min) through the pure, undiluted liquid odorants contained in 200 ml plastic bottles. Odors from the different channel lines emerged at a funnel placed in front of the chin rest, under the participant's nose.

In each trial, participants were presented with one odor and one image. The visual stimuli took the form of a 2 × 2 design, with factors of Object type (odor-related object or non-odor-related object) and Image color (colored or grayscale). Three different odor conditions were presented with each of the visual stimuli (Figure 1A). For odor-related objects, odors were classified as congruent when they matched the visual object depicted (e.g., rose odor with a picture of a rose). For colored objects, odors were classified as congruent when they matched the color of the image (e.g., orange odor with a picture of an orange baseball cap, rose odor with a picture of a red box, etc.), in accordance with previous research revealing cross-modal correspondences between colors and odors (Osterbauer et al., 2005; Morrot, Brochet, & Dubourdieu, 2001; Gilbert, Martin, & Kemp, 1996).

By contrast, trials were classified as incongruent if the odor did not match the visual object depicted. There were two distinct incongruent conditions based on whether the odor was relevant or irrelevant with respect to the visual stimuli. The incongruent-relevant odors had a matching visual object within the overall design matrix (Figure 1A), whereas the incongruent-irrelevant condition consisted of the visual images paired with coffee odor, which never matched any of the odor-related objects on the task. The incongruent-irrelevant odor condition was included to control for any nonspecific effect of odor presentation on ERPs.

Each participant was exposed to only two critical odors (orange and rose, rose and mint, or orange and mint) and their associated images (e.g., rose odor associated with images of roses and red boxes) to avoid any olfactory stimulus being more probable than another, as well as to allow equal numbers of congruent- and incongruent-relevant trials. Odors were counterbalanced across the congruent- and incongruent-relevant conditions. There was no congruency manipulation for grayscale non-odor-related objects because all odors were nonmatching with respect to the visual stimuli, but each odor was presented equally with each image (e.g., rose, orange, and coffee odors with image of grayscale box) to investigate effects of odor on processing of unrelated visual objects. Overall, each odor and image combination was equally probable throughout the course of the experiment.

There were 640 trials in the experiment, consisting of five trials for each combination of object condition (odor-related, non-odor-related), object type per object condition (two; e.g., mint and rose), color (colored, grayscale), odor (congruent, incongruent-relevant, incongruent-irrelevant, no-odor), border shape (square, diamond), and border color (white, black). Trials were completely randomized and split into 10 blocks of 64 trials.

Procedure

Odor Discrimination Screening

Participants first completed a four-alternative forced-choice odor discrimination task. Four different odors were presented to participants; coffee, no odor, and the two critical odors (e.g., rose and mint). Each odor was repeated three times, and the 12 trials were randomized. On each trial, participants were given 3 sec to prepare for inhalation, and the odor was subsequently presented for 4 sec. Participants had to make a button press response to indicate which odor they perceived. The next trial began when participants made their response.

Olfactory–Visual Task

On each trial, participants were required to inhale an odor while being presented with an individual visual image, from which ERPs were measured using EEG (Figure 1B). At the start of each trial, participants were presented with the instruction "get ready for odor" for 3000 msec, and then a 400 Hz sine wave tone was presented for 50 msec as a cue to inhale through their nose. When the tone sounded, a black fixation cross appeared in the center of the display and an odor was presented for 2000 msec. Immediately following the odor, an image appeared that either matched the odor in terms of its shape and/or color (congruent trials) or did not match the odor (incongruent trials). All visual stimuli were presented on a uniform light gray background. A critical aspect of the task was that participants never had to identify the odors or visual objects, or judge whether the odors and images matched. Instead, participants performed an orthogonal task in which they determined whether a thin black or white border surrounding the image was a square or a diamond (Figure 1B). They used the index and middle fingers of their right hand to press the left or right arrow keys on a standard keyboard to indicate whether they saw a square or diamond border, respectively. They were asked to respond as quickly and accurately as possible, and the button press signified the end of the trial. No feedback was given regarding accuracy.

EEG Acquisition

Continuous EEG data were recorded using a BioSemi Active Two system (BioSemi, Amsterdam, Netherlands), digitized at a 1024-Hz sample rate with 24-bit A/D conversion. The 64 electrodes were arranged according to the international standard 10–20 system for electrode placement using a nylon head cap. During recording, all scalp electrodes were referenced to the standard BioSemi reference electrodes. Eye movements were monitored using bipolar horizontal EOG electrodes placed at the outer canthi of each eye and bipolar vertical EOG electrodes placed above and below the left eye.

Data Analysis

EEG data analysis was performed offline using Brain Electrical Source Acquisition (BESA 5.3; MEGIS Software GmbH, Grafelfing, Germany). The data were referenced to the mastoids and subjected to low-pass (0.1 Hz, 6 dB/oct, zero phase shift) and high-pass (45 Hz, 12 db/oct, zero phase shift) digital filters. Noisy channels were identified by visual inspection of the data and were interpolated. A blink correction was applied to the data based on the EOG recordings.

ERP data were compiled from 100 msec before image onset to 1000 msec after image onset. We focused on the P1, N1, P2, and P3 components of the visual ERP at posterior scalp electrodes. The P1 peak was largest bilaterally and was observed from 60 to 120 msec after image onset. The N1 peak was largest centrally and was calculated as the average amplitude between 100 and 170 msec after image onset. The P2 and P3 components were observed bilaterally at 190–260 and 300–500 msec, respectively. All participants showed typical ERP waveforms, with pronounced P1, N1, P2, and P3 peaks.

For each component of interest, the ERP data from 160 “no-odor” trials (pooled across image type) were inspected per participant to determine the electrodes that elicited the largest peak amplitudes in response to the visual stimuli. For each participant, the three electrodes that resulted in the largest peak amplitude in the no-odor condition were chosen for subsequent analyses of the critical odor conditions. The same three electrodes were used for a given participant for all analyses per component. Importantly, the electrodes were chosen from a completely independent data set (no odor trials), which ensured there was no bias in analysis. The electrodes included in the analyses were as follows: For the P1 component—P2, P4, P6, P7, P8, PO3, PO4, PO7, PO8, Oz, O1, and O2; for the N1 component—Pz, P1, P2, P3, P4, POz, PO3, PO4, PO7, PO8, Oz, O1, and O2; for the P2 component—Pz, P2, P4, P6, P8, POz, PO3, PO4, PO7, PO8, O1, and O2; and for the P3 component—Pz, P1, P2, P3, P4, P5, P6, P7, P8, PO3, PO4, PO7, PO8, and O1.

RESULTS

Behavioral Results

Odor Discrimination Screening

Accuracy on the odor discrimination task was calculated as a proportion of correct trials. Chance performance was 25%. Performance was significantly higher than chance for women (76.92%, $t(12) = 15.78$, $p < .001$) and for men (69.23%, $t(12) = 11.58$, $p < .001$). Accuracy did not vary between women and men, $t(24) = 1.53$, $p = .140$.

Olfactory–Visual Task

Accuracy on the visual discrimination task (square vs. diamond) was calculated as a percentage of total trials answered correctly. Participants identified the shape of the border correctly on 97.94% of trials. Accuracy did not vary between women (98.50%) and men (97.37%), $t(18.51) = 1.45$, $p = .165$.

RT was calculated as the median RT per condition per participant. Importantly, there were no significant differences in RT between men and women, and there was no interaction between sex and any of the other factors.

ERP Results

The principal goal of the ERP analyses was to determine whether neural responses to the visual stimuli varied with the congruency of the accompanying but task-irrelevant odor. Visual processing can be considered as a two-stage process, encompassing early low-level perceptual processing and later, cognitive-related processing (VanRullen & Thorpe, 2001). It was hypothesized that odor congruency would influence an early stage of visual processing. We therefore analyzed the P1 and N1 components to determine the effects of odors on early perceptual processing as well as the P2 and P3 components involved in later cognitive processing. Mean ERP amplitudes were analyzed separately for each component using mixed model ANOVAs. As a measure of effect size, partial eta-square (η_p^2) is reported for each F value and Cohen’s d_z is reported for each within-subject t value (Lakens, 2013).

Incongruent Odors: Irrelevant versus Relevant Odors

In an initial analysis, the incongruent-relevant and incongruent-irrelevant conditions were compared to determine if context relevance of the nonmatching odor influenced visual ERPs. Relevance of the incongruent odor did not influence visual processing for colored objects or odor-related objects for any ERP component. For odor-related objects, 2 × 2 × 2 mixed model ANOVAs revealed no significant main effects of Odor condition, Fs(1, 24) $\leq$ .31, ps $\geq$ .585, and no significant interactions between Odor condition and factors Color and Sex, Fs(1, 24) $\leq$ 1.27, ps $\geq$ .271. Similarly, for colored objects, 2 × 2 × 2 ANOVAs revealed no significant main effects of Odor condition, Fs(1, 24) $\leq$ .49, ps $\geq$ .491, and no significant interactions between Odor condition and the factors Sex and Object type, Fs(1, 24) $\leq$ 2.65, ps $\geq$ .117. The two incongruent odor conditions were therefore combined into one "incongruent" odor condition for subsequent analyses.

The Effect of Odor Congruency on Visual ERPs

Two critical analyses were conducted per ERP component to determine whether visual processes might be modulated by odors because of a specialized association between (i) odors and colors or (ii) odors and object forms. To investigate the effect of odor congruency on perception of odor-related objects (e.g., gray mint leaves, green mint leaves), 2 × 2 × 2 ANOVAs were conducted with factors of Odor (congruent, incongruent), Image color (colored, grayscale), and Sex. To investigate the effect of odor congruency on perception of colored objects (e.g., green folder, green mint leaves), 2 × 2 × 2 ANOVAs were conducted with factors of Odor (congruent, incongruent), Object type (odor-related, non-odor-related), and Sex. Colored odor-related objects (e.g., green mint leaves) were included in both analyses, so a Bonferroni correction was applied ($\alpha = .025$) for all statistical tests.

The effect of odor on ERPs evoked by odor-related objects. In women, but not men, the N1 peak was enhanced for odor-related objects accompanied by a congruent odor (e.g., mint odor with image of mint leaves) relative to an incongruent odor, irrespective of whether the object was colored or in grayscale (Figure 2). A 2 × 2 × 2 ANOVA with factors of Odor condition, Color, and Sex revealed that N1 amplitude significantly varied across Odor condition, $F(1, 24) = 6.60$, $p = .017$, $\eta_p^2 = .22$, and as an interaction between Odor condition and Sex, $F(1, 24) = 9.28$, $p = .006$, $\eta_p^2 = .28$. To follow up the two-way interaction, the effect of Odor condition on N1 amplitude was analyzed separately for men and women using paired t tests with Bonferroni correction ($\alpha = .0125$). In women, the congruent odor condition resulted in a significantly more negative N1 peak than the incongruent condition, $t(12) = -3.16$, $p = .008$, $d_z = .88$. By contrast, in men there was no significant difference between the congruent and incongruent odor conditions, $t(12) = .52$, $p = .613$, $d_z = .14$. Thus, to summarize, as shown in Figure 2, a congruent odor enhanced the N1 peak for odor-related objects relative to an incongruent odor irrespective of the object's color, but this effect was evident only in women.

Strikingly, despite the clear effect of odors on the early N1 response to congruent visual stimuli in women, there was no evidence for any such modulation of other ERP components (P1, P2, P3; Figure 3). For the P1 component, there were no significant main effects or interactions, Fs(1, 24) $\leq$ 2.57, ps $\geq$ .122, $\eta_p^2 \leq .10$ (Figure 3A). Similarly, analysis of the P2 component revealed no significant main effects or interactions, Fs(1, 24) $\leq$ 2.94, ps $\geq$ .099, $\eta_p^2 \leq .11$ (Figure 3B). Finally, analysis of P3 amplitude revealed a significant main effect of Image color, $F(1, 24) = 6.96$, $p = .014$, $\eta_p^2 = .22$, such that colored objects evoked an enhanced P3 amplitude ($M = 6.88$) overall compared with grayscale objects ($M = 6.58$), but there were no significant main effects of Odor condition or Sex and no significant interactions, Fs(1, 24) $\leq$ 1.49, ps $\geq$ .234, $\eta_p^2 \leq .06$ (Figure 3C).

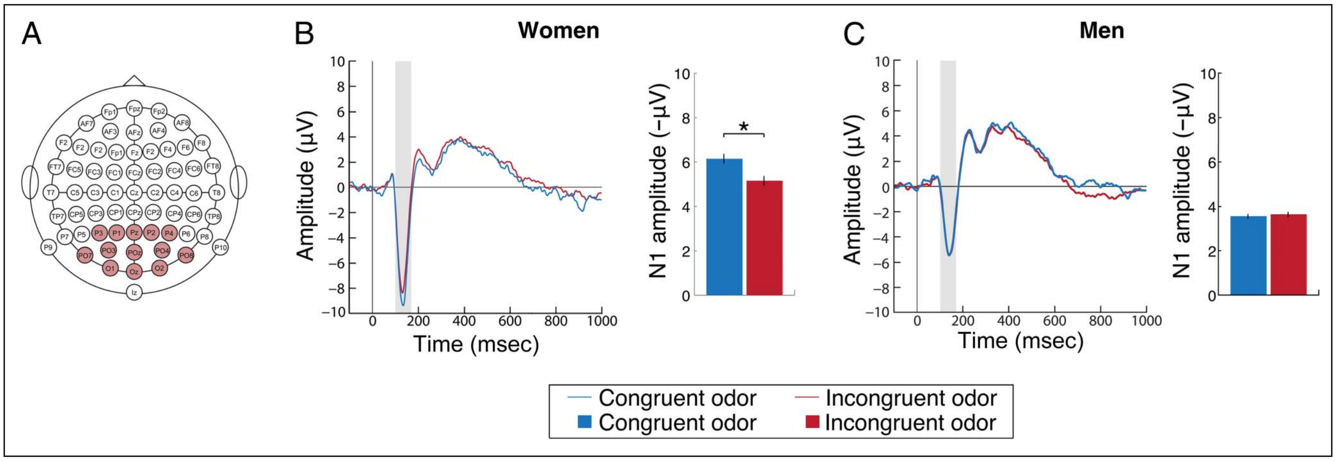

Figure 2. Plots showing ERP waveforms and average N1 amplitudes for odor-related objects (e.g., mint, rose, orange), collapsed across different colors. (A) Headmap showing electrode montage. Shaded electrodes were chosen for analysis of the N1 component. (B) ERP results for women, shown separately for each of the odor conditions. Left plot shows mean ERP waveforms, with shaded rectangle indicating time window for N1 peak. Right plot shows mean amplitude of N1 component for the two odor conditions. (C) ERP results for men, shown separately for each of the odor conditions. Left plot shows ERP waveforms, with shaded rectangle indicating time window for N1 peak. Right plot shows mean amplitude of N1 component for the two odor conditions.

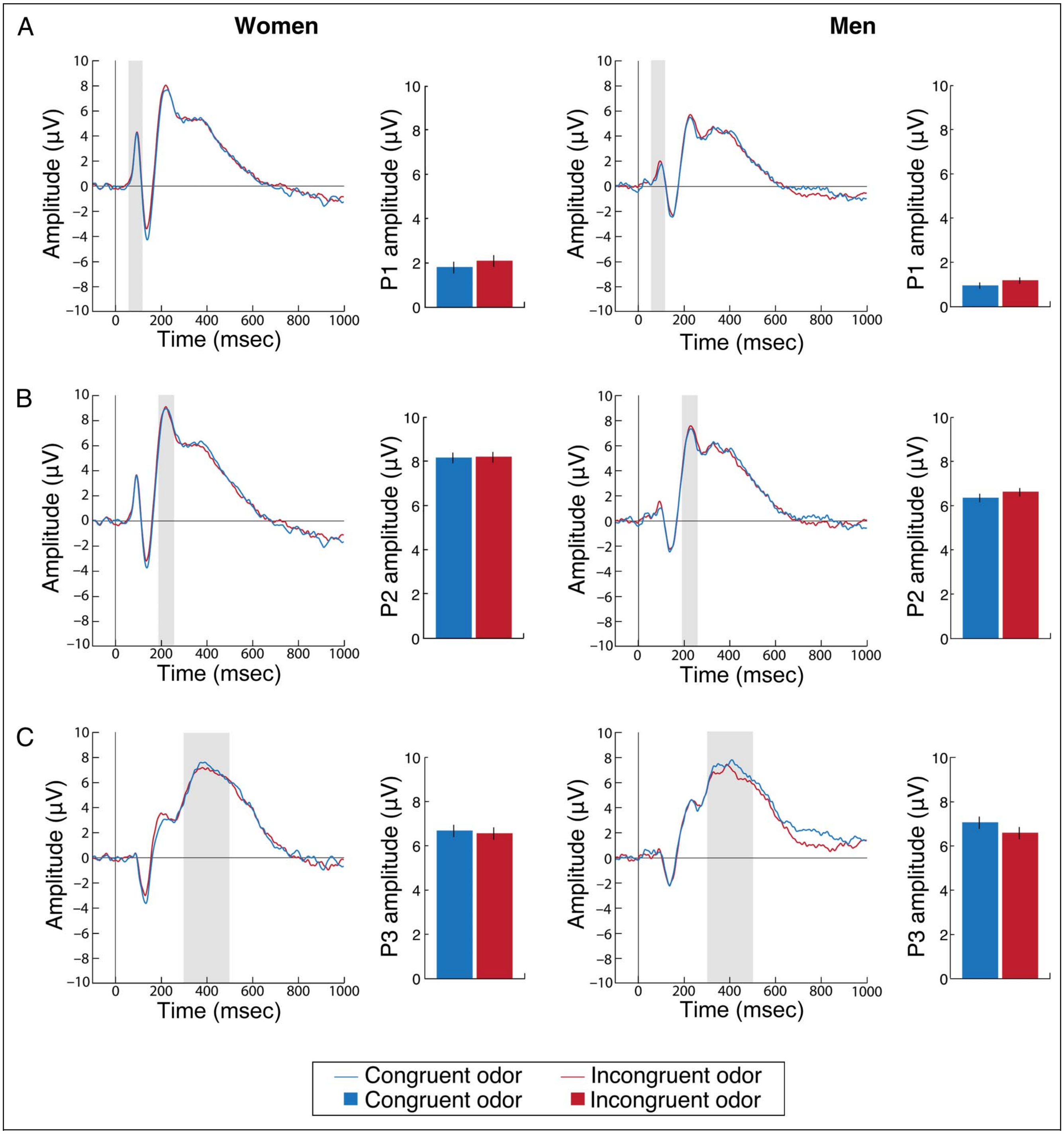

Figure 3. Plots showing ERP waveforms and average P1, P2, and P3 amplitudes for odor-related objects (e.g., mint, rose, orange), collapsed across different colors. (A) ERP results for P1 component, plotted separately for women and men. Left plot for each sex shows mean ERP waveforms, with shaded rectangle indicating time window of P1 peak. Right plot shows mean amplitude of P1 component for the two odor conditions. (B) ERP results for P2 component, plotted separately for women and men. Left plot for each sex shows mean ERP waveforms, with shaded rectangle indicating time window of P2 peak. Right plot shows mean amplitude of P1 component for the two odor conditions. (C) ERP results for P3 component, plotted separately for women and men. Left plot for each sex shows mean ERP waveforms, with shaded rectangle indicating time window of P3 peak. Right plot shows mean amplitude of P1 component for the two odor conditions.

The effect of odor on ERPs evoked by colored objects. In women, the N1 peak for colored images was enhanced by a congruent odor relative to an incongruent odor, but only when the image was an odor-related object. No odor congruency effect was found for men. A 2 × 2 × 2 ANOVA for colored images revealed N1 amplitude varied across odor condition such that amplitude was more negative for the congruent ($M = -5.00$) than incongruent condition ($M = -4.66$), $F(1, 24) = 5.62$, $p = .026$, $p_{\text{corrected}} = .052$, $\eta_p^2 = .19$. Critically, however, there was a significant

Object × Odor × Sex interaction, $F(1, 24) = 13.76$, $p = .001$, $\eta_p^2 = .36$. To follow up the three-way interaction, paired t tests ($\alpha = .025/4 = .006$) were conducted to determine how the congruent and incongruent conditions differed across colored odor-related and colored non-odor-related images in women and men. In women, N1 amplitude was larger for the congruent ($M = -6.37$) than incongruent condition ($M = -5.12$) for colored odor-related objects (e.g., red rose, green mint leaves), but this was only marginally significant after stringent Bonferroni correction, $t(12) = -3.11$, $p = .009$, $p_{\text{corrected}} = .072$, $d_z = .86$. There were no significant differences between the congruent and incongruent odor conditions for colored non-odor-related objects, $t(12) = 1.26$, $p = .232$, $d_z = .35$. In men, there was no significant difference between the congruent and incongruent odor conditions for colored odor-related objects, $t(12) = 1.37$, $p = .197$, $d_z = .38$, or for colored non-odor-related objects, $t(12) = -2.92$, $p = .013$, $d_z = .81$. In summary, the N1 peak for colored odor-related images was enhanced with a congruent odor relative to an incongruent odor for women, which is consistent with the results of the odor-related object analysis. No reliable effect was found in men for colored odor-related objects or for colored non-odor-related objects.

There was no evidence for odor modulation of the other ERP components (P1, P2, P3). A 2 × 2 × 2 ANOVA revealed that P1 amplitude varied significantly as a three-way interaction between Odor condition, Object type, and Sex, $F(1, 24) = 6.02$, $p = .022$, $\eta_p^2 = .20$, but follow-up tests revealed no differences between the congruent and incongruent conditions for any combination of sex and object type. Paired t tests ($\alpha = .006$) revealed that P1 amplitude in women did not significantly vary between the congruent odor condition and the incongruent odor condition for colored odor-related objects, $t(12) = -1.62$, $p = .132$, $d_z = .45$, or for colored non-odor-related objects, $t(12) = 1.42$, $p = .180$, $d_z = .39$. Similarly in men, P1 amplitude did not vary between the congruent and incongruent conditions for colored odor-related objects, $t(12) = -1.26$, $p = .231$, $d_z = .35$, or colored non-odor-related objects, $t(12) = -2.81$, $p = .016$, $d_z = .78$.

The amplitudes of the P2 and P3 components did not vary with odor congruency. For the P2 component, a 2 × 2 × 2 ANOVA revealed a significant main effect of Object type, $F(1, 24) = 10.69$, $p = .003$, $\eta_p^2 = .31$, such that P2 amplitude was larger for odor-related objects ($M = 7.33$) than non-odor-related objects ($M = 6.22$), but there were no significant main effects of Odor condition or Sex and no significant higher-order interactions, $F\text{s}(1, 24) \leq 1.78$, $p\text{s} \geq .194$, $\eta_p^2 \leq .07$. For the P3 component, an omnibus ANOVA also revealed a significant main effect of Object type, $F(1, 24) = 16.35$, $p < .001$, $\eta_p^2 = .41$, such that odor-related objects evoked a larger P3 amplitude ($M = 7.07$) overall compared with non-odor-related objects ($M = 6.05$). However, there were no significant main effects of Odor condition or Sex and no significant interactions, $F\text{s}(1, 24) \leq 2.04$, $p\text{s} \geq .167$, $\eta_p^2 \leq .08$.

The Effect of Odor on ERPs Evoked by Grayscale Non-odor-related Objects

In a final set of analyses, we tested for any effect of odors on visual processing of non-odor-related grayscale objects to verify that ERPs for these control stimuli were not affected by the olfactory stimuli. One-way ANOVAs were conducted to investigate the effect of Odor identity (e.g., coffee, orange, mint odor) on ERPs evoked by grayscale non-odor-related objects (e.g., gray cap). Separate analyses were run for each group of participants exposed to the same three odors: rose/mint/coffee ($n = 10$), rose/orange/coffee ($n = 8$), and orange/mint/coffee ($n = 8$). There was no indication that odor identity reliably influenced ERPs evoked by unrelated visual objects for any ERP component for two of the three groups (rose/mint/coffee participants, $F\text{s}(2, 18)$ æ .64, $p\text{s} \geq .541$, $\eta^2 \leq .07$; orange/mint/coffee participants, $F\text{s}(2, 14) \leq 1.99$, $p\text{s} \geq .174$, $\eta^2 \leq .22$. For orange/rose/coffee participants, although the odors did not influence amplitudes of the P1, N1, or P3 components, $F\text{s}(2, 14) \leq 3.17$, $p\text{s} \geq .073$, $\eta^2 \leq .31$, there was a significant main effect of odor for the P2 component, $F(2, 14) = 4.69$, $p = .028$, $\eta^2 = .40$. Follow-up tests ($\alpha = .017$) revealed orange odor trials resulted in a slightly larger P2 amplitude ($M = 7.08$) than rose trials ($M = 6.19$), $t(7) = 3.22$, $p = .015$, but there were no significant differences between coffee ($M = 7.05$) and the other odors, $t\text{s}(7) \leq 2.22$, $p\text{s} \geq .062$. Taken together, our analyses of ERPs evoked by grayscale, non-odor-related objects revealed no consistent influence of odors. Crucially, there was no effect of odor on the N1 component evoked by these control images, in contrast to the significant N1 effect of odor congruency observed for odor-related objects in female participants (as depicted in Figure 2B).

DISCUSSION

We measured evoked neural activity using EEG to determine whether familiar odors can influence early object identification processes in vision. Previous ERP studies have shown that odors influence processing of matching images at a late ("cognitive") stage of processing (Grigor et al., 1999; Sarfarazi et al., 1999). However, recent behavioral evidence has suggested that congruent odors can influence conscious perception of visual stimuli during binocular rivalry (Zhou et al., 2010, 2012) and can attenuate the attentional blink during rapid serial visual presentations (Robinson, Mattingley, & Reinhard, 2013). These findings suggest that convergent olfactory information can modulate earlier perceptual stages of visual processing. The results of this study reveal that odors can indeed alter evoked neural responses to matching objects at an early stage of visual processing. In women, but not men, early perceptual responses reflected in the N1 component were significantly enhanced for matching object–odor pairs relative to nonmatching combinations.

Critically, we held visual stimuli constant across the odor conditions, thus ruling out any explanation for the effect in terms of visual stimulus differences. Furthermore, odor did not modulate early visual responses (P1 or N1 amplitude) for grayscale non-odor-related objects, which also ruled out any olfactory-driven visual modulation based on inherent olfactory stimulus differences, such as valence or saliency. It is also important to note that participants were unlikely to have experienced habituation to the odors in this study, as the odors were randomized and no-odor trials were intermingled with odor trials. Furthermore, participants were able to distinguish between the odors in the odor discrimination screening task when the odors were presented in a similar fashion. Therefore, olfactory–visual object-based interactions are the most likely explanation for the modulation of visual ERPs by matching and nonmatching odors.

Importantly, we had participants engage their attention on a secondary task that required them to discriminate the shape of a border surrounding the visual objects. Participants were never required explicitly to identify the odors or the visual objects, thus minimizing any influence of deliberate cognitive strategies on olfactory–visual interactions. The enhanced early visual response for women in the congruent odor condition reflects an incidental effect rather than a task-related effect and implies that olfactory–visual integration might be relatively automatic under appropriate conditions. Our finding thus adds to a growing body of evidence that olfaction influences vision in a nonvoluntary manner (Zhou et al., 2010, 2012).

We found that odors influenced the processing of matching images during the N1 component of ERPs, a relatively early stage of visual processing (Mishra & Hillyard, 2009). The N1 peak has been linked to visual discrimination processes, as targets at an attended location result in larger N1 peak amplitudes than targets at an unattended location (Mangun & Hillyard, 1991) and visual stimuli evoke a larger N1 peak when associated with a discrimination task than a detection task (Vogel & Luck, 2000). Furthermore, it has been shown that object category is extracted approximately 150 msec after onset of a visual stimulus (VanRullen & Thorpe, 2001). The relatively larger N1 amplitude we observed for odor-related objects in the congruent condition is consistent with the idea that odor processing can enhance visual discrimination of matching objects. To test this prediction, future studies could measure identification accuracy for brief, masked visual objects under congruent and incongruent odor conditions.

Whereas olfactory–visual congruency modulated an early stage of visual processing, no effect was found for the later stage ERP components. Late components of ERPs are associated with cognitive stages of processing (VanRullen & Thorpe, 2001) and are likely to reflect higher level perceptual processes, such as extraction of meaning. Failure to find modulation of P2 and P3 amplitude in our study therefore indicates that odors did not impact on the semantic processing of images. It is important to note that, although we observed typical P2 and P3 peaks, we did not observe strong N400 components of ERPs. N400 amplitude has been shown to decrease in response to nonmatching images relative to matching images following an odor "prime" (Castle, Van Toller, & Milligan, 2000; Grigor et al., 1999; Sarfarazi et al., 1999). In these studies, however, participants were asked explicitly to determine whether the picture and the odor were congruent or incongruent (Castle et al., 2000; Grigor et al., 1999) or to categorize the visual images (Sarfarazi et al., 1999). It is therefore likely that previous observations of N400 changes for matching olfactory–visual stimuli arose from cross-modal semantic priming, similar to that found with picture and spoken word pairs (Pratarelli, 1994). By contrast, the absence of any effect of congruency on the later components in our study is most likely because of the nonsemantic nature of the behavioral task; participants judged the shape of a visual border (square vs. diamond) but did not have to identify the visual objects themselves or judge the congruency of the olfactory–visual pairs.

In addition to determining the time course of olfactory–visual integration, we asked whether any odor-related modulation of visual processes is because of a specialized connection between odors and colors or between odors and object forms. Interestingly, we found that odors enhanced the N1 response for images that matched in terms of their visual form (e.g., the shape of roses), but the congruency effect did not depend on the color of the images. Therefore, the learned connection between odors and object form (e.g., a rose odor with the image of a rose flower) seems to be more important than the connection between an odor and its characteristic color. This is particularly interesting because color is a potent cue for olfactory functioning; for example, it is known that image color can influence olfactory detection, discrimination, and perceived pleasantness of odors (Dematte et al., 2009; Dematte, Sanabria, & Spence, 2006). It is possible that the relationship between color and odor is driven by cognitive factors, rather than by early multisensory interactions. Here we have shown that odors can enhance early processing of images with matching object form but not matching color, which lends support to the idea that odors can enhance discrimination of matching visual images.

Interestingly, women exhibited odor-related modulation of the N1 response to visual objects, but men did not. To our knowledge this is the first investigation to uncover a sex difference in the neural integration of olfactory and visual information, although many studies have documented sex differences in olfactory functioning more generally (Doty & Cameron, 2009; Garcia-Falgueras et al., 2006). Women have a better memory for odors than men (Zucco, Aiello, Turuani, & Koster, 2012; Choudhury, Moberg, & Doty, 2003), which might contribute to the stronger influence of odors on object form observed here. Furthermore, women perform better on tasks of olfactory detection, discrimination, and identification (Doty &

Cameron, 2009). It is important to note, however, that we found no significant difference in the overall amplitude of ERP waveforms or performance on the border discrimination task between men and women, and there was no significant difference between men and women in the odor discrimination screening test, indicating that the cross-modal effect was not driven by differences in olfactory sensitivity between men and women. One alternative possibility is that men have a different time course of olfactory perception than women. Men have been found to display longer latencies for components of chemosensory ERPs, suggesting a slower time course for olfactory perception relative to women (Olofsson & Nordin, 2004). It would be interesting to probe whether the delay between the presentation of olfactory and visual stimuli affects olfactory-driven visual enhancement for men and women to determine if the optimal timing for olfactory–visual integration varies across the sexes. Nevertheless, in our study, it is clear that women displayed enhanced early processing for matching olfactory–visual stimuli and men did not show this effect.

Although we have found that olfaction can enhance early visual processing, little is known about the specific brain regions involved in olfactory–visual integration. In a cross-modal olfactory–visual fMRI study, Gottfried and Dolan (2003) found that rostromedial OFC and anterior hippocampus were significantly more active in a congruent visual–olfactory condition than in an incongruent condition. However, we observed modulation of visual processing 100–170 msec after onset of an odor-matching image, which seems too short to permit stimulus-driven feedback from these areas. Instead, it seems likely that inhalation of an odor causes an object context to be established in brain areas closer to visual cortex. In accordance with Jadauji et al. (2012), higher-order olfactory processes appear to require visual cortex processing. Perhaps the same neural processes in visual areas are involved in both olfactory and visual processing, so that concurrent odor–image perception results in sensory integration. It might be that an odor can activate related visual images, thus lowering the threshold for identification of any subsequent visual form that possesses critical features of the odor-related object. Olfactory–visual integration in visual cortex would account for an early effect on processing, but it is certainly possible that olfactory–visual integration arises in brain areas involved in attention or higher-order processing.

In conclusion, we have shown that odors can influence relatively early stages of visual processing for matching images, suggesting a potential role for olfaction in visual object identification. This effect was evident for women but not men, consistent with previous findings of superior olfactory abilities in women. Importantly, the congruency effect seemed to be independent of direct cognitive influences. In future studies, it will be important to elucidate the neural structures involved in such early olfactory–visual integration, perhaps by employing fMRI and a behavioral protocol similar to the one adopted in the current study.

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